An Assessment of Odonata Abundance and Impacts from Urbanization in La Crosse County, WI

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Contents

Abstract

Knowledge of the relationships between urbanization and the ecology and distribution of odonates enhances our ability to effectively assess conditions of aquatic ecosystems and nearby terrestrial habitats. With this project, the terrestrial adult odonata populations and species dynamics between urban and nonurban river habitats of La Crosse County, WI were assessed using data received by the Wisconsin Odonata Survey. Using the counts of odonates by species from 2009 to 2015, calculations for general odonate abundance as well as species abundance were generated. It was expected that nonurban habitats would yield both more overall numbers of odonates as well as a more species, though the results showed little difference between the two types of locations. There were on average about 1 more individual odonates counted in urban locations. However, a t-test of these means yielded the data to not be considered statistically different (p-value 0.06). There was also little change in species counts for urban habitats, but there was a spike in counts of nonurban locations from 2009 – 2012, where there were 16 counted in 2009 up to 38 in 2012. Though the r-squared values of the corresponding trendlines suggest a low goodness of fit (< 0.001 and 0.27 for nonurban and urban locations), the low values were to be expected, given the variability of the data in terms of how uneven the counts were performed. The data itself was not gathered with regard to a study, as it has been the culmination of citizen scientists recording their own findings as they visited locations. The low values could reflect the bias toward sampling done for the survey, where the surveyor frequented more urban locations. Despite this, research done with regard to adult odonate ecology and

distribution is helping to broaden the lacking knowledge we currently have with regard to odonate population ecology, as well as increase our knowledge of the effects on urbanization on populations and habitats.

Introduction

A key group of organisms used to assess water quality is that of the odonates, or dragonflies and damselflies (Khelifa 2017, Corbet 1962, 1999; Cordoba-Aguilar 2008). According to the University of California Museum of Paleontology, there are about 5000 species of odonates. A large amount of research on their larval stages with regard to water quality and riparian habitat distribution has come about in the last century, and this information has been crucial in assessing water system health (Samways 2008). Thus, most conservation strategies for threatened dragonfly species are designed to protect freshwater habitats (Kalkman et al 2010). However, the protection of the terrestrial environments surrounding natal habitats is also key for adult populations, as adults can also be sensitive to changes in their environment (Oppel 2006, Dolny 2012, Kutcher 2014). Unfortunately, there is significantly less research on adult odonate distribution, biodiversity, and general ecology, of which could be used to better preserve both water systems and the terrestrial border zones around them (Zebsa *et al* 2015, Dolny *et al* 2014). This study aims to assess the general population abundance and species richness of odonates within the La Crosse County, WI region. To begin the discussion, the first place to start is what we already understand with regard to their physical anatomy and behavior.

Life Cycle

When trying to understand odonate ecology, it helps to understand how they live. Odonates have three life stages: egg, larval, and adult. The following section describes the growth and development for each life stage, as well as reproductive behaviors. Figure 1 below illustrates the growth and development of the odonate life cycle using the growth stages of a dragonfly.

Figure 1: Life Cycle of Dragonfly. 1 shows eggs, 2 and 3 are larvae are different growth stages and 4 and 5 are both male and female adults. The two nymph stages are shown to illustrate the nymph's growth. The nymph stages shown are the husks left behind from molting. Image from https://www.abacused.com.au/media/catalog/product/cache/1/image/9df78eab33525d08d6e5fb8d27136e95/2/e/2e082.jpg

Egg and Larvae

Eggs, as pictured above on 1 on the diagram of Figure 1, are deposited into open water sources, where the larvae (2 and 3 of Figure 1) hatch and develop. Larvae breathe through tracheal gills and are susceptible to changes in dissolved oxygen levels in aquatic habitats (Tillyard 1917, Zebsa *et al* 2015). They are also noted as being active hunters, seeking out prey within their habitat and feeding regularly. Structurally, they are noted as being campodeiforms, which is a term used to describe the shape of insect larvae that have well developed legs, antennae, and a flattened body. They have no true pupal or resting-stage in their life cycle but do have a drastic change in structure with metamorphosis. Despite this lack of a resting stage, larvae can take anywhere from a few months to several years before going through metamorphosis, depending on the species. It is this prolonged exposure to specific stretches of waterways that makes odonates model organisms for their aquatic habitats ().

Odonate larvae are similar to the adult stage in structure, with a few exceptions. The antennae are larger than the adult stages. Compound eyes are present, but ocelli (simple eyes) that are seen in adults are absent for most of larval life. The legs are longer and stronger than that of adults. The wing sheaths develop externally and are supplied with numerous tracheae during development.

One of the most distinctive physical traits of odonate larvae is their highly specialized labium (the fused mouthpart that forms the floor of the mouth of an insect) that forms a “mask” that is used to capture prey (illustrated in Figure 2). The specific structure can vary from species to species. Some common-named skimmer nymphs have a scoop-like labium, where the darner nymphs can have an extending labium with graspers at the end, as shown in Figure 2. These structures are an outstanding feature of the larval stage and are impressive adaptations for predation. Prey includes most other aquatic species, such as other larvae, tadpoles, and fish, among others. Healthy water systems are able to support more variety of species, and thus increase the number of prey available. Odonate larvae themselves provide a substantial food source for many other larger predators, including fish, amphibians, and aquatic reptiles.

Figure 2: Darner nymph labium extension. Labium arm is jointed, and at rest is held under the chin and close to body of the nymph. It can extend out to grasp a target in a fraction of a second. Images are screenshots from Deep Look's youtube video "A Baby Dragonfly's Mouth Will Give You Nightmares", https://www.youtube.com/watch?v=EHo_9wnnUTE.

Adult

Larvae go through a metamorphosis and develop into terrestrial, flying adults. With that, they instead breathe air directly through spiracles. They have strong biting mouth parts, where the mandibles are thick and strongly toothed. The antennae they had as larvae are significantly reduced and more threadlike (or filiform). They have three ocelli as well as the two compound eyes. The thorax is comprised of a small movable prothorax and a large oblique synthorax. These structures are formed by the fusion of the meso- and metathorax. Two spiracles for breathing are located on the thorax. The legs are placed forward and are used primarily for perching and not walking. Wings are placed farther down on the back, just before the abdomen, and are in two unfolded pairs. The wings are heavily veined. The abdomen has ten complete segments with terminal appendages and is overall narrow in shape and elongated. There are eight pairs of spiracles along the abdomen.

Dragonflies and damselflies are biologically very similar between both life stages, with differences only being in general size, wing placement, and eye shape as adults. Adult dragonflies hold their wings vertically across their backs when at rest, whereas damselflies perch their wings vertically. The structural differences between dragonflies and damselflies are illustrated in Figure 3.

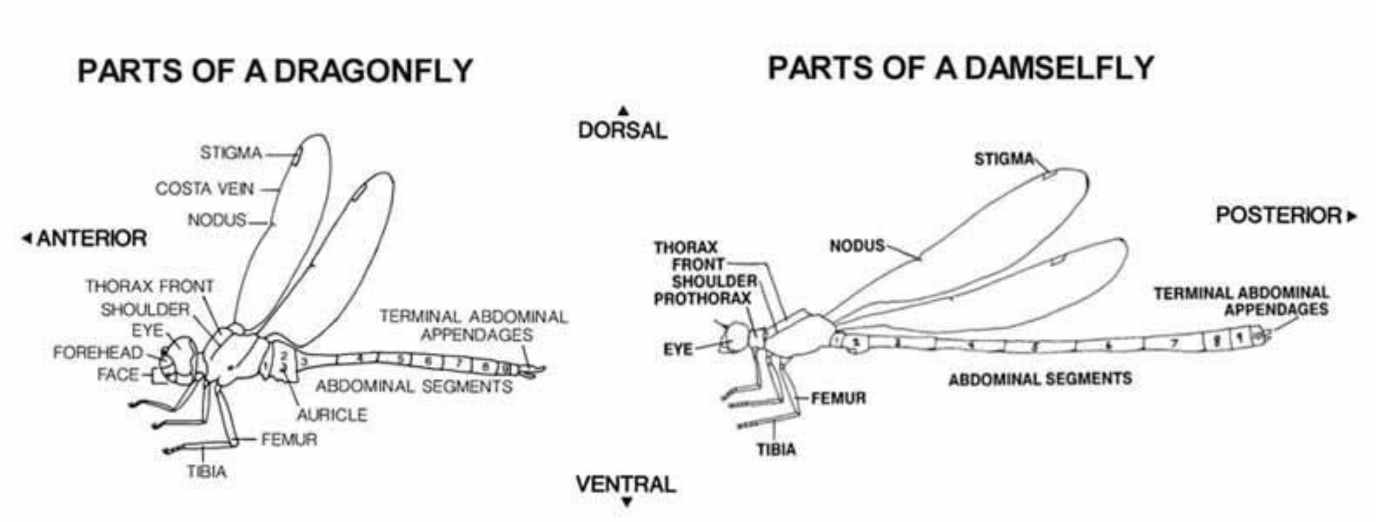


Figure 3. Illustration of differences in structure between dragonflies and damselflies. Retrieved from <http://kaweahoaks.com/html/dragonfly_partsof.jpg>

Reproductive Behavior

Odonate mating behaviors are well documented, and though they can vary slightly by species, there are behaviors that overlap. Generally, males are territorial and can spend significant amounts of time defending quality egg-laying sites near ponds or streams. Female dragonflies will seek out these prime habitats, and upon entering will be grabbed by males. The male copulatory organ is peculiar and is found on the second abdominal segment (on the anterior portion of the abdomen). Before copulating, sperm is transferred from the genital opening to the separate copulatory organ, which allows freedom for the male to hold onto the female. Males will hold onto females with their legs until they can grasp them behind the head using claspers at the end of their abdomen. When the male makes contact, the female responds by bending her abdomen down and forward to contact the male's copulatory organ. This action is called tandem flight, or as the characteristic wheel position, pictured in Figure 4.

Figure 4. Lance-tipped darner pair in wheel. © Dan Jackson.
<http://wiatri.net/inventory/odonata/SpeciesAccounts/SpeciesDetail.cfm?TaxaID=3>

As with all forms of life, odonates are dependent upon the quality of their habitats to survive. It is important to assess the quality of terrestrial habitats, as they are needed for maturation of foraging sites and potential refuge for copulation among odonates (Zebsa *et al* 2015, Dolny *et al* 2014). A broader base of knowledge of terrestrial sites is equally as important as that of the aquatic systems inhabited by nymphs.

Urbanization and Ecological Impact

As the world's population urbanizes at a faster rate, the anthropogenic changes in land use, water quality, climate, connectivity of natural lands, and inputs of excess nutrients and pollutants become ever present (Dauer et al 2000, Kalnay & Cai 2003, Theobald et al 1997, Groffman et al 2004, Hatt et al 2004). These changes are one of the leading causes of overall species population and diversity decline, and biological diversity and available habitat are closely linked (Puth 2017). The more viable habitat that is polluted or destroyed, the less biodiverse and area becomes.

Some research had shown that there are a higher number of plant species in urban areas, but the reverse trend has been shown for other organisms (Puth 2017). It is known that land use changes from urbanization cause a decrease in water clarity in aquatic habitats along with decreased taxonomic richness in species, including odonates (Usio et al 2017). Also, that landscape uses have shown a decrease in water clarity and taxonomic richness within water systems (Usio et al 2017).

This project aims to assess terrestrial adult odonata population and species dynamics between urban and nonurban habitats to increase the general understanding of odonate ecology and the effects of urbanization on odonata populations. Due to the pre-existing knowledge of habitat degradation and impacts of urbanization on odonates and other species, it is predicted that habitats with less urbanization will yield higher species abundance than more urban locations.

Methods

In order to evaluate general odonate population dynamics, individual odonata were counted by species by citizen scientist Dan Jackson and recorded for the Wisconsin Odonata Survey from 2009-2015 in La Crosse County, WI. Data was recorded from 2016 and early 2017, but more precise counts were not made. All counts of “100s” or more were excluded, as the numbers were too large to be considered precise. At least 2 counts were excluded from the analysis as the species sections were left blank.

There was no previous column for categorizing the locations as “nonurban” and “urban,” and were thusly added after looking at each location by coordinate given. Coordinates were put into Google Maps using the Earth feature. “Nonurban” locations were decided as such if they were at least a half a mile or so away from concentrated man-made buildings or structures. Some of the locations were considered “urban” because they were along the airport at French Island, despite being away from housing or businesses. There was a total of 10 different locations along the Mississippi River or other river systems used for making counts: 5 considered nonurban, and 5 considered urban.

Study Area

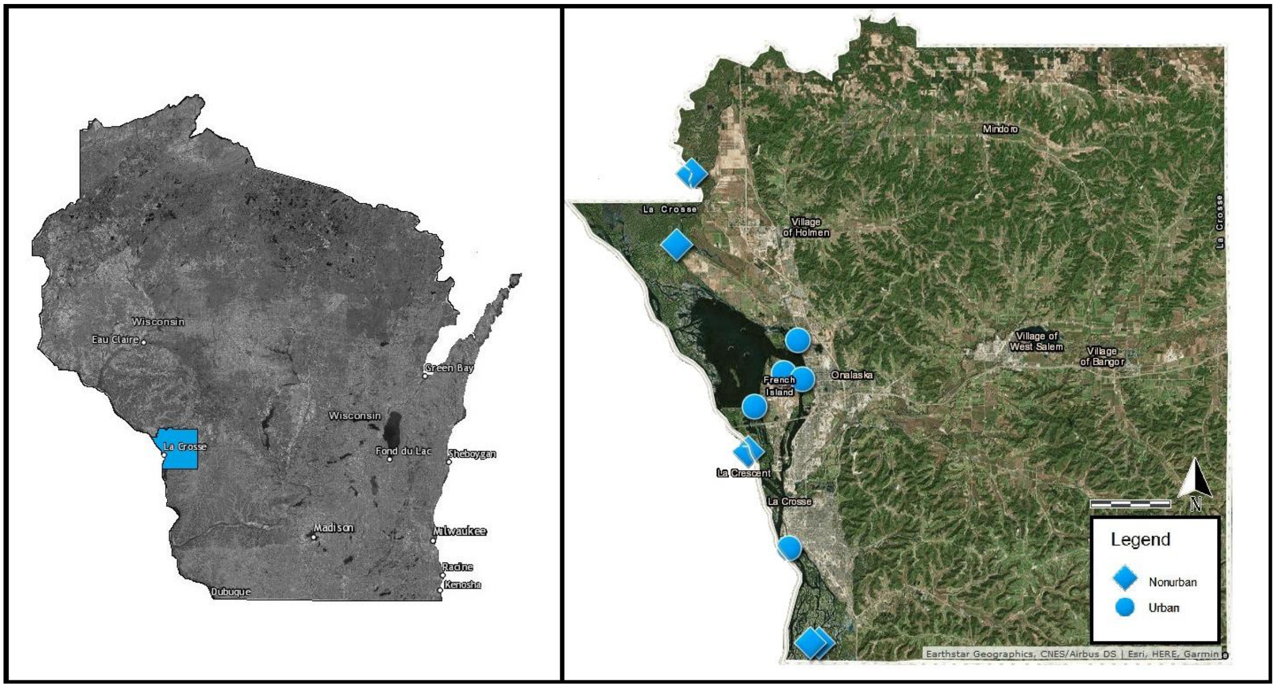


Figure 5: Study Area Map. Map shows the study area of La Crosse County, Wisconsin. The right side shows the specific sites used from the data, where nonurban locations are marked with a blue diamond shape, and urban sites are marked with a blue circle. Map was created using ArcGIS online with USA basemaps from Earthstar Geographics, CNES/Airbus DS and Esri, HERE, and Garmin.

Calculations and Statistics

Population Abundance

The mean number of individual odonates was calculated between nonurban and urban habitats from 2009-2015 using Microsoft Excel. A corresponding graph was made (Figure 6) from said means to illustrate the differences. From this information, a t-test was also performed using Excel. Along with the t-test calculations, the descriptive statistics for urban and nonurban counts was also calculated (Table 1).

Species Richness

Species richness was calculated by identifying the number of different organisms' present. Next the total number of each organism was counted. These numbers were used to calculate the total number of different species present (species richness). The corresponding numbers were totaled by year and used to create a line graph (Figure 7). The graphs include the calculated regression lines and r-squared equations to assess goodness of fit of the data.

Results

Population Abundance

The mean number of odonates counted for nonurban habitats was 6.27, and the same for urban habitats was 7.24 (Tables 1 & 2, Figure 6). The difference in means is thus a value of 0.97. A t-test using the same means yielded a one-tailed p-value of 0.06 and a two-tailed p-value of 0.12 (Table 2). The calculated standard error was 0.45 for nonurban and 0.43 for urban habitats. The standard deviation was 10.29 and 11.74 for nonurban and urban, respectively. There was a sum of 3340 odonates counted for nonurban locations and 5337 for urban, though the range, min, and max were the same (Table 1).

Table 1: Descriptives of Odonata Counts from Nonurban and Urban Locations from 2009-2015		
	Nonurban	Urban
Mean	6.27	7.24
Standard Error	0.45	0.43
Median	3.00	3.00
Mode	1.00	1.00
Standard Deviation	10.29	11.74
Sample Variance	105.86	137.94
Kurtosis	26.79	21.79
Skewness	4.16	3.87
Range	99.00	99.00
Minimum	1.00	1.00
Maximum	100.00	100.00
Sum	3340.00	5337.00
Count	533.00	737.00

Table 2: Result of t-Test: Two-Sample Assuming Unequal Variances. Mean Odonata Counts between Nonurban and Urban Habitats from 2009-2015 in La Crosse County, WI		
	Nonurban	Urban
Mean	6.27	7.24
Variance	105.86	137.94
Observations	533.00	737.00
df	1222.00	
t Stat	-1.57	
P(T<=t) one-tail	0.06	
t Critical one-tail	1.65	
P(T<=t) two-tail	0.12	
t Critical two-tail	1.96	

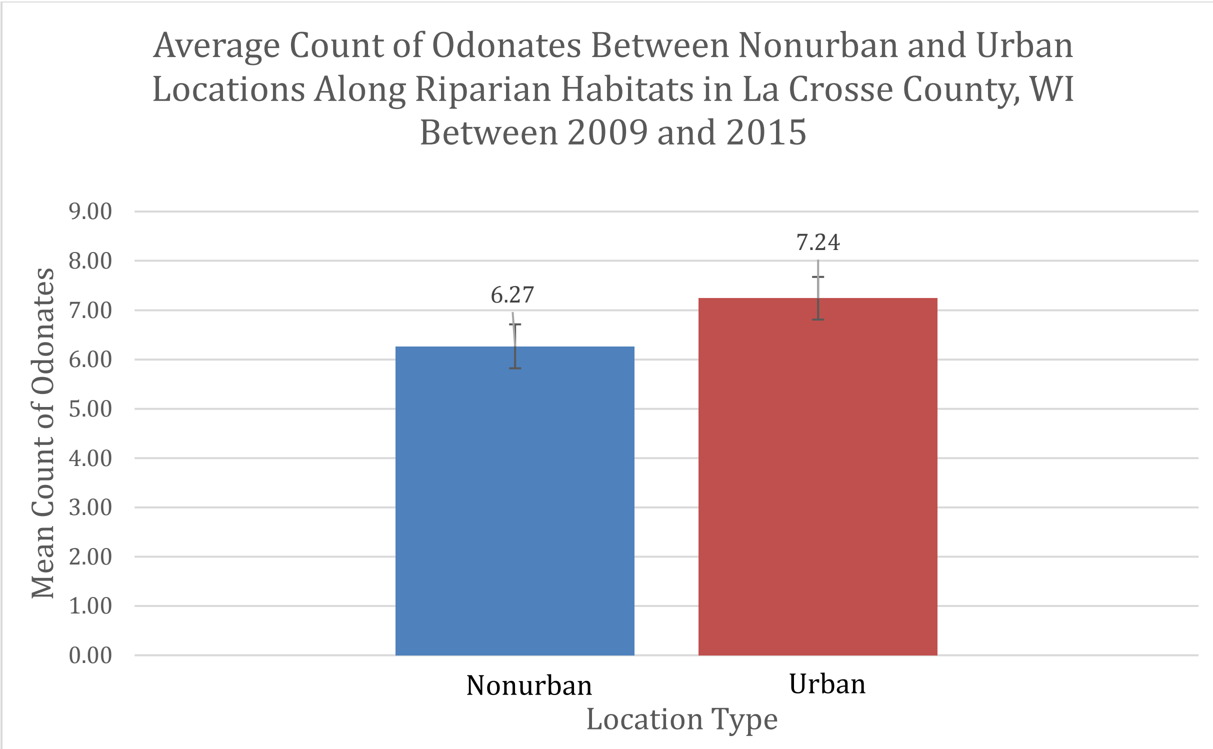


Figure 6: Average odonate count between urban and nonurban locations along river habitats in La Crosse County, WI between 2009 and 2015. Error bars were included using standard error calculated with excel and descriptives, where nonurban = 0.45 and urban = 0.43. The mean count of odonates for the nonurban locations was 6.27, whereas the mean count of odonates in urban locations was 7.24.

Species Richness

The linear regression equation for nonurban species counts was $y = 0.1071x – 188.71$, and the calculated R-squared value was < 0.001. The same for urban species counts was $y = 0.6071x – 1195.6$, with an R-squared of 0.27 (Figure 7). In both cases, the calculated R-squared value is very low, suggesting close to no goodness of fit. The R-squared value represents the fraction of the variation in one variable that may be explained by the other. In this case, there is no correlation between location type and species counts.

The number of species present within the nonurban locations showed a general increase between 2009 and 2012, followed by a sharp decline between 2012 and

2013 (Figure 7). By contrast, the number of species for urban locations shows very little fluctuation over time.

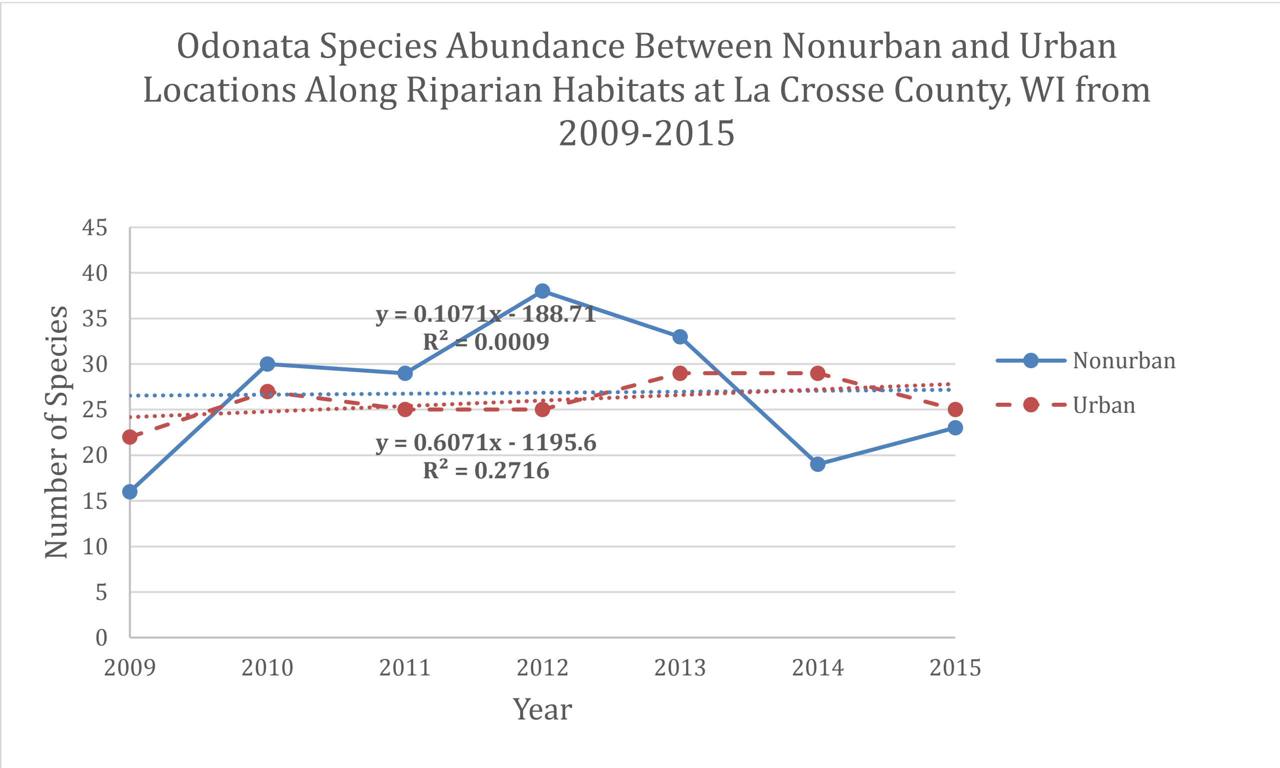


Figure 7: Odonata species abundance between nonurban and urban river locations at La Crosse County, WI from 2009 to 2015. Species richness was tested using a regression analysis with trendlines. The equations for each trendline are as follows: for nonurban locations, the equation was $y = 0.107x – 188.71$, and for urban was $0.6071x – 1195.6$. The r-squared values for nonurban locations was calculated as 0.0009, or <0.001, and was 0.27 for urban locations.

Discussion

Reflection of Results

The goal of this study was to see if there was a difference in the number of odonates present between nonurban and urban habitats, as well as any difference seen in the numbers of species present. It was expected that urban locations would consist of lesser quality water and terrestrial habitat than nonurban ones, and thus the number of individuals and species would be drastically higher in nonurban locations. However, there was only a slight difference in the total number of odonates counted between the two habitat types. The mean number of odonates counted for nonurban habitats was 6.27, and the same for urban habitats was 7.24 – a difference of just 0.97. However, the t-test using the same means yielded a one-tailed p-value of 0.06 and a two-tailed p-value of 0.12, which also suggests that there was no statistically significant difference between counts in nonurban and urban habitats.

As for the comparison of species counts, it was expected that nonurban habitats would hold higher numbers. The results show that was the case between 2010 and 2013, where the total number of species counted ranged from 30 to 38 at the highest (Figure 7). For the same time frame, the species counts for urban locations was between 26-28. Though the R-squared values suggest very little goodness of fit, there was an outstanding result from the test. It was not expected that the variation of species counts would be more or less stable between habitats. However, the species counts from nonurban locations showed much more variation, whereas the counts in urban locations remained about the same over time. There could be more research done to assess migration patterns between sites to see how fragmentation could play a role in odonate population dynamics.

The Data

There were a number of issues with the data. To start, there was data recorded for 2016 up to late summer of 2017, but Jackson had stopped reporting actual numbers for counts. Instead of counts of “12 or so,” counts were recorded as “a few,” or “many.” Thus, the data for those two years was not included in the analysis. Another related issue was that locations were marked by different coordinates for the same place. All locations had to be sorted to ensure that the names were the same. This could be an example of the difficulties of using citizen-gathered data.

Citizen science can be used in a way to promote random sampling techniques. In hindsight, it would have been best to devise a way to “randomly sample” from a specific number of data points. One of the main issues with the data used in this study was that the number of observations was not the same between all sites. Some sites were visited more often than others, which could have ultimately skewed the results. For example, Jackson could have spent ten consecutive days counting in one site, then three in another. If instead the locations were numbered, and a certain number of samples was randomly chosen using a random number generator in Excel, the chance of bias could have been reduced drastically.

Each of the coordinates given by Dan Jackson was looked at using Google Maps to assess if the location was considered nonurban or urban. This was first done in early fall of 2017, and again at the beginning of 2018. After looking back again, it would seem that one of the drainage ponds visited by Jackson for the data had been filled in sometime recently. Though, as with google maps, it isn't known what year the satellite images were actually taken, but it did seem that there were signs of land use changes at some point within the last few years. This pond was not included in the statistical analysis, as the data focused on just river locations, but it is important to note that there was evidence of a more drastic land use change with regard to the numerous suburban drainage ponds within La Crosse city.

Urban Ponds

It may be beneficial to have analyzed odonata counts between the more natural river locations and the urban ponds and human-altered drainage basins. The land preserved for conservation of species including odonates is often solely done in protected natural areas, though there has been increasing research that shows that management of human-altered landscapes is just as important (Lundholm and Richardson 2010, Chester and Robson 2013). More recent studies have shown that water bodies in agricultural and urban landscapes play important roles in biodiversity conservation and in particular is that of agricultural ponds (Akasaka et al., 2010). These studies have demonstrated that smaller sized agricultural ponds tend to be the most biodiverse water bodies, as they have shallower water depth and more aquatic vegetation (Willams et al. 2004, Davies et al. 2008).

Trophic state changes via increased concentration of phosphorus and/or nitrogen seem to be associated with abiotic and biotic stresses. The trophic state is defined as the total weight of biomass in a given water body at a specific time. The Carlson index uses the algal biomass as an objective classifier of a lake or other water body's trophic status (Usio 2017). As an example of an abiotic stress, land-use changes such as deforestation in the surrounding area and input of agrochemicals through agricultural intensification have been shown to deteriorate water quality and reduce the species richness of aquatic plants in farm ponds (Akasaka et al., 2010). An example of a biotic stress includes that of trophic cascades via fish predation on zooplankton. A trophic cascade is an ecological phenomenon triggered by the addition or removal of top predators and involves reciprocal changes in the relative populations of predator and prey through a food chain. This often results in dramatic changes in ecosystem structure and nutrient cycling (Usio 2017).

In large areas of the Midwestern U.S., most of the natural floodplain wetlands and lowland areas have been converted into agricultural or urban areas (Puth 2017). The once native species of these areas now find these fragmented microhabitats as refuge, and in practice a number of farm ponds in Japan have been noted for containing many indigenous and endangered species that are absent from natural wetland habitats (Usio 2017). However even these habitats face biodiversity threats from increased land consolidation and changes in management styles of ponds over time, further enforcing the need for better agricultural management practices.

Statistical Analysis

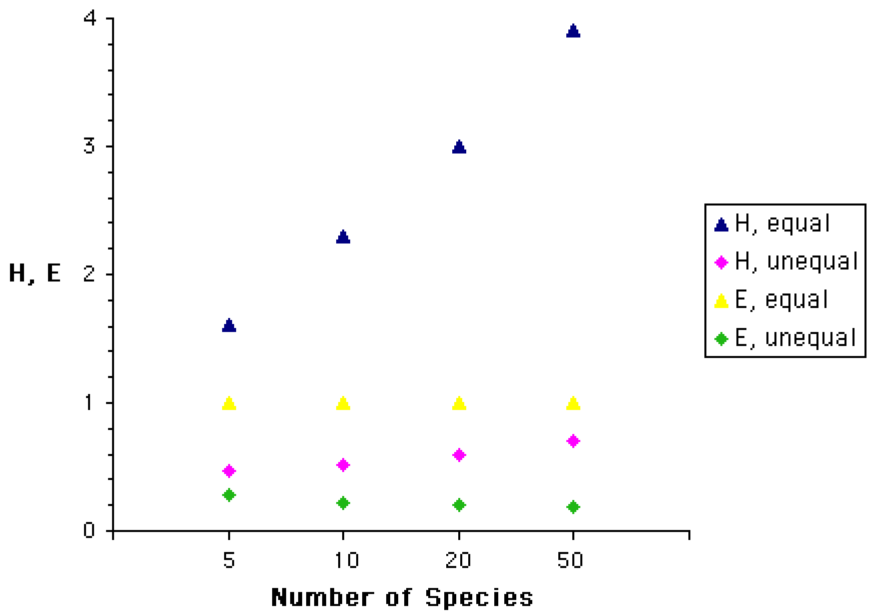
ArcGIS and ArcMaps could be used to show differences of urbanization between 2009 and 2015 of La Crosse County area, if any. If there was any data available, map layers could be made to show any differences in land use changes with data provided.

This information is rare to come by, and any analysis that can be performed could prove vital in understanding any impacts on odonata population dynamics. Combined with an improved method of sampling, ArcMaps could also be used to calculate a Shannon-Weiner index.

The simple species richness calculation used with this study does not take into account the proportion and distribution of each species within a local community, and this can be made more complicated with flying species. By contrast, with a Shannon-Weiner Index, the richness and the percent of each species from a sample within a community are taken into account. This index assumes that the proportion of individuals in an area indicate their importance to diversity.

The Shannon-Weiner index takes into account species richness and proportion of each species within a given area using measurements of the sampling space (or evenness). The Institute of Environmental Modeling (TIEM) lists the equation for the Shannon diversity index as: $H = -\sum_{i=1}^{S} p_i \ln p_i$. In this equation, H is Shannon's diversity index, S is the total number of species in the community (richness), p_i is the proportion of S made up of the *i*th species, and E_H is the equitability (evenness). Here, the proportion of species (*i)* relative to the total number of species (p_i) is calculated. Then that is multiplied by the natural log ($\ln p_i$), and the resulting product is summed across species and multiplied by -1. Shannon's equitability (E_H) can be calculated by dividing H by H_{max} (=lnS). Equitability assumes a value between 0 and 1 with 1 being complete evenness. The equation would look as follows: $E_H = H / H_{max} = H / \ln S$.

A graph was created on the TIEM website to better explain the relationship between *H* and E_H:



With this example, four hypothetical communities of 100 individuals are shown. The communities are composed of 5, 10, 20, and 50 species, respectively. It assumes that individuals are distributed evenly among the different species (each species makes up an equal proportion of S). For the case of where one species has 90% of the individuals, the remaining individuals are assumed to be distributed evenly. The diamonds represent *H* and E_H values for the first case (equal proportions), and the triangles represent values for *H* and E_H for the second case (unequal proportions).

For the first case, E_H is always equal to one (complete evenness), but *H* increases dramatically as the number of species increases, as we would expect. When one species makes up 90% of the community, we can see that although *H* does increase with increasing numbers of species, it does so much more slowly than in the first case. Additionally, E_H decreases as species number increases (since one species always makes up 90% of the community in the second case of this hypothetical example, the remaining species make up some fraction of 10% of the community; as species number increases this fraction becomes smaller and evenness decreases).

H and E_H clearly give more information about these communities than would species number (richness) alone and using a comparison of one or all of these methods has been used to illustrate changes in water quality conditions within communities by the Maryland Sea Grant and other water monitoring organizations and may be applicable to terrestrial habitats as well.

Future Study

If given the resources, I would propose a more focused, in depth study. The following is an example of what I could perform to better assess odonate population and species abundance.

For the purpose of studying population abundance of odonates between two locations, a sampling of adult odonates in a marked area would have to be used. Two sampling sites of 50x50m quadrats would be setup along the Mississippi River in LaCrosse County, WI. One location would be considered non-urban, where there would be no large, concentrated manmade structures for 1-2 miles around the site. The other location would be considered urban, with man-made buildings being concentrated within a mile of the site. If possible, it would be best if the locations were far enough apart to reduce the likelihood of dispersal between the two from odonates (immigration and emigration). This could be determined based on knowledge of known migration patterns of odonates species in the area.

Sampling within each quadrat would consist of netting odonates within sites. With this in mind, it would be best to have sampling occur at the same time, since it is known that odonates have varying activity levels throughout the day. Each site would have a group of just 2 each so there would only need to be 4 people doing sampling at a time. Groups would have to begin at the same time and end at the same time, and the best time for sampling could be determined based on prior knowledge of adult odonate behavior. Because the odonates are not stationary targets, they themselves would have to be considered the points within the samples. Recordings on odonates would be simple and include species identified and if they were recaptures or not. With every capture, a marker would be used to mark a point on the wings, and each point style and color would be noted ahead of time to make sure there was no confusion in sampling. For example, a guide would be made for each group that lists an order for different marks to use on the dragonflies as they were captured: first capture = orange star, for example. This is because samples would be re-released. Other variables would also be recorded, such as weather, air temperature, humidity, wind speed, gust speed, and wind direction.

Each group would capture and release odonates from within a time frame. If both groups start at 8 am, then the sampling could end by 10 am or sooner. But whatever time frame is chosen, it has to be the same between both groups. Groups would also have to determine how long the study were to take place. Ideally, sampling would occur for multiple years, for 1 week during each active season. Active seasons for odonates are from early-late spring, through the summer, and into mid-late fall. Using known information on odonate activity levels, one week for each season would be determined for sampling. Thus, for one whole week in each season, sampling would occur. And this could be done over the course of a number of years. The groups doing the sampling could be comprised of citizen scientists and possibly even organized through groups such as the Wisconsin Odonata Survey.

It would be impossible to capture every individual odonate in a given area, for their sheer numbers as well as their ability to fly. Thus, a representative sampling technique needs to be used, and a quadrat sample would be best. This is because of odonates being sampled as moving targets. It would be best to setup an area of sampling such as with a quadrat, though there would have to be some differences. The odonates themselves would have to be considered the “points” within the quadrat. The location of capture within the quadrat would not be as important as the odonates themselves. The specimens would be the data points as they hold the information needed (species, perhaps wing size, etc).

From the data recorded, population abundance can be calculated and also species abundance. Population abundance could be the total counts between each site (urban/non-urban) over each season and/or over the years. Since sampling would occur within a 50x50m plot, the species abundance could be calculated using a Simpson Index. This measurement accounts for the richness and percent of species from a biodiversity sample within a local community. The index assumes that the proportion of individuals in an area indicate their importance to diversity.

Ultimately, general knowledge of odonate ecology and population dynamics is still lacking in information. However, the expansion of interest with freshwater aquatic habitats and their surrounding terrestrial zones is ever increasing. As conservation efforts move to more broad areas, so to does the understanding of odonates.

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