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APROACHES TO ARTHROPOD CONSERVATION: LANDSCAPE GENETICS, COMMUNITY ASSESSMENT, AND PREDICTION OF EXTINCTION RISK

By

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B.S., Baylor University, 2011

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A Dissertation Approved on

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DEDICATION

To Dad

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ABSTRACT

APROACHES TO ARTHROPOD CONSERVATION: LANDSCAPE GENETICS, COMMUNITY ASSESSMENT, AND PREDICTION OF EXTINCTION RISK

Victoria A. Prescott

October 28, 2016

Although urbanization is a leading cause of species extinction throughout the world, the impact of urban development on arthropods is little studied and, as a result, poorly understood. I used three distinct approaches to studying arthropod conservation in North America. First, I used landscape genetics techniques to study the impact of urbanization on gene flow among populations of *Rabidosa rabida*, the rabid wolf spider. While gene flow was not detrimentally reduced, urban development correlated with a reduction in migration rates among populations, and to my knowledge, this is the first study to document isolation by resistance in spiders. Next, I examined how lentic and lotic odonate communities within the same landscape were affected by urbanization. Due to the inherent differences between lentic and lotic ecosystems and between dragonflies and damselflies, different environmental factors contributed to the persistence of particular species and thus to the makeup of adult odonate communities in urban areas. The different responses of dragonflies, damselflies, and spiders to urban development suggested that dispersal abilities strongly predict resilience to altered landscapes. Finally, I identified ecological correlates of an extinction risk assessment for North American odonates. Two of those correlates, geographic range size and length of flight period, are surrogate measures of dispersal. Both dragonfly and damselfly extinction risk assessments correlated with these two traits, but dragonfly assessments also correlated with the interactions between length of flight period and both geographic range size and habitat breadth. Collectively, this research showed that not all arthropods are negatively affected by urban development and that even closely related taxa are not always similarly affected. These differing responses were likely due to interspecific differences in dispersal abilities and life-history patterns, and possibly in odonates to taxonomic differences in flight capability and voltinism. These results highlight the need for further research on identifying the mechanisms driving urban biodiversity patterns and gaining a better understanding of the basic ecology of invertebrates.

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CHAPTER 1

INTRODUCTION

The world is currently suffering its sixth mass extinction (Barnosky *et al.* 2011), and this extinction event is unlike those of the past in that contemporary extinction rates are vastly higher. In previous extinction events, the extinction of 75% of species occurred over a period of 2 million years, but currently that same percentage of species will be lost in just 300 years (Barnosky *et al.* 2011), with an average of eight species lost each day (Cardoso *et al.* 2011a). The predominant drivers of today's mass extinction are habitat degradation and loss via anthropogenic causes (Leakey and Lewin 1995) such as deforestation, mining, agriculture, and urbanization, with urbanization being the leading cause (Vale and Vale 1976; Czech *et al.* 2000; Marzluff 2001; McDonald *et al*. 2008; Aronson *et al*. 2014). The amount of urban land cover is expected to expand by 1.2 million km^2 between the years 2000 and 2030, which is a 185% increase over current land cover values (Seto *et al.* 2012).

Urbanization affects all aspects of both aquatic and terrestrial environments (Paul and Meyer 2001, Brönmark and Hansson 2002, Allan 2004, Foley *et al.* 2005; Grimm *et al.* 2008; Hassall 2014) and results in permanent land transformations (McKinney 2002, 2006). Habitat fragmentation (Fahrig 2003; Fuller *et al.* 2015; Haddad *et al.* 2015), exotic species (Gurevitch and Padilla 2004; Havel *et al.* 2015), and increased temperatures (Pickett *et al.* 2001; Grimm *et al.* 2008; Somers *et al.* 2013) are among the factors that most strongly affect ecosystems in urban areas. In addition, urbanization makes the landscape unsuitable for most species because it replaces native landscapes with novel and uniquely inhospitable ones (Unfried *et al.* 2013), and most native species cannot adapt to the altered and novel disturbance regimes that also occur in urban areas (Alberti 2005). Further, not only are important habitat patches degraded in quality, the corridors between those patches also become degraded (Verbeylen *et al.* 2003; Unfried *et al.* 2013).

A vast majority of conservation and wildlife studies focus on vertebrates (McIntyre 2000; Clark and May 2002; Cardoso *et al.* 2011a; Magle *et al.* 2012; D'Amen *et al.* 2013; Grodsky *et al.* 2015). As a result, our current understanding of how urban development affects invertebrates is poor even though arthropods alone make up half of the species on the planet (Redak 2000) and suffer a higher rate of extinction than do vertebrates (Cardoso *et al.* 2011a). Further, because conservation studies center on vertebrates, conservation management practices also cater to vertebrate conservation (Cardoso *et al.* 2011b, Barua *et al.* 2012) even though extinction patterns in vertebrates do not necessarily mirror those in invertebrates (Clausnitzer *et al.* 2009), and the needs of vertebrates drive the development and maintenance of nature reserves (D'Amen *et al.* 2013). The bias toward studying and conserving vertebrates is strong and clear. In North America alone, an estimated 200,000 species of insects and arachnids are believed to exist, yet only half are scientifically described (Redak 2000). This is a stark contrast from vertebrates, of which 45,000 species have been scientifically described and another 5,000 are estimated undescribed (Black *et al.* 2002). Additionally, only 0.5% of scientifically-described arthropod species have been assessed by the IUCN Red List compared to 42% of vertebrates (Leather 2009; Cardoso *et al.* 2011b; D'Amen *et al.* 2013). While urbanization has been directly linked to insect extinction (Fattorini 2011), it is still unknown how other arthropods, such as spiders, respond to urbanization because only 10% of urban animal studies focused on arthropods (Magle *et al.* 2012).

Arthropods also provide numerous benefits to the planet. Arthropods provide a majority of ecosystem processes (Kim 1993, Redak 2000, Leather *et al.* 2008, Kotz *et al.* 2011), and because urbanization affects arthropods, ecosystem function is likely to also be affected (McIntyre 2000; McIntyre *et al.* 2001). For example, urbanization is leading to population declines of a variety of pollinators which will result in steep declines of plant diversity (Vanbergen 2013). Arthropods also provide numerous benefits to humans; despite a general negative perception of insects (Barua *et al.* 2012), they provide over $57 billion in global revenue to the United States annually (Losey and Vaughn 2006). Finally, from a purely biological standpoint, arthropods, as with all other living creatures, have a right to exist even without conveying any sort of benefit to humans (Samways 2005).

In my dissertation, I take three distinct approaches to the study of arthropod conservation. In the first chapter, I use landscape genetic techniques to study the impact of urbanization on gene flow among populations of the wolf spider species *Rabidosa rabida*. Even with great advances in genetic analysis techniques and tools, very few studies have examined how urban land use affects the population genetics of arthropod species (Bond *et al.* 2006). Urbanization reduces gene flow in a variety of vertebrate species (*e.g.* lizards: Delaney *et al.* 2010; salamanders: Noël and Lapointe 2010; frogs:

Hitchings and Beebee 1997, Mikulíček and Pišút 2012; birds: Delaney *et al.* 2010; Björklund *et al.* 2010, Unfried *et al.* 2013; and mammals: Epps *et al.* 2005, Lee *et al.* 2012, Munshi-South 2012, Santonastaso *et al.* 2012), but the results vary in arthropod studies. For example, conflicting results have emerged from studies on beetles, with one species being greatly affected (Keller and Largiadèr 2003) but others showing no effect of urbanization on gene flow (Desender *et al.* 2005). Additional studies are needed to gain insight into the responses of arthropods to urban development.

In my second chapter, I examined how urbanization alters dragonfly communities of both lentic and lotic ecosystems. Generally, vertebrate species richness tends to decrease with increasing urbanization (Ishitani *et al.* 2003; Urban *et al.* 2006; Pillsbury and Miller 2008; Van Nuland and Whitlow 2014; reviewed in McKinney 2008). Invertebrates exhibit a wide range of responses to urbanization despite the relatively low number of studies focused on this group. Invertebrate responses to urbanization often follow the vertebrate pattern, with species richness showing a consistent decline along rural to urban gradients (Hansen *et al*. 2005; reviewed by McKinney 2008). However, urbanization has neutral effects on invertebrate species richness in varied taxa (reviewed by Faeth *et al.* 2011; Jones and Leather 2012), and some studies found that invertebrate species richness increases in urban areas (Magura *et al.* 2004; Magura *et al.* 2010). Even though species richness may not always change due to urbanization, community composition consistently differs between urban and rural habitats in both vertebrates and invertebrates (Urban *et al.* 2006; Pillsbury and Miller 2008; Van Nuland and Whitlow 2014; reviewed in McKinney 2008). Urban animal communities typically have lower diversity than those in less altered habitats (McKinney 2002; Shochat *et al.* 2006; Luck and Smallbone 2010), and often widespread, non-native generalist species replace native species, resulting in homogenization at urban sites (McKinney and Lockwood 2001; Blair 2004; McKinney 2006; McDonnell and Hahs 2008; Horsák *et al.* 2013; Hassall 2014; Knop 2016; but see Olden and Rooney 2006).

In my third chapter, I identified three dragonfly traits that correlate with an extinction risk assessment. Population responses to changing habitats vary across odonates. *Pantala flavescens*, a dragonfly species that has a global migratory pattern, experiences gene flow on a global scale (Troast *et al.* 2016) while three damselfly species are somewhat negatively affected (Sato *et al.* 2008). These contrasting responses to urbanization may be due to species-specific biological and life-history traits that affect their resiliency to disturbance in the landscape (Prevedello and Vieira 2010), but comparative studies focusing on how ecological traits of arthropods correlate with extinction risk are largely unknown (McKinney 1997; Reynolds 2003; Hutchings *et al.* 2012; Jeppsson and Forslund 2014). The differences in the biological and life-history traits that frequently correlate with extinction risk (McKinney 1997; Reynolds 2003; Hutchings *et al.* 2012; Jeppsson and Forslund 2014) can be identified and used to assess which taxa are most at risk (Foufopoulos and Ives 1998). From there, conservation priorities can be established (Reynolds 2003; Jeppsson and Forslund 2014) and implemented (Nylin and Bergström 2009).

By investigating how arthropods are affected by urban land use and identifying ecological correlates with extinction risk, my dissertation provides insight into and future directions for the conservation of arthropods in North America.

CHAPTER II

LANDSCAPE GENETICS OF *RABIDOSA RABIDA* ACROSS AN URBAN LANDSCAPE

SUMMARY

Urbanization is a leading cause of habitat fragmentation and isolation because the urban matrix is typically of poor quality for most species and increases the resistance of the matrix to dispersal. This often reduces gene flow among populations. I used landscape genetic techniques to investigate the impact of urban development on gene flow among populations of the rabid wolf spider, *Rabidosa rabida.* Urbanization correlated with isolation by resistance and generally reduced migration rates among populations. However, the proportion of genetic variation among populations and estimates of genetic differentiation were low, and there were high degrees of admixture, suggesting that urban development does not drastically reduce gene flow among populations. Thus, urbanization does not greatly affect gene flow in this species. Two modes of dispersal, aerial and cursorial, likely maintain gene flow among populations.

INTRODUCTION

Anthropogenic land uses break up large swaths of continuous habitat into smaller patches that isolate animal populations. The degree of isolation is affected by several factors, including the number and features of traversable corridors linking habitat patches and the quality of the matrix surrounding those corridors (Ricketts 2001; Prugh *et al.* 2008; Prevedello and Vieira 2010). Populations become increasingly isolated when corridors are narrow (Andreassen *et al.* 1996) or composed of degraded habitat (Anderson and Danielson 1997; Henein and Merriam 1990). Isolation also increases when habitat patches are distant from one another and long corridors are required to promote connectivity. The quality of the matrix is determined by its similarity to occupied patches of habitat. The matrix habitat can be a primary determinant of population connectivity, with the matrix becoming increasingly inhospitable for native species as its characteristics diverge from inhabited areas (Öckinger and Smith 2008; Prevedello and Vieira 2010).

Habitat fragmentation and isolation caused by urbanization is of particular interest to conservation biologists because urbanization is the leading driver of species extinction (Czech *et al.* 2000; McKinney 2006) and is expected to continue to rapidly spread across the world (Alig *et al.* 2004; UN 2014). The urban matrix is typically of very poor quality for most species because it replaces native habitat (Unfried *et al.* 2013) with landscapes that typically lack or are very low in basic requirements for survival, such as appropriate food resources. In addition to making survival more difficult, urban development also increases the resistance of the matrix, thereby making animal dispersal more difficult and reducing gene flow among populations (Verbeylen *et al.* 2003; Unfried *et al.* 2013). Isolated populations have reduced genetic diversity and increased genetic differentiation due to forces such as inbreeding and genetic drift. When genetic variability is reduced, populations may suffer from lower survival and fitness (Reed and Frankham 2003) and may be unable to adequately respond to sudden changes in the environment (Hedrick

2011). This is especially problematic in urban areas where natural disturbance regimes are altered and novel disturbances are introduced (Alberti 2005).

Most studies that investigate the effect of isolation on gene flow among populations use an isolation-by-distance framework (McRae 2006), which assumes the genetic difference between pairs of populations positively correlates with the geographic distances separating them (Wright 1943; Rousset 1997). However, using only the straight-line distance between populations ignores the heterogeneity of the matrix (Verbeylen *et al.* 2003) and may be particularly unsuitable for urban population genetics studies because of the intense resistance of the urban matrix to movement (Verbeylen *et al.* 2003). Including analyses assessing the quality of the corridors, which has been little studied in urban areas (Braaker et al. 2014), and landscape resistance results in a more in-depth understanding of how urbanization affects animal populations. Isolation by resistance assesses the relationship between genetic differentiation among populations and the resistance of the landscape to migration based on electrical circuit theory (McRae 2006), with differentiation expected to increase with increasing resistance. In urban areas, corridors are likely to be highly degraded, resulting in greater genetic differentiation among populations than in less disturbed areas.

Surprisingly few studies have examined how urbanization affects population genetic dynamics in animals (Noël and Lapointe 2010), and those that have usually focused on genetic differentiation among urban populations as a function of geographic distance. Furthermore, among these studies, most have focused on vertebrate taxa (*e.g.* salamanders: Noël and Lapointe 2010; frogs: Hitchings and Beebee 1997, Mikulíček and Pišút 2012; lizards: Delaney *et al.* 2010; birds: Delaney *et al.* 2010; Björklund *et al.*

2010, Unfried *et al.* 2013; and mammals: Epps *et al.* 2005, Lee *et al.* 2012, Munshi-South 2012, Santonastaso *et al.* 2012). The general pattern emerging from these studies is that vertebrate populations in urban areas experience a reduction in gene flow.

How urbanization affects the population genetics of arthropods is not well understood (Bond *et al.* 2006). Studies of invertebrates have focused predominately on insects, especially those with strong flying capabilities, such as butterflies (Kronfrost and Fleming 2001; Takami *et al.* 2004), bees (Jha and Kremen 2013), and damselflies (Watts *et al.* 2004). These studies suggest that urbanization reduces gene flow among volant species (but see Kronfrost and Fleming 2001). To my knowledge, the only study to have tested for isolation by resistance in arthropods was done on bees (Jha and Kremen 2013). Studies on beetles, which are typically less mobile, have yielded conflicting results, with urbanization greatly reducing gene flow in one species (Keller and Largiadèr 2003) but not reducing it in others (Desender *et al.* 2005). The effects of anthropogenic landscapes on gene flow in spiders have not been well studied (*e.g.,* Schäfer *et al.* 2001; Stefani and Del-Claro 2015, Bond *et al.* 2006), and no study has investigated isolation by resistance in this taxon.

Corridor quality and barriers in urban areas affect most ground-dwelling vertebrates and invertebrates (Vandergast *et al.* 2009; Braaker *et al.* 2014, Unfried *et al.* 2013). However, spiders may respond differently to a hostile, urban matrix because responses to matrix type are species-specific (Prevedello and Vieira 2010) and spiders are not strictly ground-dwelling. The genetic studies that have examined the impact of urbanization on spiders have shown that the effects vary with species. For example, Stefani and Del-Carlo (2015) found no detectable levels of genetic differentiation between urban and rural populations of funnel-web spiders, while Bond *et al.* (2006) found that urbanization resulted in the extinction of populations of different mygalomorph spider species through loss of adaptability associated with reductions in genetic diversity.

Wolf spiders are wandering predators possessing two modes of dispersal that enable movement on different scales. First, wolf spiders move short distances terrestrially (Bonte *et al.* 2006). Second, wolf spiders disperse aerially via a behavior known as ballooning—which entails the release of silk threads that enables wind to pick up and carry the spider to a new location. Typically ballooning only takes place during the juvenile phase (Bell *et al.* 2005) and the spider largely does not control the outcome (Bonte *et al.* 2007). As such, using this method of dispersal within a highly resistant landscape could limit gene flow among populations because the probability of reaching a suitable patch may be low. Thus, wolf spiders may be at least partially dependent on landscape connectivity for movement and gene flow, as is the case with ground-dwelling mammals (Braaker *et al.* 2014). While relatively little is known about the molecular ecology of wolf spiders, Reed *et al.* (2011) examined gene flow in *Rabidosa rabida* across fragmented patches in Mississippi and found significant levels of isolation by distance, suggesting that anthropogenic land use affects gene flow in this species. In this study, I investigated gene flow and isolation by resistance in *R. rabida* in the greater Louisville area in order to better understand how urbanization affects this species.

METHODS

Study Species

Rabidosa rabida (Walckenaer 1837) is a wolf spider species that predominantly inhabits grasslands (Brady and McKinley 1994; Reed *et al.* 2007a), although this species can also be found in disturbed, suburban habitats. I chose to study *R. rabida* because it is abundant and easy to collect and genetic resources have been developed for this species (Reed *et al.* 2011). While the level of dispersal exhibited by this species is not well understood, Reed *et al.* (2011) suggested that aerial dispersal via ballooning is likely to be the predominant mode of dispersal for this species. With respect to terrestrial movement, lycosid spiders travel between 1 m (Framenau 2005) and 8 m (Bonte *et al.* 2003) per day.

Study Sites

From August through September 2013, I collected spiders from four urban and three rural sites in and around Louisville, Kentucky, with sites located within Interstate 265 classified as "urban" and those outside of I265 classified as "rural" (Figure 1, Table 1). I chose to use Interstate 265 as my delineation between urban and rural sites because it is a perimeter highway that surrounds the majority of the Louisville Metropolitan Area (population 763,623). The use of Interstate 265 as a delineation line between urban and rural sites is supported by the quantification of the amount of urbanization around each site, as all urban sites are surrounded by more than 45% urban land use while all rural sites are surrounded by less than 22% urban land use, as determined by the National Land Cover Database (Homer *et al.* 2015; Table 1). Distances between sites ranged from 6.94 km to 54.17 km.

Collection Methods

Between 15 and 28 *R. rabida* were collected from each site. I collected spiders exclusively at night following the methods of Reed *et al.* (2007b). Specifically, I located spiders by scanning the ground and vegetation for their eyeshine in the light of a headlamp. Once captured, spiders were placed in labeled collection vials, and their GPS coordinates were recorded with a Garmin Dakota 10. Spiders were then taken to the lab where they were euthanized via freezing at -20°C.

DNA Isolation and Genotyping

DNA was isolated from each spider using a slight modification of the protocol described by Fetzner (1999). DNA isolates were used to genotype each spider at five microsatellite loci that were described by Reed *et al.* (2007a). I used the nested PCR approach described by Schuelke (2000) to label PCR products with 6-FAM. The forward or reverse primer for each locus was modified by appending a M13(-21) DNA sequence (TGT-AAA-ACG-GCC-AGT) to the 5' end of one of the primers in each respective primer pair based on the results of a hairpin analysis performed via the Integrated DNA Technology (IDT) website.

I amplified each locus with 25 µl PCRs as follows: 1x buffer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.2 µM M13(-21)-labeled species specific primer, 0.8 µM untwinned primer, 0.8 µM of M13(-21) labeled with 6-FAM , 0.625 units GoTaq DNA polymerase

(Promega), 20-100ng DNA template. Reaction conditions were: 94°C for two minutes followed by 21 cycles of (1) 94°C for 30 seconds (2) 60°C for 30 seconds (3) 72°C for 40 seconds, followed by 8 additional cycles of (1) 94°C for 30 seconds (2) 53°C for 30 seconds (3) 72°C for 40 seconds and a final cleanup step of 72°C for 30 minutes. I shipped labeled PCR products to the Arizona State University DNA Lab where fragment analysis was performed using an ABI 3730. Scoring and binning were performed using GENEIOUS version 9.0.4 (Biomatters).

Genetic Analysis

I tested for deviations from Hardy-Weinberg equilibrium and pairwise genotypic disequilibrium using GenePop v4.2 (Rousset 2008) with 1000 dememorization steps, 100 batches, and 1000 iterations per batch. I then used GenAlEx (Peakall and Smouse 2012) to calculate G_{ST} and G''_{ST} (Meirmans and Hedrick 2011) and test for isolation by distance via a Mantel test. I also used GenAlEx to perform an analysis of molecular variance, AMOVA, (Excoffier *et al.* 1992) to determine how genetic variation is hierarchically partitioned among populations, among individuals within populations, and within individuals. All *P*-values were estimated from 9999 permutations, and when necessary, I corrected for multiple testing using Holm's (1979) procedure.

To determine whether urban development has reduced gene flow among populations, I used MIGRATE v3.6 (Beerli and Felsenstein 1999, 2001; Beerli 2009) and BAYESASS+ v1.3 (Wilson and Rannala 2003) to compare current and historical levels of migration among populations, respectively. Both programs use Markov chain Monte

Carlo algorithms to infer migration rates between populations; however MIGRATE estimates migration rates based on a coalescent model (Beerli and Felsenstein 1999) while BAYESASS+ uses transient linkage disequilibrium to estimate migration rates (Wilson and Rannala 2003). Although, MIGRATE is not the only population genetics software package to use a coalescent framework (*e.g.* Nath and Griffiths 1993, Slatkin and Maddison 1989), MIGRATE differs from other methods because it estimates migration rates from all possible genealogies and can be used under various mutation models and data types (Beerli and Felsenstein 1999). I ran MIGRATE under a Brownian motion model, using 1 long chain of 5,000,000 iterations, a burn-in period of 10,000 and 50,000 recorded steps. MIGRATE estimates the mutation-scaled migration rate (*M*) (*M*=m/μ, where m=immigration rate, μ=mutation rate) and the mutation-scaled effective population size ($\Theta=4N_e\mu$, where N_e is the average effective population size over $4N_e$ generations). Because MIGRATE and BAYESASS+ report similar but distinct parameters, I calculated m from the *M* parameter estimated via MIGRATE by multiplying by a range of mutation rates that bracket empirical estimates from a variety of systems (Li *et al.* 2002).

BAYESASS+ and other methods of estimating contemporary migration rates have fewer assumptions than estimators of historical migration rates (*e.g.* BAYESASS+ does not assume constant population size; Wilson and Rannala 2003). BAYESASS+ differs from other contemporary methods in that it does not assume that genotypes within a population are in Hardy-Weinberg equilibrium (Wilson and Rannala 2003). BAYESASS+ estimates the migration rate of the last three generations (Wilson and Rannala 2003), and I ran this software with 3,000,000 iterations, a burn-in period of

1,000,000, and a sampling number of 2,000. As recommended by Meirmans (2014), I used the model with the lowest Bayesian deviance.

Landscape Analysis

GENELAND (Guillot *et al.* 2005) is an R package that conducts spatially-explicit genetic clustering, and I used this software to gain insight into which landscape features within my study area that may be acting as barriers to gene flow among populations. I ran GENELAND with an uncertainty of 0.05 m, a minimum of 1 population and a maximum of 7 populations, 100,000 iterations, and a thinning of 100 iterations. The allele frequency model option was set to correlated, the spatial model options was set to true, and the null allele model was set to true. I also tested for admixture with 20,000 iterations and a thinning of 10.

To identify key barriers and corridors within the landscape, I implemented an array of software programs in ArcMap Student Edition 10.2 (ESRI 2015). I first created a 106 km by 88 km^2 area that encompassed all sites, and then used the National Land Cover Database 2011 (Homer *et al.* 2015; NLCD) to classify the landscape characteristics within that area. The NLCD catalogs the earth's surface into 21 different land categories at a resolution of 30m. The NLCD describes four urban land use categories, which are based on the percentage of impervious surface within that 30m resolution (Table 1). Within my buffer, I found 15 different land cover classifications (Table 2)

In order to find corridors through the urban matrix and then determine the quality of these corridors, I quantified the amount of resistance found throughout the landscape. In addition to this, I also created habitat rasters to examine where the most suitable habitat within the landscape is located. To produce habitat and resistance rasters, I used Gnarly Landscape Utilities v0.1.0 (McRae *et al.* 2013a). To create the rasters, I gave habitat and resistance scores to each NLCD classification found in the landscape (Table 2). Habitat scores must range between zero and one, with one being the most suitable habitat (McRae *et al.* 2013a). The scores given are based on published papers and my knowledge of the biology of *R. rabida*. Because *R. rabida* is a grassland species, I gave the herbaceous classification a habitat value of one. While spiders can be found along the margins of forested areas that border meadow areas, they do not inhabit forested areas. Therefore, forested areas were given a habitat value of zero. The developed open intensity and developed low intensity land use classifications were given values of 0.8 and 0.7, respectively, because *R. rabida* occurs in these types of habitat (personal observation).

Unlike habitat scores, resistance scores were not capped at a value of one (McRae *et al.* 2013a), and higher values were given to land uses that greatly impede dispersal. I reasoned that developed, high intensity land cover deserves a high resistance score because the tall grasses or shrubs that *R. rabida* requires are not found in commercial areas. As recommended by the creators of the software, the lowest resistance was 1, which I assigned to the grassland category. This is necessary because Linkage Mapper v1.0 (McRae and Kavanagh 2011), which is used in the next step, cannot read resistance values of zero. For both types of rasters created, cells were not expanded.

After creating the rasters, I implemented Linkage Mapper v1.0 to identify least-cost corridors between the sites. Linkage Mapper uses the resistance raster created in Gnarly Landscape Utilities to identify important corridors among sites. To obtain all pairwise resistance values, I unchecked Step 1, which only finds corridors (and subsequently resistance values) between adjacent populations. Next, I identified important barriers within those corridors using Barrier Mapper v1.0 (McRae 2012a). When using Barrier Mapper, I set the minimum search radius to 90m, the maximum radius to 270m, and the radius step value to 90m. This tells the software to search for barriers within the corridors at an initial radius of 90m, and then search again after increasing the radius by 90m until the radius is 270m. The resolution of the resistance raster was 90m, which accordingly had to be the minimum radius. Gnarly Landscape Utilities established the resolution of the resistance raster as 90m, limiting the minimum search radius to 90m; Barrier Mapper only identified barriers at and above the resolution of the resistance raster (McRae 2012a).

Once this was done, I used Centrality Mapper v1.0 (McRae 2012b) to identify the most important corridors for maintaining connectivity between populations. Centrality Mapper does this by implementing Circuitscape v1.0 (McRae *et al.* 2013b) to send a one amp current across the corridors and core areas and then determining the current flow centrality. Next, I used Pinchpoint Mapper v1.0 (McRae 2012c) to identify areas within the corridors that are restricting movement. Like Centrality Mapper, Pinchpoint Mapper uses Circuitscape to send electrical currents through the corridors, but it then identifies specific areas within the corridors experiencing pinch points (bottlenecks). Circuitscape also calculates effective resistances between pairwise cores. To determine if isolation by resistance is present, I conducted a Mantel test on the G''_{ST} pairwise values and the pairwise resistance values.

RESULTS

Genetic Analysis

After I corrected for multiple testing, three of the five loci tested in each of the seven sites (a total of 35 tests), deviated from Hardy-Weinberg equilibrium: locus 3 in Iroquois Park and locus 1 in Rural Sites B and C. We found no evidence for pair-wise genotypic disequilibrium between any pair of loci in any of the populations. Because no locus presented systemic problems across a majority of populations, I conducted my analyses using all five loci. Summary statistics for each population are presented in Table 3.

Pairwise G_{ST} values range from -0.003 to 0.019 (Table 4), and pairwise G''_{ST} values range from -0.019 to 0.103. After correcting for multiple testing, no comparisons were significant (Table 5). The global G_{ST}, which provides the average G''_{ST} value across all loci, was 0.009 (p=0.014), and the global G''_{ST} was 0.034 (p=0.012). The AMOVA results presented in Table 6 show that differences among populations accounted for 4.3% of the variation in the data. The Mantel test provided no evidence of isolation by geographic distance (r=0.085, p= 0.388).

GENELAND detected three spatially explicit genetic clusters based on posterior probabilities (Figure 2). The posterior probabilities (Figure 2) indicate the likelihood that an individual belongs to a certain genetic cluster based on its geographic location.

Spiders from the four urban sites grouped into two clusters and spiders from the three rural sites belong to a third cluster (Figure 2). With respect to the urban sites, GENELAND grouped the Iroquois Park and Thurman-Hutchins Park populations into one cluster and the E.P. “Tom” Sawyer Park and Blackacre State Nature Preserve populations into another cluster. Additionally, the analysis I performed in GENELAND indicated that all individuals were admixed (Figure 3), further underscoring that the populations I sampled were not well differentiated from one another. These results align with the posterior probabilities associated with cluster assignment, as no probabilities appeared above 0.60, indicating that the assignment of each individual to its respective cluster was not particularly robust.

After assuming mutation rates to 1×10^{-4}, 1×10^{-5}, and 1×10^{-6} per generation per locus, MIGRATE estimated average proportions of migrants in each population as 6.463, 0.646, and 0.065. Mutation rates of 1×10^{-4} and 1×10^{-5} resulted in proportions that were > 1.0, indicating that these values are higher than the actual mutation rate in *R. rabida*. Accordingly, I conducted analyses using a mutation rate of 1×10^{-6} (Table 7). The highest proportions of migrants were from Rural Site B and Thurman-Hutchins Park to Blackacre State Nature Preserve, and the lowest proportions of migrants were all from Horner Wildlife Refuge. The proportion of migrants to and from each population were fairly uniform and varied between 0.053 and 0.105. I calculated the proportion of non-migrants in each population by subtracting the total proportion of migrants in each population from one, and proportions of non-migrants ranged from 0.540 to 0.648.

Current estimates of the proportion of migrants and non-migrants in each population as calculated by BAYESASS+ are presented in Table 8. 70% of non-migrants comprised most of the populations, except Rural Site C, which contained a high proportion of non-migrants (.872). Generally, the proportions of migrants from one population to another ranged from 0.012 to 0.049. However, Rural Site C had the largest proportion of non-migrants, and the proportion of migrants from this population was high relative to all other populations. Rural Site B contributed the lowest proportion of migrants to Blackacre State Nature Preserve and Thurman-Hutchins Park, and Thurman-Hutchins Park and Rural Site B received the highest proportion from Rural Site C. A one-tailed paired t-test comparing current versus historical proportions of migrants was significant (t=3.629, df=41, p=0.043), with average historical proportions being higher (0.065) than current mean proportion (0.046).

Landscape Analysis

Figure 4 displays the habitat raster showing that the urban landscape had less suitable habitat than rural areas, and Figure 5 displays the corridors (least-cost paths) between all sites found by Linkage Mapper as well as Pinchpoint Mapper's current flows within those pathways. Table 9 shows the least-cost path lengths and effective resistance of those pathways. The mean least-cost path length is 30.89 km (SD=17.56 km). The longest corridor is 52.56 km, which connects Iroquois Park and Rural Site C, while the shortest corridor is 7.90 km, between E.P. "Tom" Sawyer Park and Horner Wildlife Refuge.

The average pairwise resistance score (*e.g.* the average resistance for all linkages) was 52,749 (SD=32,384.8). The link between Iroquois Park and Horner Wildlife Refuge had the highest resistance score, 120,186.1. Linkages associated with Iroquois Park contained the top five resistance scores. The link between Rural Site B and Rural Site C had the lowest score, 12,587. I failed to identify any corridors free of strong barriers, as Pinchpoint Mapper identified pinch points in all corridors, even those with low resistances and in rural areas. As mentioned above, these spiders are grassland habitat specialists, and a forested landscape may therefore create natural pinch points within the corridors. While a Mantel test did not detect a significant association between the geographic and genetic distance matrices (r=0.085; p= 0.388), there was a significant association between the resistance and genetic distance matrices (r = 0.599; p=0.046; Figure 6).

DISCUSSION

The results of this research suggest that urbanization correlates with isolation by resistance and has generally reduced gene flow among *R. rabida* populations. Historical rates of gene flow appear somewhat higher than contemporary rates, and a positive association exists between genetic distance and landscape resistance—a predictor variable correlated with the degree of urbanization. Nevertheless, according to BAYESASS+ immigrants constitute at least 12% of every population. Thus, despite the inhibitory effects urbanization may have on gene flow in *R. rabida*, substantial connectivity among the populations appears to still exist. Low G_{ST} estimates, a low proportion of variation being attributable to differences among populations (AMOVA), high degrees of admixture among spatially explicit clusters, and a high proportion of migrants in each population from Rural Site C support this conclusion. *Rabidosa rabida* often occurs in suburban gardens and homes (pers. obs.), so clearly they can persist in these partially degraded areas. Collectively, these results suggest that the two modes of dispersal found in this species, cursorial and aerial, keep the levels of genetic differentiation among the populations low.

Given the low G_{ST} estimates, gene flow among the populations is occurring and is likely maintained via a source-sink model. The populations of *R. rabida* are well connected, suggesting a source population is present (Furrer and Pasinelli 2016), and the results of this research suggest that the population at Rural Site C is the source population. Current estimates of migration rates indicate that Rural Site C contributes a large proportion of migrants to all assessed populations, and immigration rates exceed emigration rates at this site. Source populations typically possess these characteristics (Watkinson and Sutherland 1995; Manier and Arnold 2005; Schaub *et al.* 2010). However, further analyses are needed to definitively assess this pattern. The fine-scale genetic clustering detected by GENELAND does not match migration rate estimates or any G_{ST} estimates. For example, while GENELAND clustered the two urban populations together, these two populations receive more migrants from other populations than from each other, and the G''_{ST} value between these two populations was the highest value documented. These conflicting results were possibly to due to the low number of individuals sampled as well as the low number of microsatellite markers used in the analyses.

Significant isolation by resistance occurred among the sampled populations, showing the difficulty for this species of crossing both forested landscapes (Reed *et al.* 2007b) and urban areas. Interestingly, in contrast to this study, Reed *et al.* (2011) found significant levels of isolation by distance. Differences in the amounts of forested areas and urban development between populations may lead to the different conclusions of the two studies. Further, the isolation by resistance may mask any detectable isolation by distance. Not only do the migration rates suggest that long-distance dispersal occurs even at current levels of urbanization, but also other studies show that resistance in the landscape affects the detection of any isolation by distance. For example, high levels of resistance between two very closely spaced populations of striped field mice in Poland masked the detection of isolation by distance (Gortat *et al.* 2014). The possibility also exists that the sample size is too low to detect any isolation by distance, as correlations between genetic distance and geographic distance are more likely to be significant with more loci being tested (Landguth *et al.* 2012).

The high levels of gene flow found in this study suggest that dispersal allows this species to persist in urban environments. Cursorial dispersal allows spiders to move short distances, and while cursorial dispersal is only effective in matrices with low resistance (Bonte and Maelfait 2001), *R. rabida* may find enough small areas of suitable habitat to continue to traverse the urban matrix. Spiders express cursorial behaviors more often when inhabiting low-quality habitats (Kreiter and Wise 2001, Bonte *et al.* 2004, Rykken *et al.* 2011), but the results of this study suggest that aerial dispersal predominately maintains gene flow given the distances between the sites and the resistance of the landscape.

Aerial dispersal greatly contributes to maintaining gene flow across the landscape in spiders. Reed *et al.* (2011) suggested that when gene flow via cursorial dispersal fails, aerial dispersal becomes important for *R. rabida.* Although relatively little research has addressed the effects of aerial dispersal on gene flow, aerial dispersal maintained high gene flow levels among isolated populations of *Argiope trifasciata* (Ramirez and Haakonsen 2001), and colonization across the Hawaiian Islands by spiders correlated with wind patterns (Gillespie *et al.* 2012). Currently, research on the impact of disturbed, fragmented landscapes on spider ballooning behavior suggests that habitat generalists and specialists have different responses; habitat specialists less often display aerial behaviors (Bonte *et al.* 2003, 2004, Entling *et al.* 2011), especially in small isolated populations (Bonte *et al.* 2006). Further, Entling *et al.* (2011) concluded that generalist spiderlings from disturbed habitats more often aerially dispersed than those from undisturbed habitats. The low estimated levels of genetic differentiation align with the view that *R. rabida* spiderlings frequently balloon in urban areas and that aerial dispersal plays an important role in maintaining connectivity across spatial scales that are large relative to the daily movements of adult *R. rabida*. In addition, aerial dispersal potentially explains how the Iroquois Park population is not more genetically differentiated from the other populations. Pinchpoint Mapper found a high level of resistance within the northern corridor that connects the Iroquois Park population to other populations (Figure 5), and only ballooning would allow spiderlings to successfully cross this inhospitable landscape.

Intraspecific variations in dispersal behavior between *R. rabida* in Northern Mississippi and *R. rabida* in the Louisville area could explain the contrast between the results of this study and the conclusions of Reed *et al.* (2011). Populations of *R. rabida* located 10 km apart exhibited no gene flow in Mississippi (Reed *et al.* 2011), whereas the Louisville populations were separated by much greater distances and still sustained gene flow. For example, the G_{ST} value between the Iroquois Park and Rural Site C populations, located 54 km apart, was 0.009. Intraspecific variations in dispersal behaviors are frequent in nature and often reflect differences in the composition and structure of the landscape (Stevens *et al.* 2010; Matthysen 2012). Variations in dispersal behaviors have been documented in a variety of taxa including black flies (Fonesca and Hart 1996), toads (Constible *et al.* 2010), sea-snakes (Lane and Shine 2011), and spiders (Bonte *et al.* 2006). Louisville and Northern Mississippi are located in different geographic locations and also have different climatic conditions. Thus, the possibility exists that the populations in Louisville have different dispersal behaviors from populations in Mississippi. This study demonstrated how combining traditional population genetic analyses with geospatial analyses further contributes to the understanding of how altered landscapes and resistance within the landscape affect gene flow in cursorial spiders. Future studies need to investigate the differential responses of *R. rabida* and other spiders to urban development across the United States and identify the mechanisms that are driving these responses.

Table 1. List of sites and their respective development category, geographic coordinates, habitat size, and name abbreviations. Sites located within Interstate 265 are considered urban, while those located outside the interstate are rural.

Site	Development Category	Coordinates		Size (m^2)	Abbreviation
Iroquois Park	Urban	38°09'42"N	085°47'15"W	64533.54	IP
Thurman-Hutchins Park	Urban	38°16'54"N	085°41'26"W	24872.95	TH
Blackacre State Nature Preserve	Urban	38°11'34"N	085°31'30"W	104755.6	BA
E.P. "Tom" Sawyer Park	Urban	38°17'08"N	085°33'36"W	9266.528	TSP
Horner Wildlife Refuge	Rural	38°20'35"N	085°31'44"W	1582.946	HNR
Rural Site B	Rural	38°23'13"N	085°25'39"W	2077.007	RSB
Rural Site C	Rural	38°26'48"N	085°16'44"W	22198.66	RSC

Table 2. Land cover classifications found within my 106km x 88km area with respective habitat and resistance values. Land cover classifications are determined by the National Land Cover Database.

Land Cover Classification	Habitat Value	Resistance
Open Water	0	50
Developed, Open Space	0.8	1
Developed, Low Intensity	0.7	2
Developed, Medium Intensity	0	60
Developed, High Intensity	0	85
Barren Land	0	2
Deciduous Forest	0	70
Evergreen Forest	0	50
Mixed Forest	0.1	25
Shrub/Scrub	0.7	2
Herbaceous	1	1
Hay/Pasture	0.9	1
Cultivated Crops	0.5	1
Woody Wetlands	0	40
Emergent Herbaceous Wetlands	0.1	30

Table 3. Summary statistics for each locus in each population and mean (standard error) across all loci in a population. N: number of individuals sampled, N_A: number of alleles, N_{EA}: number of effective alleles, H_O: observed heterozygosity, H_E: expected heterozygosity, F_{IS}: inbreeding coefficient (Weir and Cockerham 1984), M-Ratio: M-ratio (Garza and Williamson 2001). * indicates significant deviations from Hardy-Weinberg Equilibrium

Population	Locus	N	N_A	N_{EA}	H_O	H_E	F_{IS}	M-Ratio
IP	1	22	12	7.118	0.864	0.860	0.019	0.706
	2	26	5	2.198	0.269	0.545	0.508	0.625
	3	23	7	3.574	0.652	0.720	0.117	0.875
	4	26	3	1.362	0.154	0.266	0.437	0.750
	5	24	19	14.961	0.875	0.933	0.084	0.613
		24.200 (0.800)	9.200 (2.871)	5.843 (2.482)	0.563 (0.150)	0.665 (0.120)	0.233 (0.100)	0.714 (0.048)
TH	1	12	8	3.740	0.583	0.733	0.245	0.615
	2	16	3	1.290	0.125	0.225	0.469	1.000
	3	16	6	2.338	0.500	0.572	0.158	0.750
	4	16	4	1.690	0.438	0.408	-0.040	1.000
	5	15	12	8.824	0.800	0.887	0.132	0.400
		15.000 (0.775)	6.600 (1.600)	3.576 (1.376)	0.489 (0.110)	0.565 (0.117)	0.193 (0.083)	0.753 (0.115)
TSP	1	12	9	6.545	0.667	0.847	0.254	0.900
	2	12	4	1.419	0.250	0.295	0.195	0.667
	3	15	6	4.500	0.533	0.778	0.345	0.750
	4	4	5	3.200	0.750	0.688	0.053	0.625
	5	15	16	11.250	0.733	0.911	0.228	0.727
		11.600 (2.015)	8.000 (2.168)	5.383 (1.689)	0.587 (0.092)	0.703 (0.109)	0.215 (0.048)	0.734 (0.047)
BA	1	13	8	4.694	0.692	0.787	0.160	0.727
	2	16	6	2.462	0.438	0.594	0.293	0.667
	3	15	7	4.327	0.733	0.769	0.081	0.636
	4	10	6	1.961	0.500	0.490	0.032	0.750

	5	15	12	8.491	0.800	0.882	0.127	0.750
		13.800 (1.68)	7.800 (1.114)	4.437 (1.151)	0.633 (0.070)	0.704 (0.071)	0.139 (0.044)	0.706 (0.023)
HNR	1	23	11	6.116	0.565	0.836	0.344	0.786
	2	24	5	1.867	0.333	0.464	0.302	0.833
	3	20	8	4.469	0.550	0.776	0.315	0.615
	4	20	5	1.709	0.300	0.415	0.301	0.714
	5	15	13	8.491	0.667	0.882	0.277	0.650
		20.400 (1.568)	8.400 (1.600)	4.530 (1.289)	0.483 (0.071)	0.675 (0.098)	0.308 (0.011)	0.720 (0.041)
RSB	1	22	11	6.630	0.636	0.849	0.272	1.000
	2	25	4	1.758	0.320	0.431	0.277	1.000
	3	25	7	3.655	0.560	0.726	0.248	0.875
	4	21	6	2.023	0.429	0.506	0.176	1.000
	5	18	13	10.286	1.000	0.903	-0.079	0.448
		22.200 (1.319)	8.200 (1.655)	4.870 (1.608)	0.589 (0.116)	0.683 (0.093)	0.179 (0.067)	0.865 (0.107)
RSC	1	13	10	6.377	0.615	0.843	0.307	0.909
	2	24	4	1.354	0.250	0.261	0.064	0.800
	3	24	8	2.946	0.542	0.661	0.201	1.000
	4	25	5	1.460	0.240	0.315	0.258	0.714
	5	16	14	11.130	0.875	0.910	0.071	0.737
		20.400 (2.462)	8.200 (1.800)	4.653 (1.856)	0.598 (0.133)	0.598 (0.133)	0.180 (0.049)	0.832 (0.054)

Table 4. Pairwise G_{ST} values and uncorrected *P*-values among all sites. G_{ST} values are below the diagonal and *P*-values are above.

	IP	**TH**	**TSP**	**BA**	**HNR**	**RSB**	**RSC**
IP		0.002	0.020	0.075	0.052	0.011	0.028
TH	0.019		0.071	0.184	0.062	0.071	0.495
TSP	0.014	0.011		0.574	0.344	0.131	0.303
BA	0.007	0.006	-0.001		0.685	0.243	0.391
HNR	0.008	0.010	0.002	-0.003		0.199	0.567
RSB	0.011	0.009	0.007	0.003	0.004		0.110
RSC	0.009	0.002	0.004	0.002	0.000	0.007	

Table 5. Pairwise G″$_{ST}$ values and uncorrected p-values among all sites. G″$_{ST}$ values are below the diagonal and *P*-values are above. After correcting for multiple testing, no values are significant.

	IP	**TH**	**TSP**	**BA**	**HNR**	**RSB**	**RSC**
IP		0.004	0.014	0.070	0.046	0.013	0.030
TH	0.103		0.064	0.185	0.067	0.080	0.492
TSP	0.095	0.067		0.580	0.330	0.126	0.276
BA	0.051	0.033	-0.011		0.689	0.235	0.382
HNR	0.049	0.057	0.013	-0.019		0.202	0.556
RSB	0.069	0.052	0.048	0.024	0.025		0.102
RSC	0.053	0.008	0.023	0.013	0.000	0.038	

Table 6. AMOVA results examining genetic variation at different scales. Variation among populations accounted for only 4.3% of the variation found, with 34.7% of the variation found among individuals and the majority (61.0%) of the variation within individuals.

	df	**SS**	**MS**	**Variance Component**	**Percent Variation**	**Fixation Index**	**P-value**
Among Populations	6	34.423	5.737	0.078	4.284	F_{ST}=0.043	< 0.001
Among Individuals	144	343.809	2.388	0.636	34.743	F_{IS}=0.363	< 0.001
Within Individuals	151	168.500	1.116	1.116	60.973	F_{IT}=0.390	< 0.001
Total	301	546.732		1.830	100.000		

Table 7. Historical mean estimates of proportion of migrants and non-migrants within each population as estimated from MIGRATE. Values along the diagonal represent the proportion of non-migrants within the population, and values above and below the diagonal represent the proportion of migrants within the population. Column names indicate source population and row names indicate sampled population.

Historical estimates have been calculated with a mutation rate of 1×10^{-6}. The highest proportions of migrants were from Rural Site B and Thurman-Hutchins Park to Blackacre State Nature Preserve, and the lowest proportions of migrants were all from Horner Wildlife Refuge. The proportion of migrants to and from each population ranged from 0.053 to 0.105. Note, MIGRATE does not provide standard deviations.

	IP	**TH**	**TSP**	**BA**	**HNR**	**RSB**	**RSC**
IP	0.591	0.083	0.073	0.070	0.053	0.075	0.056
TH	0.055	0.648	0.058	0.063	0.053	0.066	0.056
TSP	0.062	0.062	0.648	0.055	0.053	0.060	0.060
BA	0.060	0.100	0.071	0.540	0.053	0.105	0.070
HNR	0.064	0.070	0.071	0.058	0.618	0.055	0.063
RSB	0.058	0.085	0.062	0.059	0.053	0.629	0.054
RSC	0.064	0.074	0.072	0.059	0.053	0.067	0.611

Table 8. Current mean (SD) proportion of migrants and non-migrants within each population as estimated from BAYESASS+. Row names indicate the populations that the migrants disperse to, and column names indicate the source population. Values along the diagonal show the number of non-migrants within each population. Most populations contained approximately 70% non-migrants, except Rural Site C, which contained a high percentage (87.2%) of non-migrants.

	IP	**TH**	**TSP**	**BA**	**HNR**	**RSB**	**RSC**
IP	0.732 (0.045)	0.013 (0.013)	0.015 (0.014)	0.013 (0.012)	0.018 (0.018)	0.018 (0.018)	0.192 (0.046)
TH	0.020 (0.019)	0.682 (0.014)	0.016 (0.015)	0.015 (0.015)	0.016 (0.015)	0.017 (0.016)	0.235 (0.033)
TSP	0.049 (0.037)	0.024 (0.023)	0.699 (0.029)	0.021 (0.020)	0.034 (0.029)	0.036 (0.032)	0.137 (0.048)
BA	0.029 (0.025)	0.021 (0.020)	0.021 (0.019)	0.689 (0.020)	0.029 (0.024)	0.021 (0.020)	0.192 (0.039)
HNR	0.028 (0.024)	0.014 (0.013)	0.016 (0.014)	0.014 (0.013)	0.695 (0.026)	0.020 (0.018)	0.214 (0.040)
RSB	0.018 (0.017)	0.012 (0.012)	0.015 (0.014)	0.012 (0.011)	0.016 (0.015)	0.696 (0.024)	0.231 (0.035)
RSC	0.034 (0.030)	0.016 (0.015)	0.017 (0.016)	0.016 (0.015)	0.022 (0.021)	0.024 (0.020)	0.872 (0.040)

Table 9. List of the least-cost path length (meters, LCP Length) and effective resistance of all linkages between sites, as calculated by Circuitscape. Linkages associated with Iroquois Park contained the top five resistance scores. The link between Rural Site B and Rural Site C had the lowest score, 12,587. All corridors had strong barriers,

Population 1	Population 2	LCP Length	Effective Resistance
Iroquois Park	Thurman Hutchins Park	20980	100509.66
Iroquois Park	E.P. "Tom" Sawyer Park	28192	89223.17
Iroquois Park	Blackacre State Nature Preserve	35842	55384.10
Iroquois Park	Horner Wildlife Refuge	35441	120186.07
Iroquois Park	Rural Site B	49530	111845.24
Iroquois Park	Rural Site C	84658	83142.84
Thurman Hutchins Park	E.P. "Tom" Sawyer Park	14217	40078.29
Thurman Hutchins Park	Blackacre State Nature Preserve	25296	43088.57
Thurman Hutchins Park	Horner Wildlife Refuge	19153	64823.65
Thurman Hutchins Park	Rural Site B	33242	56395.64
Thurman Hutchins Park	Rural Site C	52562	68582.23
E.P. "Tom" Sawyer Park	Blackacre State Nature Preserve	13166	14874.88
E.P. "Tom" Sawyer Park	Horner Wildlife Refuge	7904	28555.87
E.P. "Tom" Sawyer Park	Rural Site B	20553	18263.02
E.P. "Tom" Sawyer Park	Rural Site C	39873	30460.21
Blackacre State Nature Preserve	Horner Wildlife Refuge	22769	49617.42
Blackacre State Nature Preserve	Rural Site B	30848	43835.43
Blackacre State Nature Preserve	Rural Site C	48838	27564.31
Horner Wildlife Refuge	Rural Site B	13059	18252.63
Horner Wildlife Refuge	Rural Site C	32379	30449.82
Rural Site B	Rural Site C	20219	12587.24

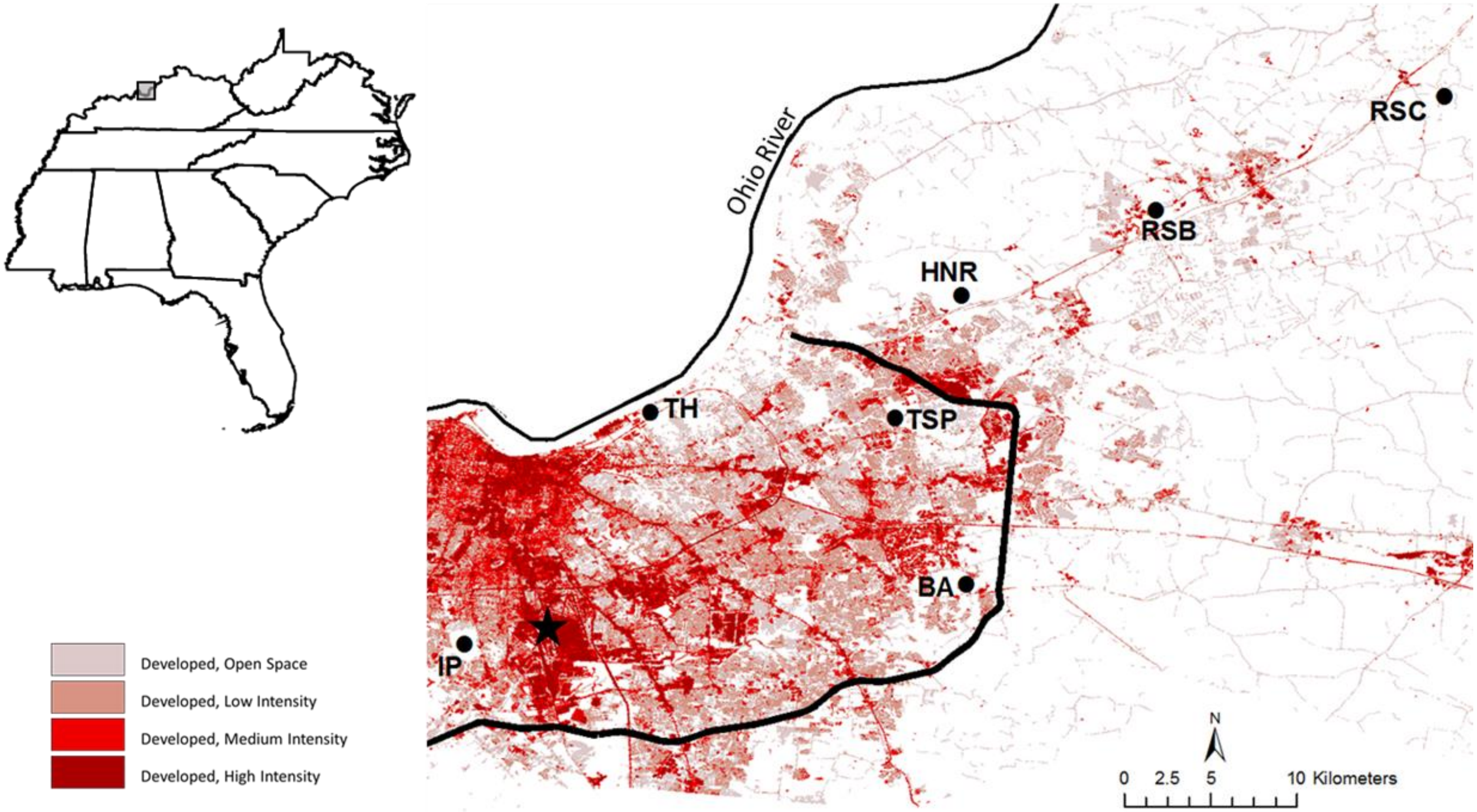


Figure 1. A map of the seven field sites with Interstate 265 separating urban and rural sites and urbanization intensity across the landscape. The star shows the location of the Louisville International Airport, and the heavy bold line shows Interstate 265. See Table 1 for list of site abbreviations. Urban development categories are from the National Land Cover Database.

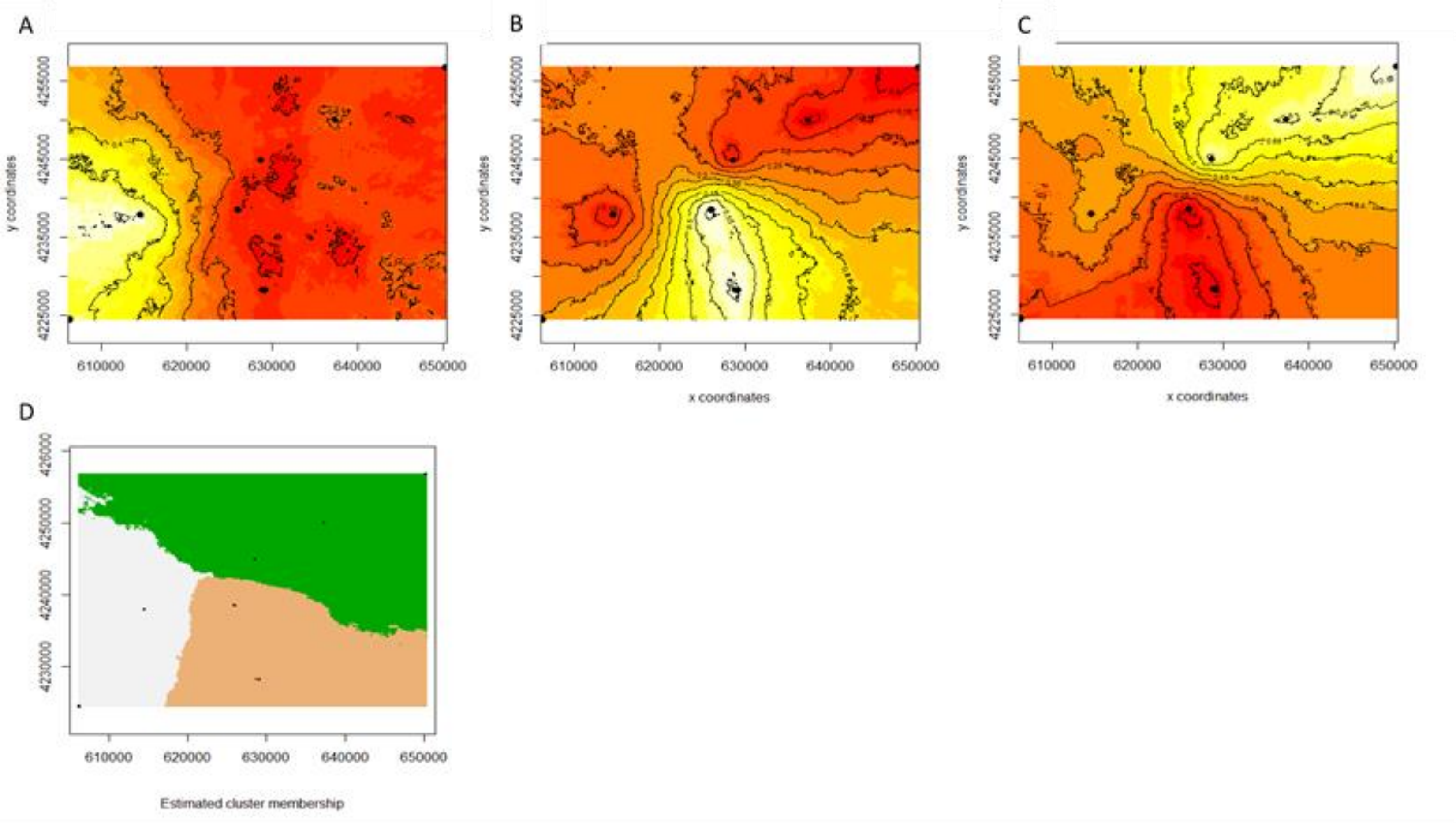


Figure 2. (A-C) Posterior probabilities of the likelihood of an individual belonging to a certain genetic cluster. White to light yellow areas indicate a high likelihood and red areas indicate a low likelihood. (D) Genetic clustering of all sites. Spiders from the four urban sites grouped into two clusters, which are shown in pink (Iroquois Park and Thurman-Hutchins Park) and

green (E.P. “Tom” Sawyer Park and Blackacre State Nature Preserve). Spiders from the three rural sites (Horner Wildlife Refuge, Rural Site B, and Rural Site C) belong to a third cluster, shown in grey.

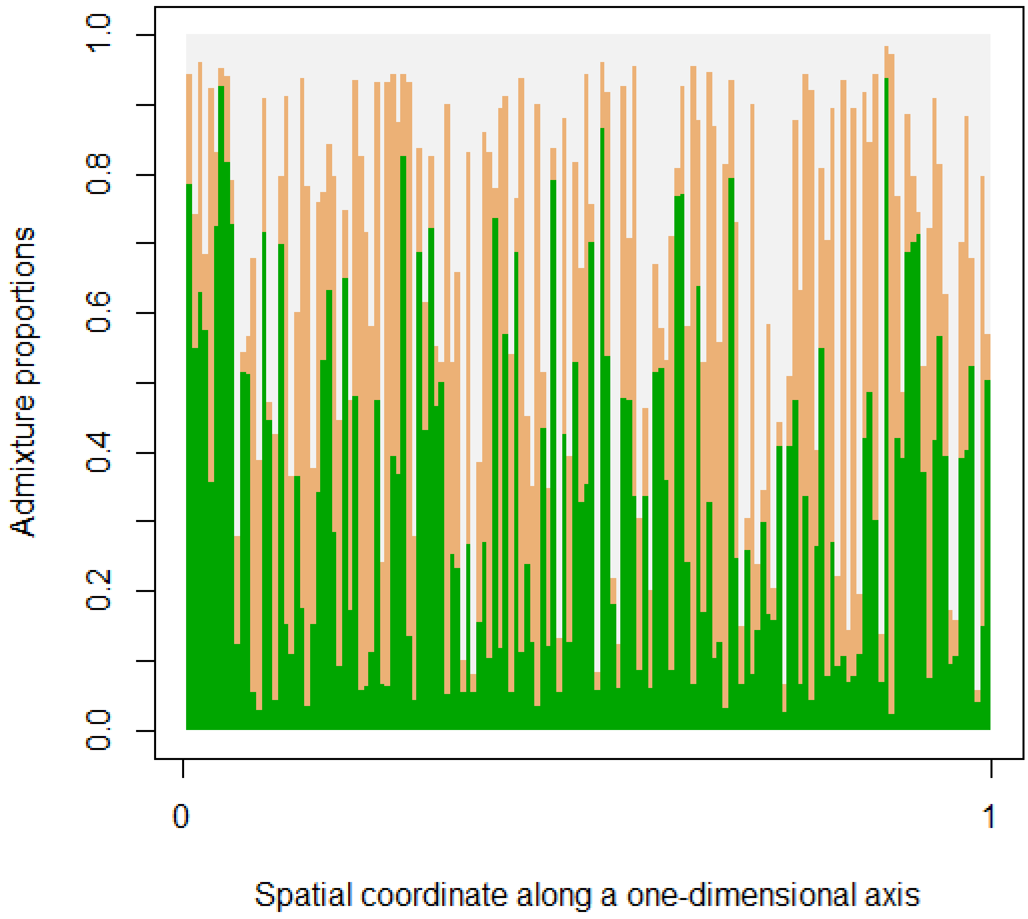


Figure 3. Admixture proportions estimated from GENELAND. Each column represents an individual; each bar within the column reflects the proportion of the individual's genotype that is genetically similar to any of the three genetic clusters. Pink bands indicate genetic similarities to cluster 1, green bands indicate genetic similarities to cluster 2, and grey bands indicate genetic similarities to cluster 3. The x-axis represents the geographical line across which admixture is tested, east (0) to west (1). All individuals were admixed, showing that the sampled populations were not well differentiated from one another.

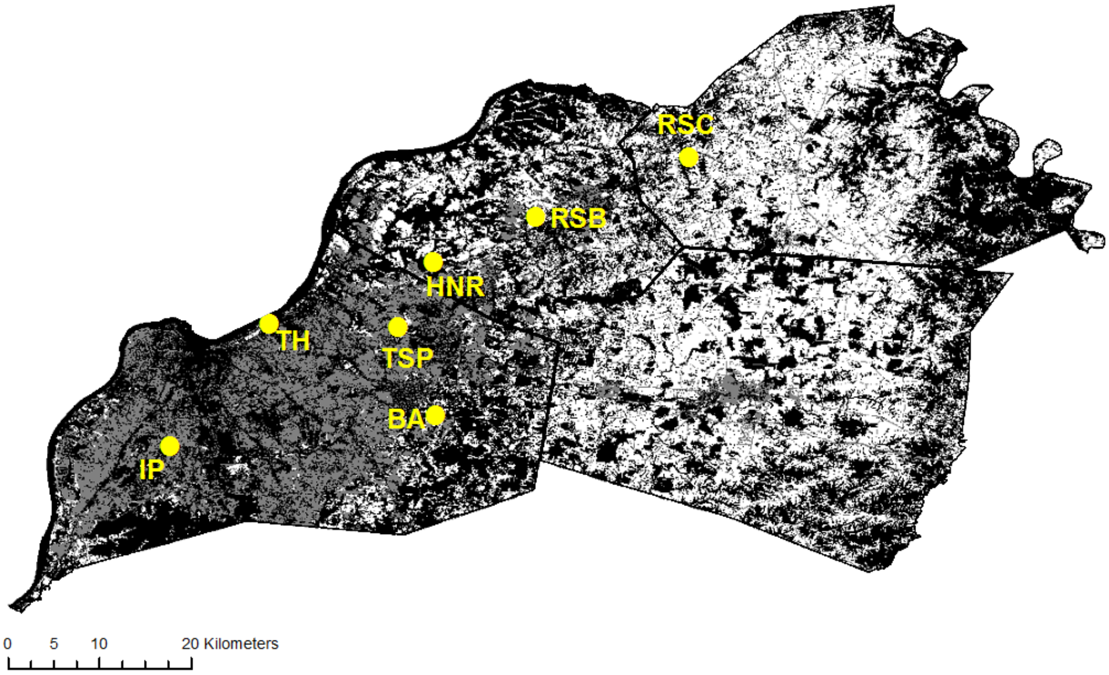


Figure 4. Habitat raster, developed by Gnarly Landscape Utilities, depicting quality of the landscape for suitable habitat. The lighter the color, the more suitable the habitat. Rural areas had more suitable habitat than do urban areas.

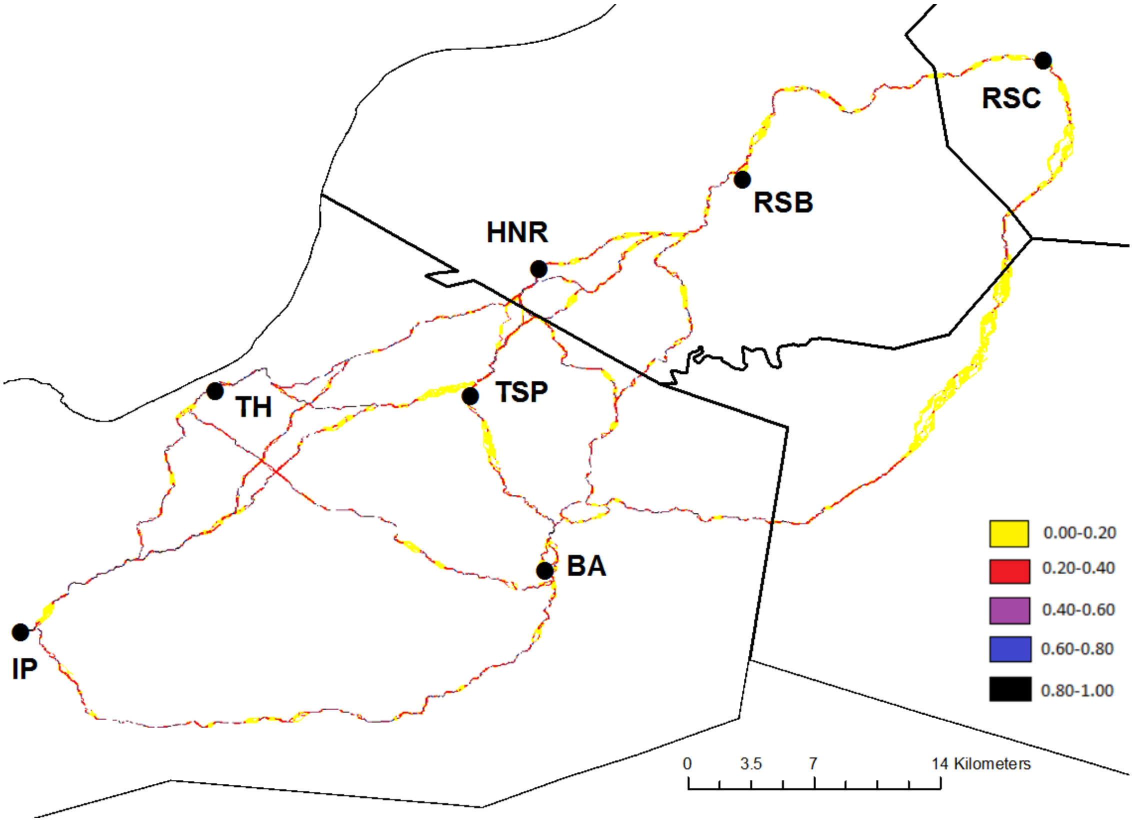


Figure 5. Least-cost paths identified from Linkage Mapper incorporated with Pinchpoint Mapper's current flows. Higher values indicate higher currents indicating locations where the corridor narrows and dispersal becomes more difficult. There is a high level of resistance within the northern path connecting Iroquois Park (IP) with other parks.

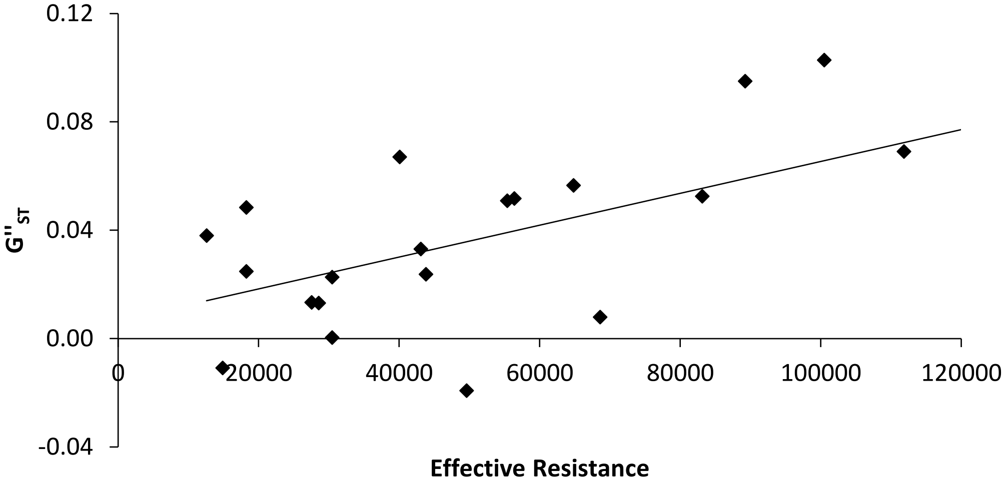


Figure 6. Mantel test showing a significant association between the resistance and genetic distance matrices (r = 0.599; p=0.046).

CHAPTER III

URBANIZATION DIFFERENTLY AFFECTS POND AND STREAM ODONATE COMMUNITIES

SUMMARY

Habitat alteration via urbanization has very different effects on even closely related taxa. However, most research investigating the ecological effects of urbanization focuses on birds or mammals, resulting in a poor understanding of the responses of invertebrate populations. I quantified the differences in the diversity of odonates (dragonflies and damselflies) at lentic and lotic sites between urban and rural landscapes and examined environmental factors that might affect community composition. Urbanization significantly lowered lentic damselfly species richness but did not alter lentic dragonfly species richness. Changes in lentic odonate community composition were associated with the amount of urban development within 150 of each site, mean algal coverage, and distance to the urban center. At lotic sites, water temperature and distance to the urban center influenced odonate communities. Inherent differences between dragonflies versus damselflies and between lentic versus lotic ecosystems likely drive the differing responses to urbanization observed in this study. Given that different environmental factors affect taxa differently in lentic and lotic sites, maintaining the highest level of odonate diversity possible across a landscape will require the use of different management practices for each ecosystem type.

INTRODUCTION

Urbanization profoundly affects biodiversity, and as cities continue to grow, the impact increases. Approximately 3.9 billion people currently inhabit urban areas; projections expect that number to rise to 6.3 billion by 2050 (United Nations 2015) and the land area occupied by cities will triple from 2000 to 2030 (Seto *et al.* 2012). The consequences of urbanization for animal species depend on the degree of urbanization and vary among taxa and ecosystems. In part, because of this complexity, our understanding of how urbanization affects animal communities remains inadequate, although major drivers of extinction include habitat loss and fragmentation (Wilcox and Murphy 1985; Fahrig 1997; Heinrichs *et al.* 2016). Further, urban development results in high rates of extinction for many native taxa (Vale and Vale 1976; Marzluff 2001; McDonald *et al.* 2008; Aronson *et al.* 2014). Taxonomic bias in research has hampered our understanding of the effects of urbanization on animal taxa—only 10-12% of studies of urban wildlife in the 1990s and 2000s focused on arthropods, for example, while 38% focused on mammals and 43% on birds (Magle *et al.* 2012).

Urbanization commonly affects both species richness and community composition. In vertebrates, species richness typically declines along a rural to urban gradient (reviewed in McKinney 2008; Urban *et al.* 2006; Pillsbury and Miller 2008; Van Nuland and Whitlow 2014), although sites with intermediate levels of urbanization hold higher avian species richness levels than rural or highly urbanized areas (Chace and Walsh 2006). Although relatively little studied, invertebrate responses to urbanization are complex and vary across taxa. Similar to the vertebrate pattern, invertebrate species richness generally declines along rural to urban gradients (Hansen *et al.* 2005; reviewed by McKinney 2008). However, some species richness patterns also show neutral responses (reviewed by Faeth *et al.* 2011; Jones and Leather 2012), such as in nematodes (Pavao-Zuckerman and Coleman 2007), isopods (Hornung *et al.* 2007), and wasps (Christie and Hochuli 2009), and other taxa experience increased species richness in urban areas (carabids: Magura *et al.* 2004; spiders: Magura *et al.* 2010). In butterflies, the highest species richness can occur at intermediate levels of urbanization (Blair 1999), and tropical gardens hold more species than primary or secondary forests (Kudavidanage *et al.* 2011).

Urbanization also affects community composition for both vertebrates and invertebrates, and the ability of species to persist in urban areas depends on species-specific traits. (Chace and Walsh 2006; Scott 2006; Thompson and McLachlan 2007; Pillsbury and Miller 2008; Alexandre *et al.* 2010). Urban animal communities typically have lower diversity than those in less altered habitats (McKinney 2002; Shochat *et al.* 2006; Luck and Smallbone 2010), and often widespread, non-native species replace native species, resulting in homogenization at urban sites (McKinney and Lockwood 1999; Blair 2004; McKinney 2006; Horsák *et al.* 2013; Knop 2016; but see Olden and Rooney 2006). Habitat specialization may relate to species persistence in urban areas, with urban species possessing broader habitat tolerances (McKinney and Lockwood 1999; Devictor *et al.* 2007). Dispersal ability also affects species persistence; species with strong dispersal capabilities can traverse urban matrices (Bierwagen 2007) and thus may be more likely to persist. Differences in dispersal capability explained variation in the responses of some terrestrial and aquatic arthropods to urbanization (Vergnes *et al.*

2012; Smith *et al.* 2105), but did not affect urban carabid beetle communities (Weller and Ganzhorn 2004).

Urbanization negatively influences aquatic and terrestrial ecosystems (Paul and Meyer 2001; Hassall 2014), although studies predominantly focus on terrestrial habitats (Abel 2002; Dudgeon *et al*. 2006). Habitat fragmentation (Fahrig 2003; Fuller *et al.* 2015; Haddad *et al.* 2015), exotic species introductions (Gurevitch and Padilla 2004; Havel *et al.* 2015) and increased temperatures (Pickett *et al.* 2001; Grimm *et al*. 2008; Somers *et al.* 2013) alter both aquatic and terrestrial communities in urbanized environments. In aquatic habitats, because impervious surface cover replaces native vegetation, freshwater systems suffer from increased run-off of pollutants and nutrients into the water (Booth and Jackson 1997) and increased water temperatures driven by increases in air temperatures (Brönmark and Hansson 2002; Nelson and Palmer 2007). Decreased canopy cover further increases water temperatures (Somers *et al*. 2013). These anthropogenic factors reduce species richness and alter community composition in aquatic communities (Roy *et al*. 2003; Morse *et al*. 2003; Moore and Palmer 2005; Cuffney *et al.* 2010; Collier and Clements 2011; de Jesús-Crespo and Ramírez 2011). However, lentic and lotic habitats do not always suffer the same degradation or respond in the same ways to urbanization. Unlike ponds, streams additionally suffer from increased erosion and higher flow rates (Booth and Jackson 1997; Paul and Meyer 2001; Allan 2004), which further contribute to altered communities and reduced species richness in urbanized areas (Kennen *et al*. 2010; Marshall *et al.* 2010). Just as urbanization differently affects a single taxon inhabiting different terrestrial ecosystems

(Ogai and Kenta 2015), the inherent differences in lentic and lotic ecosystems may drive dissimilar responses of aquatic invertebrates inhabiting both systems.

Important predictors of odonate species richness and community composition in urban ponds (Aliberti Lubertazzi and Ginsberg 2010; Goertzen and Suhling 2013; Jeanmougin *et al.* 2014) and streams (Samways and Steytler 1996; Monteiro-Júnior 2013, 2014, 2015) include pH levels and the presence and characteristics of surrounding vegetation (for example canopy cover and emergent vegetation). Few studies have examined odonate communities across aquatic habitat types within an urban landscape, and most did not consider which environmental variables drove detected differences between lentic and lotic communities. One study identified locations of endangered species and which habitats possessed high odonate diversity (Küry and Christ 2010) and another merely identified how many odonate species inhabited an urban area (Craves and O'Brien 2013). Only Willigalla and Fartmann (2012) examined both lentic and lotic ecosystems, and they found that overall odonate species richness correlated with climate factors, but this study did not analyze lentic and lotic ecosystems separately. Thus, we still do not fully understand whether pond and stream communities respond in a similar manner to urban development. Additional studies will not only contribute to the understanding of how ecosystem degradation threatens odonates specifically, but will also provide further insight into the general response of insects to urban development.

Because the life histories of dragonflies and damselflies include both an aquatic larval stage and a terrestrial adult stage, odonate communities should reflect the effects of urbanization on ecosystems (Samways and Steytler 1996; Corbet 1999; Goertzen and Suhling 2013, 2015; Jeanmougin *et al.* 2014; Villalobos-Jiménez *et al.* 2016). However, previous research shows that odonate communities vary in their response to urbanization. A recent review concluded that urban development usually lowers odonate species richness (Villalobos-Jiménez *et al.* 2016), although urbanization had no effect or a positive effect on richness in approximately one-third of studies. Further, even small, urban bodies of water can maintain high odonate species richness (Aliberti Lubertazzi and Ginsberg 2010; Craves and O'Brien 2013; Goertzen and Suhling 2013; but see Fattorini 2014).

In this study, I examined whether odonate communities at lentic and lotic habitats within the same landscape respond similarly to urbanization. The objectives were to examine whether odonate species richness and community composition significantly differ between urban and rural areas and to identify which environmental variables are associated with any changes in community composition.

METHODS

Study Sites

I surveyed ten ponds (five urban and five rural) and ten streams (five urban and five rural) in and around Louisville, Kentucky (38°15'N - 85°45'W; population: 763,623 Figure 7; Table 10; US Census Bureau 2010). I categorized a site as urban if more than 30% of a 150-m zone surrounding the stream or pond consisted of urban development. The sites were primarily located within city parks, but four were located on private lands and two were on state or federal property. To decrease the possibility of odonates travelling between survey sites, I selected sites at least 1 km away from other sites, with the exception of one pond and one stream site (Angler Lake and Floyds Fork), which were located 0.2 km apart. Pond size ranged from 0.3 to 28.1 hectares. Because most ponds in Louisville contain stocked or released pet fishes, I surveyed only ponds and streams that contained fishes, which are predators of odonate larvae. Shoreline vegetation, an important factor for larval odonate emergence (Corbet 1999), was present at all surveyed ponds, but not in streams. Surveyed streams were perennial and varied from 1.6 m to 35.9 m in width. All the streams are located within the Salt River Basin and are direct or indirect tributaries of the Ohio River.

Surveys

To encompass the flight seasons of local odonate species, I surveyed all sites three times during May-August 2015, with at least one month between visits to the same site (Jeanmougin *et al.* 2014). To ensure high odonate diversity during my surveys, I conducted them between 09:00 and 16:30 hours when the temperature was over 17.5°C in the shade and when I estimated cloud cover to be less than 50% (Jeanmougin *et al.* 2014). For surveys, I walked 10-m linear transects along the water's edge and identified each odonate I encountered to species. A distance of one meter separated transects at a site, and I walked each transect in 6 minutes. I followed a rule-based stopping protocol (Watson 2003) to determine when a survey was complete so that my surveys accurately reflected the diversity of each site. A survey ended when three consecutive transects revealed no new species for a given site on that day. If I could not immediately identify an individual, I paused the survey until I made the identification. I used binoculars to identify distant individuals, and if I was unable to identify an individual, when possible I used a standard insect net to capture it and then identified it using a field guide. I combined *Tramea onusta* and *T. carolina* as *Tramea* sp. because I was unable to reliably distinguish or capture them for identification, but I left the distinctive *T. lacerata* as a single species.

Environmental Variables

I measured several environmental factors at each site. I used a Hydrolab Surveyor4 with an MS5 sonde to obtain the temperature and luminescent dissolved oxygen of the water at each site during each visit. To assess the availability of perching and oviposition sites at each site, I assessed the amount of emergent vegetation, algae, and miscellaneous debris along the edge of the water for every meter surveyed during a visit. Miscellaneous debris consisted of all items floating on the water that were not plants or algae, *e.g.*, floating/emergent sticks, leaves, and anthropogenic litter. I placed a 1 m^2 square quadrat made of PVC pipe over the water at each meter surveyed and estimated to the nearest ten percent the percentage of the quadrat covered by each of emergent vegetation, algae, and miscellaneous debris. For analysis, I averaged all environmental variables measured at each site across all three sampling times, with the exception of water temperature and dissolved oxygen, which we measured only during the second and third surveys at each site.

Using data from the National Land Cover Database 2011 (NLCD) (Homer *et al.* 2015), I quantified the proportion of urban land use within 150m of each study site

(Kutcher and Bried 2014). The NLCD classifies the landscape into 16 possible land-use categories at a resolution of 30m, with four of those categories describing urban land use: 1) developed, open space; 2) developed, low intensity; 3) developed, medium intensity; and 4) developed, high intensity. Open space urban development consists of mowed areas and <20% impervious surface cover; low intensity urban development consists of 20% to 49% impervious surface cover. Medium intensity urban development consists of 50 to 79% impervious surface cover, and high intensity urban development consists of 80-100% impervious surface cover. I ground-truthed each site to ensure that the NLCD produced accurate information, and I corrected cell categories as needed. In particular, I corrected the tendency of the NLCD to place cells located within parks into the "herbaceous" category when those cells should be in the "developed, open space" category, which by definition includes the open spaces of parks. I then calculated the proportion of urban cells within the 150-m buffer zone around each study site.

Statistical Analysis

I reported all means with standard deviations and performed all statistical analyses using the statistical software R v 3.1.1 (R Core Development Team 2015). I performed all analyses on community data summed across all seasons. First, I conducted a correlation of species richness with site size to determine whether site size should be included in further analyses. I then performed generalized linear mixed models using the lme4 package v 1.1-122 (Bates *et al.* 2015) to compare odonate species richness between urban and rural sites for each ecosystem type. I also did this separately for the two suborders Anisoptera and Zygoptera. I next determined whether pond and stream community compositions differed, using a two-factor permutational multivariate analysis of variance (PERMANOVA) with the factors being type of aquatic ecosystem (pond or stream) and urbanization level (urban or rural). This PERMANOVA yielded a significant p-value ($p = 0.037$), so I then compared urban versus rural sites within each ecosystem using one-factor PERMANOVAs. All tests used Jaccard's measure of similarity and ran with 9999 permutations in the Vegan package v 2.0-10 (Oksanen *et al.* 2013). I used non-metric multidimensional scaling (NMDS) to visualize the data for each PERMANOVA.

To examine the effects of environmental variables on dragonfly community composition, I first log-transformed the environmental data to linearize the relationship between the variables and community composition. I then performed separate forward-selection canonical correspondence analyses (CCA) (Ter Braak 1986) for ponds and streams, using significance of $p \leq 0.10$ as the cut-off value for inclusion in further models. I ran each analysis with 1000 permutations in each step. To determine whether the variation explained by the axes was significant, I performed a permutational ANOVA on each axis in the final model.

Finally, I conducted indicator species analyses to investigate whether certain species were characteristic of either ecosystem (pond versus stream) or land use type (urban versus rural) within each ecosystem. I ran all tests with 9999 permutations in the indicspecies package v 1.7.5 (De Caceres and Legendre 2009). To reduce the likelihood of a Type I error, I used Holm's (1979) correction for multiple testing on all tests that found more than four species to be significantly associated with a system or urbanization level (De Caceres and Legendre 2009).

RESULTS

I observed 50 odonate species, including 20 zygopterans and 30 anisopterans (Table 11), which is 32% of the 157 species documented in Kentucky (NatureServe Explorer 2009). Of the 50 observed species, 21 species (four zygopterans and 17 anisopterans) were only found at ponds, six species (three zygopterans and three anisopterans) were only at streams, and 23 species (13 zygopteran and 10 anisopteran) occurred at both ponds and streams. No significant correlation existed between pond species richness and pond size (r = -0.27, $p = 0.44$). Species richness significantly differed between dragonflies and damselflies at urban and rural pond sites ($p = 0.03$) but not at stream sites ($p = 0.34$). Odonate species richness did not differ significantly between rural ponds ($\bar{X} = 19.6 \pm 3.0$ species; range: 15-23 species) and urban ponds ($\bar{X} = 15.4 \pm 1.5$ species; range: 13-17 species; $p = 0.11$) nor did rural and urban stream species richness differ significantly (rural: $\bar{X} = 10.0 \pm 3.1$ species; range: 6-13 species; urban: $\bar{X} = 7.0 \pm 2.1$ species; range: 4-10 species; $p = 0.10$; Figure 8). Anisopteran species richness did not differ significantly between rural and urban ponds (rural: $\bar{X} = 12.2 \pm 3.6$ species; range: 7-17 species; urban: $\bar{X} = 12.0 \pm 1.6$ species; range: 10-14 species; $p = 0.93$) or between rural and urban streams (rural: $\bar{X} = 2.6 \pm 1.3$ species; range: 1-4 species; urban: $\bar{X} = 1.2 \pm 1.6$ species; range: 0-4 species; $p = 0.12$; Figure 8). However, rural ponds held significantly higher zygopteran species richness values ($\bar{X} = 7.4 \pm 1.3$ species; range: 6-9 species) than urban ponds ($\bar{X} = 3.4 \pm 1.5$ species; range: 2-6 species; $p = 0.01$) but did not differ significantly between rural and urban streams (rural: $\bar{X} = 7.4 \pm 1.8$ species; range: 6-13 species; urban: $\bar{X} = 5.8 \pm 1.1$ species; range: 4-10 species; $p = 0.32$; Figure 8).

Multiple environmental variables were measured for each study site (Table 12). The percent urban development surrounding urban and rural ponds ranged from 37.0 to 93.4%, and 3.8 to 14.5% respectively. Most of that development consisted of open-space development (range for urban ponds: 1.0% to 21.6; rural ponds: 0.0 to 14.0%), with low-intensity urban development covering a relatively small proportion of the area around ponds (Urban: 2.3 to 16.5%; rural: 0.0 to 0.4%). Urban and rural streams were surrounded by 36.9 to 100.0% and 0.0 to 26.0% urban development, respectively. Streams resembled ponds in that the development around them was primarily open development (urban: 8.7 to 96.2%; rural: 0.0 to 15.4%), with some low-intensity development (urban: 3.3 to 60.9%; rural: 0.0 to 6.7%).

Ponds and streams differed significantly in odonate community composition (two-way PERMANOVA; $p \leq 0.05$; Table 13). Pond communities clustered together but were distinct from stream communities along the first axis of an NMDS (Figure 9a). Pond communities of odonates differed significantly in urban versus rural sites (one-way PERMANOVA; $p = 0.01$; Table 13 and Figure 9b). Stream communities also differed significantly in urban versus rural sites (one-way PERMANOVA; $p = 0.03$; Table 13 and Figure 9c).

The environmental factors associated with the change in community composition within each ecosystem type generally differed, although distance to the urban center may have affected both pond and stream communities. For ponds, mean algal cover and distance to urban center were significant factors driving community composition (CCA; p

≤ 0.04), and proportion of urban development approached significance (CCA; *p* = 0.07) (Table 14; Figure 10). These three factors together explained 45.4 % of the variation in odonate community composition at ponds. Axis 1 of the CCA (Figure 10) depicts approximately half (49.4%) of the variation explained by these three variables (eigenvalue: 0.3111), and a permutational ANOVA found this axis to be significant (*p* = 0.04). This axis appears to represent a rural-urban gradient as well as a gradient of algal coverage. Mean algal cover and proportion of urban development had positive correlations with Axis 1 (Table 14), and all of my urban sites clustered around the vector representing urban development (Figure 10a). Distance to urban center had a negative correlation with Axis 1 (Table 14). Axes 2 and 3 of the CCA were not significant (*p* ≥ 0.13).

For stream community assemblages, the forward-step CCA found that only mean water temperature was significantly associated with community differences (*p* = 0.02; Table 14; Figure 11). Distance to urban center approached significance (*p* = 0.06), but the proportion of urban development did not appear in the final model. Mean water temperature and distance to urban center explained 30.8% of the community diversity among the stream sites. Axis 1 depicts 63.6% of the variation in community assemblage explained by these two variables (eigenvalue: 0.4342) and was significant (*p* = 0.03); Axis 2 explained 36.2% of the variation explained by the two variables (eigenvalue: 0.2463), and approached significance (*p* = 0.06). Axes 1 and 2 reflect a water temperature gradient and an urban-rural gradient, with mean water temperature negatively correlated with Axis 1 and positively correlated with Axis 2, and distance to urban center positively correlated with both axes (Table 14).

Indicator species analyses found select odonate species were indicators of ponds and streams in general and more specifically of urban versus rural ponds. After correcting for multiple testing, there were ten indicator species of pond ecosystems, all of which were anisopterans (Table 15). In contrast, the four species that were stream indicators were all zygopterans (Table 15). I found four indicator species (three Zygoptera and one Anisoptera) for rural ponds and one indicator (Anisoptera) for urban ponds, but no indicator species for rural or urban streams.

DISCUSSION

The effects of urbanization on species richness and community composition differed for dragonflies and damselflies and between ponds and streams. Urbanization altered pond damselfly species richness. However, urbanization did not alter damselfly species richness between urban and rural streams, and dragonfly species richness did not differ between urban and rural sites for either ponds or streams. Other researchers have noted that urban areas have the potential to maintain high levels of odonate diversity (Craves and O'Brien 2013; Goertzen and Suhling 2013; 2015; Ball-Damerow *et al.* 2014), but those species found in urban areas were often habitat generalists with strong dispersal abilities (Hill and Wood 2014). Habitat generality likely explains why dragonfly species richness did not significantly differ between urban and rural areas, as dragonflies are typically habitat generalists and strong dispersers (Corbet 1999; Heiser and Schmitt 2009; Monteiro-Júnior *et al.* 2014).

My analyses of indicator species also emphasize differences in the responses of dragonflies and damselflies to urbanization, as well as differences across ponds and streams. I identified indicator species for urban and rural ponds, but none for urban or rural streams. Further, my indicator species analyses found no damselfly indicators of urban ponds, yet found three for rural ponds. These findings highlight the sensitivity of lentic damselflies to urbanization. As habitat specialists, damselflies experience local extinctions in degraded areas more often than generalist dragonflies (Korkeamäki and Suhonen 2002). This difference, combined with their poorer dispersal capabilities (Clark and Samways 1996; Corbet 1999; Sahlén 2006; Heiser and Schmitt 2009) and a lack of connectivity among urban ponds, resulted in lower species richness at ponds in urban areas. I did not find a significant difference in zygopteran species richness between urban and rural streams because of the inherent connectedness of streams in both urban and rural settings, which reduces the likelihood of local extinction and allows for quicker recolonization should it occur.

The reduction in native vegetation, rather than increased levels of impervious surface cover, most likely affects odonate communities at urban ponds. The amount of urban development surrounding my pond sites ranged from 37.0 to 93%, and at least half of the total urban development surrounding any urban pond was open development (51.1 to 92.3% of the total development) which consists of less than 20% impervious surface cover. The loss of the native vegetation surrounding bodies of water can influence odonate community assemblage, especially damselfly diversity and abundance (Remsburg and Turner 2009; Dutra and De Marco 2015), and likely alters predator-prey interactions for odonates and lowers environmental quality for some odonate species. Mowing can reduce the abundance of insects (Diehl *et al.* 2013), which would reduce prey availability for odonates (Baird and May 1997), and mowing can also increase predator pressure on odonates due to the loss of potential refuges from predators. Predation by birds became the leading cause for changes in herbivorous arthropod diversity in urban areas (Faeth *et al.* 2005), and while insectivorous avian species richness declines in urban areas, omnivorous species richness increases (Allen and O'Conner 2000; Kark *et al.* 2007). Due to the increase in omnivorous species, avian predation pressures on insects remain strong in urban areas. Additionally, tenerals (immature odonates that have recently emerged from an aquatic habitat) mature in the terrestrial vegetation surrounding lentic sites, and adults use this vegetation for roosting (Corbet 1999). In addition, Lee Foote and Rice Hornung (2005) found that a reduction in plant height from grazing negatively affected odonate diversity at wetlands and that the reduction in tall vegetation especially affected damselflies because the vegetation acted as a barrier to wind. Tall vegetation also creates shade, which damselflies need for thermoregulation (Monteiro-Júnior *et al.* 2013). The perception by odonates that grazed areas are degraded habitats exacerbates the reduction in odonate diversity (Lee Foote and Rice Hornung 2005). At my study sites, adult odonates possibly viewed the surrounding mowed areas and impervious surface cover as poor-quality habitat and continued to search for suitable habitat rather than reproduce at a poor-quality site.

In addition to urban development, mean algal cover also significantly affected pond communities. Mean algal coverage in a pond should correlate with impervious surface coverage, as increased impervious surface coverage leads to higher nutrient run-off into water bodies (Paul and Meyer 2001; Allan 2004), which results in higher amounts of algal coverage. This increase in nutrient levels can be especially detrimental to lentic systems where nutrients stay within the water body and are not carried downstream (Hassall 2014). In this study, some rural ponds also had high levels of algal coverage, possibly due to nearby agricultural fields or aeration of the rural ponds. Aeration prevents nutrients from settling to the bottom of the pond, thereby providing a constant source of nutrients for algal growth (Fast *et al.* 1973). Odonates use algal mats for perching and ovipositioning (Corbet 1999), and, for this reason, certain species prefer sites with high algal coverage, regardless of the amount of urbanization around the site. For example, *Tramea* sp. had the highest positive correlation with Axis 1 (Figure 10), which represented mean algal coverage and distance from urban center. This species occurred at both urban and rural sites (Table 11), suggesting this species prefers sites with high amounts of algal cover.

Distance to the urban center significantly predicted pond community composition and neared significance for predicting stream community composition. This factor broadly reflects the overall change in anthropogenic disturbance over distance without identifying specific elements of urbanization that might affect community compositions (Kinzig *et al.* 2005). Three of the species indicators for rural ponds, *Enallagma basidens, Arigomphus villosipes,* and *Argia fumipennis*, cluster near the distance variable in Figure 9, showing that the further a lentic site is from the urban center (*e.g.* the more rural the site), the more likely these species will be present. Interestingly, in my analysis of pond communities, the distance to the urban center did not correlate with the amount of urbanization around each site as obtained from the NLCD. Although frequently used to measure urbanization (*e.g.*, Kinzig *et al.* 2005; Trammell and Carreiro 2011; Pardee and Philpott 2014), these two variables measure different aspects of urban development, resulting in differing outcomes (Raciti *et al.* 2012).

For stream communities, only mean water temperature significantly predicted odonate community composition (Table 14; Figure 11). Urban streams tend to have high water temperature (Samways and Steytler 1996; Somers *et al.* 2013). However, in this study, an urban site recorded the coolest mean water temperature while a rural site held one of the warmest mean temperatures (Table 12). Samways and Steytler (1996) suggested that shade cover likely affected water temperature, which then significantly affected odonate community composition. They reasoned that cool lotic systems with much shade slowly warm up daily, and proper larval development possibly depends on warm water temperatures. Cool sites, urban or not, will host only those species whose larval stages tolerate cooler water temperatures. Water temperature affects egg development (Corbet 1999), and due to their tropical evolutionary history, odonates likely have high water temperature tolerances (Pritchard and Leggott 1987). Thus, the problem lies in cooler stream temperatures rather than warmer ones.

Inherent differences between pond and stream habitats likely affected how pond and stream communities respond to the same environmental factors. For example, mean algal cover did not significantly affect stream communities, and this lack of effect may be due to the fact that some of the problems unique to urban streams (*e.g.* increased flow disturbance) can counteract the increased nutrient loads that would encourage extensive algal growth (Walsh *et al.* 2005). Only one stream site, compared to eight pond sites, possessed over 5% algal cover. The difference in how many pond versus stream sites possessed high levels of algal cover suggests that water flow mitigates the effects of increased nutrient loads in the stream sites.

In sum, due to inherent differences in lentic and lotic ecosystems and between dragonflies and damselflies, different environmental factors contribute to the taxonomic makeup of adult odonate communities at urban habitats, something not necessarily detected by species richness measurements alone. Urbanization altered community composition but not necessarily species richness, a pattern also found in odonates inhabiting deforested and forested streams (Monteiro-Júnior *et al.* 2013). This study thus confirms community composition provides more insight than species richness into how odonate communities respond to urbanization (Monteiro-Júnior *et al.* 2013); measuring species richness alone does not detect the homogenization of odonate communities that occurs in urban areas (Ball-Damerow *et al.* 2014). Focusing on species richness rather than community composition can lead to misinformed conclusions and ultimately, incorrect management practices (Fleishman *et al.* 2006).

Conservationists need to consider more than just the urban development when conserving or restoring freshwater systems in urban areas, and implement different management practices in the two types of ecosystems in order to conserve the highest diversity of odonates possible. The quality of habitat patches often determines insect diversity, and given the high mobility of odonates compared to many taxa, small efforts to improve urban ponds and streams for odonates could result in large gains in these sites' effectiveness as contributors to conserving odonate diversity. This study shows that different measurements of urbanization do not similarly reflect odonate communities, highlighting the need for the use of multiple variables measuring urbanization in conservation studies.

My study focused on adult community assemblages, but lentic and lotic larval stages may show different responses to urbanization. Future studies should investigate the mechanisms driving the observed responses to urbanization to provide a basis for conservation efforts and assess whether adult and larval communities in urban areas respond similarly to urbanization.

Table 10. List of pond and stream sites with their respective abbreviations, classifications, and geographic coordinates. Urban sites contain over 30% urban development within 150 m of the site. Urban development is determined from the four development categories of the National Land Cover Database.

	Category	Site	Abbreviation	Coordinates	
Pond	Urban	McNeely Lake	ML	38°06'15"N	85°38'08"W
		Waverly Pond	WA	38°07'49"N	85°49'51"W
		Iroquois Pond	IQ	38°09'23"N	85°46'45"W
		Willow Pond	WI	38°14'38"N	85°42'10"W
		Chickasaw Pond	CH	38°14'26"N	85°49'54"W
	Rural	Tom Wallace Lake	TW	38°05'09"N	85°46'20"W
		Private Pond	PP	38°19'48"N	85°35'08"W
		Lower Douglas Lake	LD	37°49'20"N	85°52'36"W
		Jackson's Pond	JK	38°11'56"N	85°32'05"W
		Angler Lake	AN	38°13'52"N	85°27'59"W
Stream	Urban	Beargrass Creek	BG	38°16'05"N	85°43'22"W
		South Fork Beargrass Creek	SF	38°12'46"N	85°42'44"W
		Weicher Creek	WC	38°14'20"N	85°38'06"W
		Middle Fork Beargrass Creek	MF	38°14'00"N	85°40'56"W
		Clark Creek	CL	38°12'52"N	85°43'36"W
	Rural	Popelick Creek	PL	38°11'19"N	85°29'17"W
		Floyds Fork	FF	38°13'47"N	85°28'07"W
		Wolf Pen Branch Creek	WP	38°19'40"N	85°35'37"W
		South Fork Harrod's Creek	SH	38°20'23"N	85°31'41"W
		Otter Creek	OT	37°55'48"N	86°01'45"W

Table 11. List of species found at each site and abbreviations for each species name. See site name abbreviations in Table 10. *Tramea sp*. includes *T. onusta* and *T. carolina*.

Dragonflies	Ponds										Streams									
	ML	WA	IQ	WI	CH	TW	PP	LD	JK	AN	BG	SF	WC	MF	CL	PL	FF	WP	SH	OT
Aeshna umbrosa (A)						●														
Aeshna verticalis (B)						●														
Anax junius (C)	●		●	●	●		●		●											
Anax longipes (D)							●													
Arigomphus villosipes (E)			●			●	●	●	●	●										
Boyeria vinosa (F)																●				
Celithemis eponina (G)										●										
Celithemis fasciata (H)						●				●										
Didymops transversa (I)		●																		
Dromogomphus spinosus (J)						●														
Dromogomphus spoliatus (DE)								●												
Dythemis velox (K)										●							●			
Epiaeschna heros (L)																		●	●	
Epitheca cynosura (M)	●	●	●	●	●	●														
Epitheca princeps (N)	●	●	●	●		●		●	●	●	●						●			
Erythemis simplicicollis (O)	●	●	●	●	●	●	●		●	●			●				●			●
Gomphus graslinellus (P)						●		●												
Hagenius brevistylus (AA)								●												
Ladona deplanata (Q)	●	●	●	●		●	●												●	
Libelulla incesta (R)	●	●	●	●		●	●		●	●									●	
Libelulla luctuosa (S)	●	●	●	●	●	●	●	●	●	●		●					●			
Libelulla pulchella (T)			●	●			●													
Macromia illinoiensis (U)											●									
Pachydiplax longipennis (V)	●	●	●	●	●	●	●		●	●	●									

Pantala flavescens (W)		●		●	●	●														
Perithemis tenera (X)	●	●	●	●	●	●	●		●	●	●									
Plathemis lydia (Y)	●	●	●	●	●	●	●	●	●	●						●			●	●
Sympetrum obtrusum (Z)									●											
Tramea sp. (BC)				●	●		●		●											
Tramea lacerata (EF)	●	●	●	●	●	●	●		●	●										

Damselflies	Ponds										Streams									
	ML	WA	IQ	WI	CH	TW	PP	LD	JK	AN	BG	SF	WC	MF	CL	PL	FF	WP	SH	OT
Argia apicalis (a)	●				●	●		●			●			●		●	●	●	●	●
Argia fumipennis (b)		●				●	●	●	●	●		●	●	●	●	●	●		●	
Argia moesta (c)												●	●	●		●	●	●	●	●
Argia sedula (d)								●		●	●			●		●	●			
Argia tibialis (e)											●	●		●		●	●			●
Argia translata (f)																		●	●	
Calopteryx maculata (g)								●					●		●	●	●	●	●	●
Enallagma aspersum (h)						●			●										●	
Enallagma basidens (i)						●	●	●	●	●						●				
Enallagma civile (j)	●		●												●					
Enallagma exsulans (k)											●	●	●	●			●	●		
Enallagma signatum (l)	●						●	●		●									●	
Enallagma traviatum (m)						●	●		●	●		●								
Hetaerina americana (n)										●						●	●			●
Ischnura hastata (o)	●							●												
Ischnura posita (p)	●	●	●	●	●	●	●		●	●	●	●	●	●	●		●		●	●
Ischnura verticalis (q)	●	●	●	●	●		●	●	●	●	●		●						●	
Lestes congeners (r)										●										
Lestes rectangularis (s)									●											
Lestes vigilax (t)									●											

Table 12. List of environmental variables and the mean values of each variable used in my analyses. Dissolved oxygen was measured in microsiemens. Pond size and stream width were measured in meters. Development percentages describe the amount of urban development within 150 m of each site. Width of streams (in meters) was not used in any analyses.

		Site	Distance (km)	Size	Development (%)	Water Temperature (°C)	Dissolved Oxygen (μS)	Emergent Vegetation (%)	Alga (%)	Miscellaneous Debris (%)
Ponds	*Urban*	ML	21.1	18.7	37.0	28.7 (0.3)	205.5 (56.1)	44.6 (14.9)	7.3 (0.4)	11.8 (3.9)
		WA	15.4	1.7	42.3	29.9 (2.7)	138.05 (55.6)	12.2 (3.3)	6.8 (11.7)	5.9 (5.2)
		IQ	11.4	0.4	65.3	26.5 (4.0)	88.9 (12.4)	19.7 (6.9)	5.2 (5.3)	8.1 (6.8)
		WI	5.8	1.9	73.0	28.9 (1.3)	116.6 (71.0)	47.6 (11.5)	5.9 (8.5)	8.7 (2.8)
		CH	6.4	0.3	93.4	27.2 (6.9)	26.95 (1.1)	35.0 (19.6)	27.7 (7.7)	17.5 (10.5)
	Mean		12.0 (6.4)	4.6 (7.9)	62.2 (23.1)	28.2 (1.34)	115.19 (65.5)	31.8 (15.4)	10.6 (9.6)	10.4 (4.5)
	Rural	TW	19.3	2.2	3.8	28.3 (1.9)	119.7 (19.8)	14.4 (8.2)	3.4 (4.1)	26.7 (23.3)
		PP	17.7	0.8	4.2	26.7 (4.9)	137.6 (115.6)	44.2 (19.9)	17.5 (20.1)	17.0 (5.7)
		LD	49.7	28.1	6.9	29.6 (1.7)	112.3 (2.8)	8.5 (4.3)	0.6 (0.8)	6.1 (4.6)
		JK	22.4	0.4	9.7	26.0 (1.5)	63.2 (49.0)	39.5 (29.5)	18.3 (16.4)	6.3 (3.1)
		AN	26.4	1.2	14.5	29.0 (2.6)	104.1 (9.8)	33.4 (17.7)	11.2 (14.1)	9.0 (6.1)
	Mean		27.1 (13.0)	6.5 (12.1)	7.8 (4.4)	28.0 (1.5)	107.4 (27.6)	28.0 (15.7)	10.2 (8.0)	13.0 (8.8)
Stream	*Urban*	BG	3.9	35.9	36.9	27.5 (5.7)	115.0 (14.6)	12.3 (20.3)	0.9 (1.6)	5.1 (3.4)
		SF	6.9	3.8	82.6	21.1 (1.6)	100.2 (15.8)	26.6 (6.4)	3.1 (1.8)	9.9 (1.9)
		WC	11.6	10.4	100.0	22.7 (1.4)	115.4 (20.2)	4.8 (6.9)	0.2 (0.1)	12.5 (7.5)
		MF	7.6	13.5	100.0	23.3 (2.2)	128.3 (25.0)	4.8 (3.6)	9.4 (8.9)	4.5 (3.9)
		CL	6.1	1.6	100.0	18.2 (1.1)	93.1 (8.3)	3.3 (3.2)	0.5 (0.9)	9.9 (2.9)
	Mean		7.2 (2.8)	13.0 (13.6)	83.0 (26.8)	22.6 (3.4)	110.4 (13.9)	10.4 (9.7)	2.8 (3.8)	8.4 (3.5)
	Rural	PL	25.5	7.4	26.0	23.7 (1.2)	118.2 (15.3)	0.1 (0.2)	2.8 (3.3)	7.3 (1.6)
		FF	26.2	21.7	17.7	26.3 (1.2)	108.7 (35.8)	14.4 (5.6)	4.6 (6.4)	4.0 (4.2)
		WP	17.2	13.9	2.9	20.3 (3.0)	92.8 (6.7)	2.0 (2.9)	0.1 (0.2)	8.5 (4.4)
		SH	22.7	6.12	0.0	21.1 (1.2)	103.6 (12.7)	3.1 (3.5)	3.4 (5.7)	5.3 (6.7)
		OT	42.3	20.7	0.0	22.5 (3.0)	141.4 (0.2)	35.8 (16.1)	0.6 (1.0)	5.2 (3.7)
	Mean		26.8 (9.3)	14.0 (7.2)	9.3 (11.9)	22.8 (2.4)	112.9 (18.4)	11.1 (14.9)	2.3 (1.9)	6.1 (1.8)

Table 13. A two-way PERMANOVA testing the effects of ecosystem type and development category on odonate community composition showed that ponds and streams differed significantly in odonate community composition (a). One-way PERMANOVAs showed that both pond (b) and stream (c) communities of odonates differed significantly in urban versus rural sites. Ecosystem = pond or stream; Development = urban or rural.

			Df	SS	F Model	R^2	P-value
a)	*Ecosystem*	Ecosystem	1	1.808	10.058	0.325	0.000
		Development	1	0.490	2.726	0.088	0.020
		Ecosystem*Development	1	0.384	2.138	0.069	0.050
		Residuals	16	2.875		1.000	
b)	*Pond*	Development	1	0.442	3.659	0.314	0.010
		Residuals	8	0.967		1.000	
c)	*Stream*	Development	1	0.432	1.810	0.185	0.030
		Residuals	8	1.908		1.000	

Table 14. Forward-selection canonical correspondence analysis parameters for pond and stream systems and intraset correlations showing correlation of environmental factors with axes. For pond communities, mean algal cover and distance to urban center were significant factors driving community composition, and proportion of urban development approached significance (CCA; *p* = 0.07). For stream communities, only mean water temperature significantly predicted odonate community composition

	Environmental Factor	F Model	P value	AXIS 1	AXIS 2
Pond	Mean algal cover	1.91	0.04	0.84	0.39
	Proportion of urban development	1.42	0.07	0.53	-0.82
	Distance to urban center	1.95	0.01	-0.86	0.37
Stream	Mean water temperature	1.57	0.02	-0.79	0.61
	Distance to urban center	1.44	0.06	0.70	0.72

Table 15. Indicator species for ponds versus streams and rural versus urban ponds. No species represented urban or rural stream systems. Indicator values represent the strength of a species being an indicator species.

	Category	Species	Indicator Value	P-value
Ecosystems	Pond	*Tramea lacerata*	90.0	0.000
		Libelulla luctuosa	83.3	0.001
		Pachydiplax longipennis	81.0	0.001
		Perithemis tenera	81.0	0.001
		Plathemis lydia	76.9	0.003
		Libelulla incesta	71.1	0.007
		Epitheca cynosura	60.0	0.010
		Anax junius	60.0	0.012
		Erythemis simplicicollis	67.5	0.020
		Epitheca princeps	64.0	0.023
	Stream	*Argia moesta*	80.0	0.001
		Argia tibialis	60.0	0.011
		Enallagma exsulans	60.0	0.011
		Calopteryx maculata	61.3	0.021
Ponds	Rural	*Enallagma basidens*	100.0	0.007
		Arigomphus villosipes	83.3	0.047
		Argia fumipennis	83.3	0.048
		Enallagma traviatum	80.0	0.048
	Urban	*Epitheca cynosura*	83.3	0.047

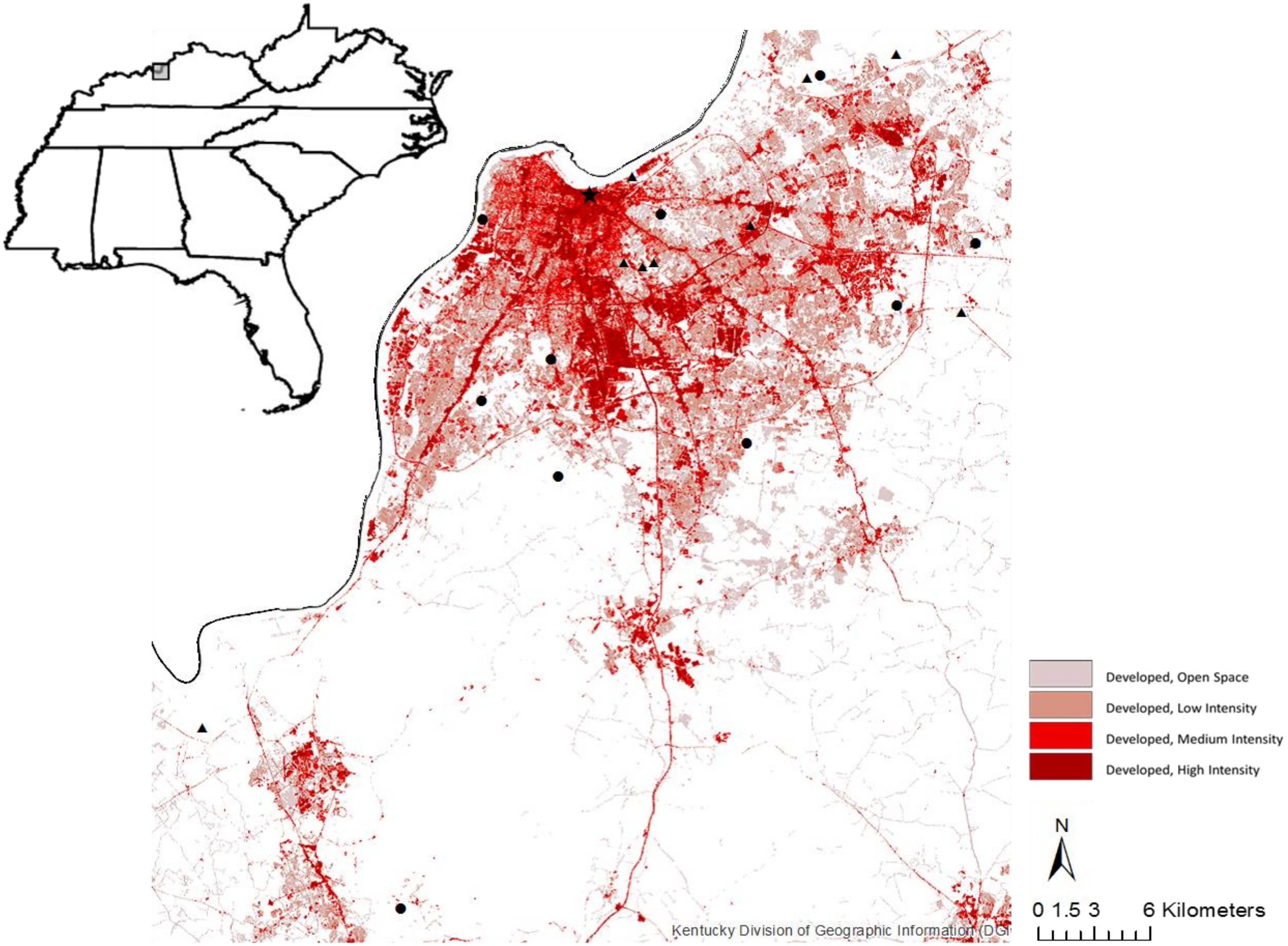


Figure 7. Map of sites. Filled circles indicate lentic sites, filled triangles indicate lotic sites, and the star locates downtown Louisville. Development categories are based on the urban development classifications of the National Land Cover Database.

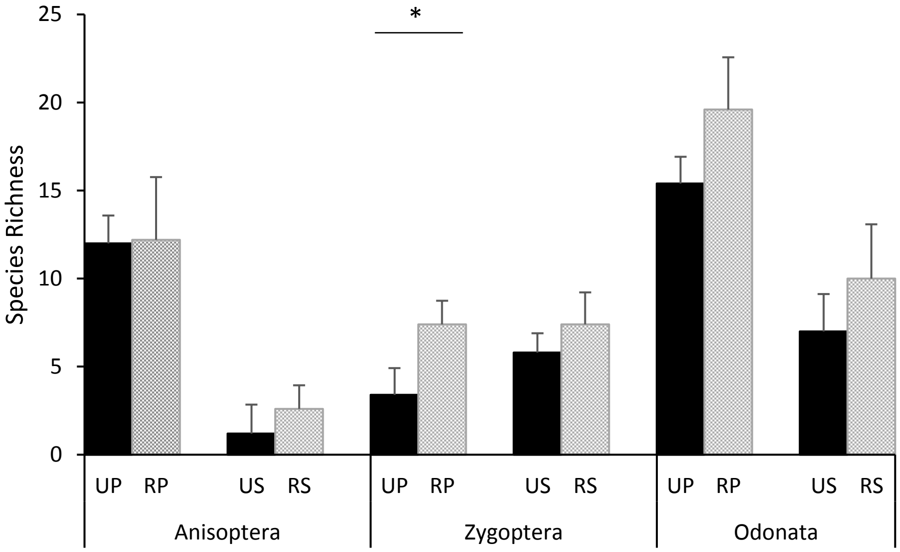
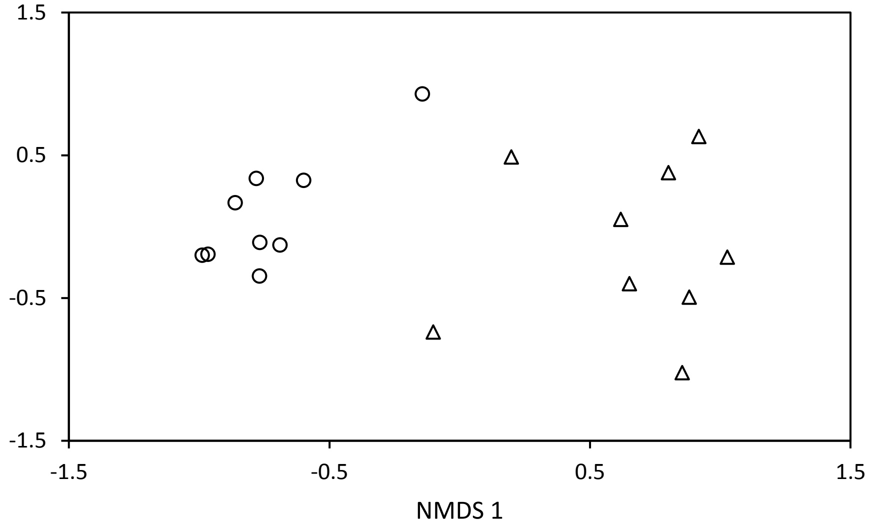
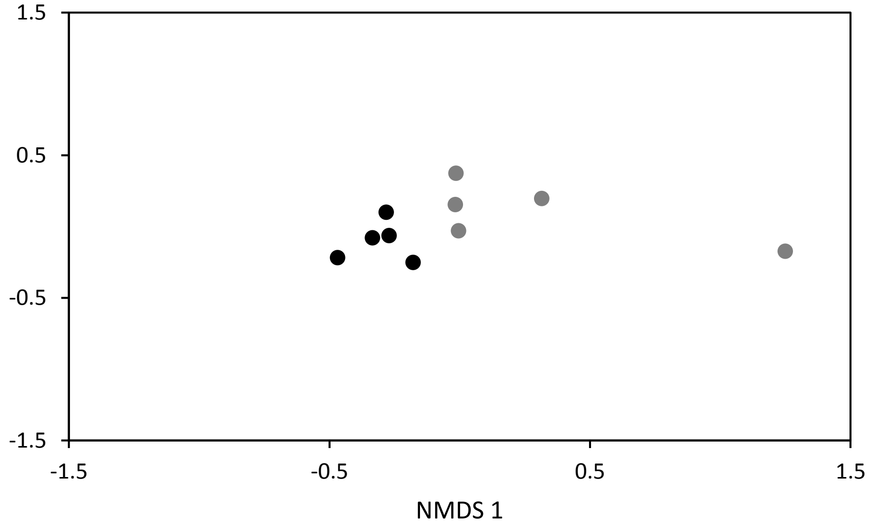


Figure 8. Mean species richness (standard deviation) of anisopteran, zygopteran, and all odonate species found in urban ponds (UP), rural ponds (RP), urban streams (US), and rural streams (RS). Each category includes five sites. Only zygopteran pond communities differed significantly (*) between urban and rural sites.

9a


1.5
0.5
-0.5
-1.5
NMDS 1
-1.5
-0.5
0.5
1.5
NMDS 1

9b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0.5
-0.5
-1.5
NMDS 2
-1.5
-0.5
0.5
1.5
NMDS 1

9c

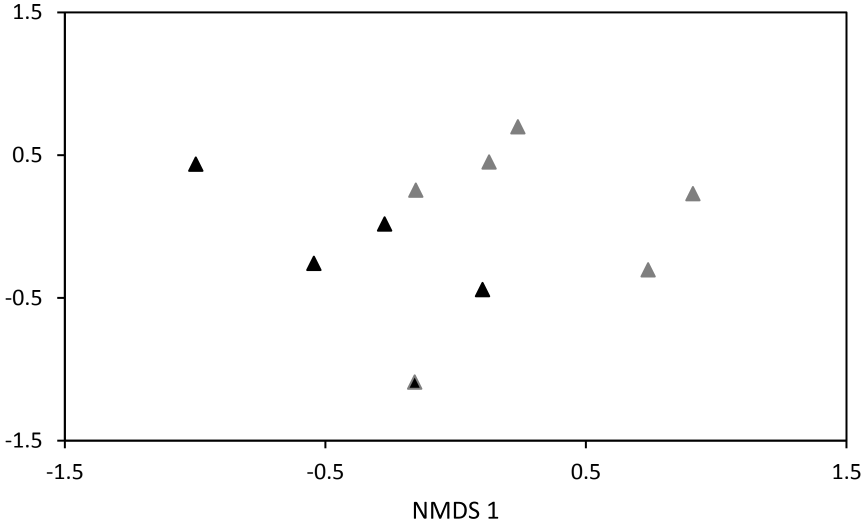

Figure 9. NMDS analysis showed that pond communities clustered together but were distinct from stream communities (a; stress= 0.13). Urban versus rural communities clustered separately at both ponds (b; stress=0.07) and streams (c; stress=0.09). Symbols: open circles, ponds; open triangles, streams; solid grey circles, rural ponds; solid black circles, urban ponds; solid grey triangles, rural streams; solid black triangles, urban streams.

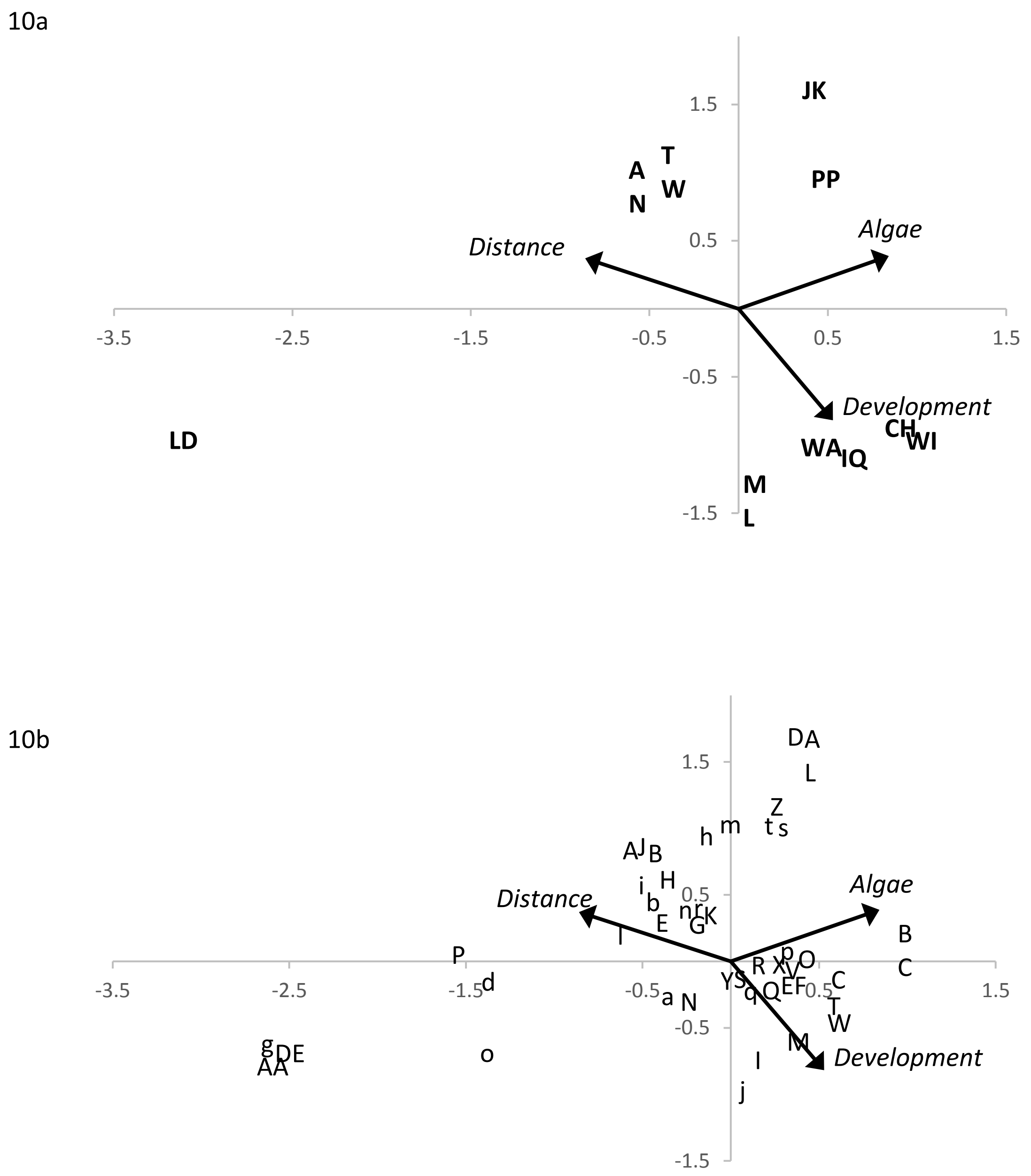

Figure 10. Plots of canonical correspondence analysis for pond communities showing sites (a) and species (b). Axis 1 represents a rural-urban gradient as well as a gradient of algal coverage and was significant. See Table 10 for site name abbreviations, which are in bold. See Table 11 for species name abbreviations. Environmental factor abbreviations: Distance= distance to urban center; Algae= mean algal cover; Development= proportion of urban development.

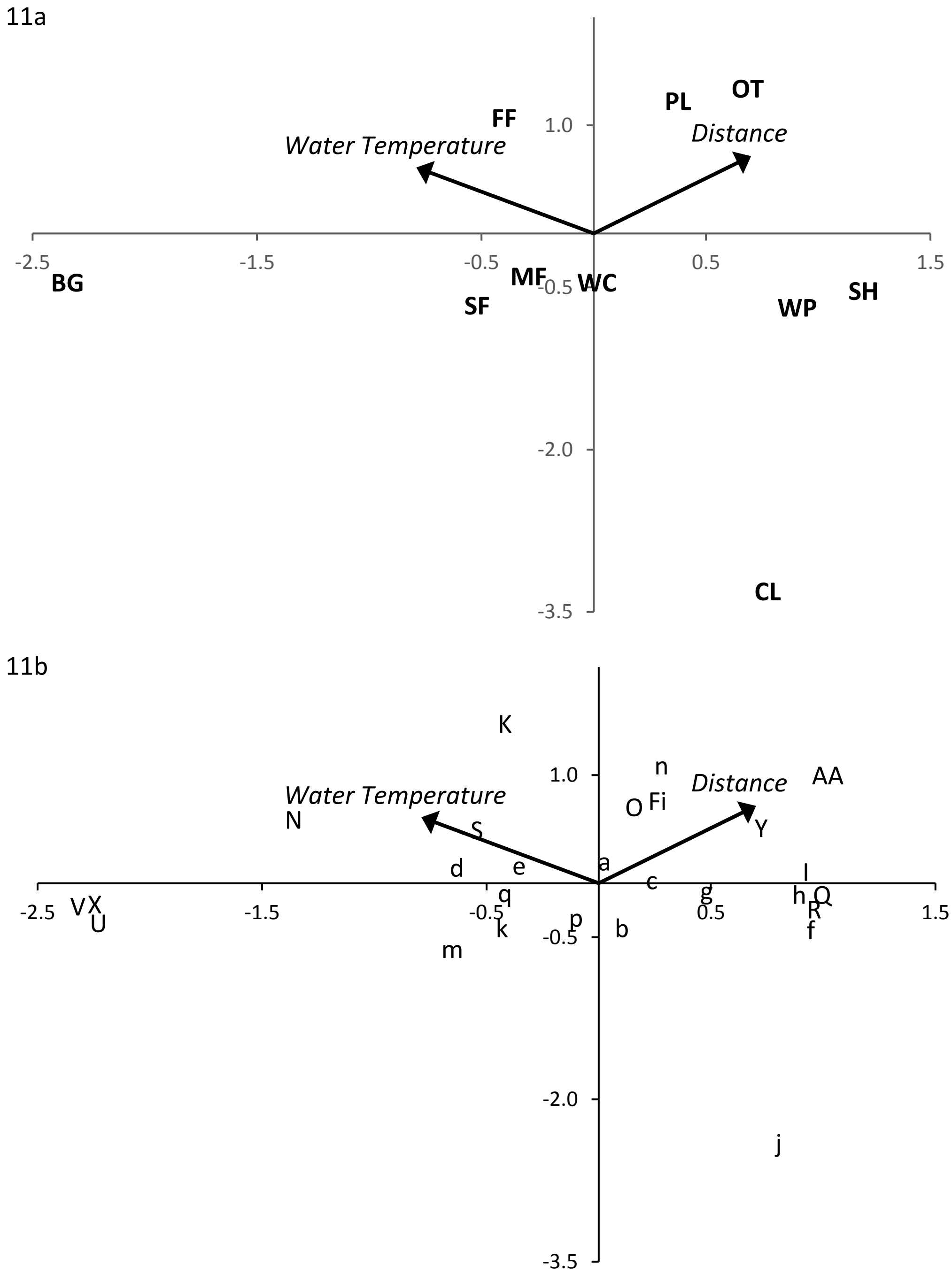

Figure 11. Plots of canonical correspondence analysis for stream communities showing sites (a) and species (b). The CCA found that only mean water temperature was significantly associated with community differences ($p = 0.02$), with distance to urban center approaching significance ($p = 0.06$). See Table 10 for site name abbreviations,

which are in bold, and Table 11 for species name abbreviations. Environmental vectors: Distance = distance to urban center; Temperature = mean water temperature.

CHAPTER IV

DRAGONFLIES AND DAMSELFLIES HAVE DIFFERENT ECOLOGICAL CORRELATES WITH AN EXTINCTION RISK ASSESSMENT

SUMMARY

Resilience against extinction is not uniform among taxa. Researchers need to be able to prioritize conservation concerns, and one effective approach is to identify species traits that correlate with extinction risk assessments. I tested for a correlation for three ecological traits (geographic range size, length of flight period, and habitat breadth) with an extinction risk assessment for North American odonates. Different traits showed different degrees of correlation with the assessment for anisopterans (dragonflies) and zygopterans (damselflies). Geographic range size and length of flight period correlated with assessments in both taxa, but dragonfly conservation rank also correlated with habitat breadth, and with the interactions between length of flight period and both geographic range size and habitat breadth. This research shows that even closely related taxa differ in their resilience to extinction, and that extinction correlates reflect interspecific variation in dispersal capabilities and voltinism among odonate taxa.

INTRODUCTION

Prioritizing conservation concern is a key aspect of conservation biology (Jeppsson and Forslund 2014) because the world is currently losing species at an increasing rate (Murray and Hose 2005). One important task is to develop cost-effective means of predicting which species are most at risk so that conservation efforts can be directed appropriately (O'Grady *et al.* 2004; Reynolds 2003; Murray and Hose 2005). Biota do not show uniform extinction risk (McKinney 1997; Fisher and Owens 2004; Cardillo *et al.* 2008) because variation in life-history traits within and among species cause differential responses of species to changes in the environment (Reynolds 2003). Differences in life-history traits can be correlated with extinction risk (McKinney 1997; Reynolds 2003; Hutchings *et al.* 2012; Jeppsson and Forslund 2014) and need to be identified across taxa and used to assess which species are most at risk (Foufopoulos and Ives 1998). Conservation priorities can then be established (Reynolds 2003; Jeppsson and Forslund 2014) and implemented (Nylin and Bergström 2009).

Our understanding of which invertebrate life-history traits and ecological factors correlate with extinction risk is currently poor (Reynolds *et al.* 2003) and with very high extinction rates among invertebrates (McKinney 1999), more efforts should focus on this group. In vertebrate species, which have been far more studied, factors such as geographic range size (Purvis *et al.* 2000; Jones *et al.* 2003; Murray and Hose 2005; Cardillo *et al.* 2005), body size (Bennett and Owens 1997; Murray and Hose 2005; García *et al.* 2008; Hutchings *et al.* 2012), and age at maturity (Bennett and Owens 1997; Webb *et al.* 2002; González-Suárez and Revilla 2013) correlate with extinction risk in a variety of both terrestrial and aquatic taxa. However, some invertebrate species do not express these traits in a measurable form. For example, certain life-history patterns such as long gestation (Purvis *et al.* 2000) and delayed maturity (Olden *et al.* 2008; Anderson *et al.* 2011) correlate with extinction risk in vertebrates, but these patterns are often not measurable in invertebrates. Further, extinction patterns in vertebrates do not necessarily mirror those in invertebrates (Clausnitzer *et al.* 2009). Thus, unique ecological correlates in invertebrates are needed to best prioritize conservation effects.

I examined whether three species traits–geographic range, mean length of flight season, and habitat breadth correlate with extinction risk in odonates with ranges including the contiguous states of the USA or Alaska. I examined species inhabiting the United States because the basic ecology of these species is well documented, which is not the case for many species found solely in Mexico. Geographic range is likely to be a strong correlate of extinction risk across all biota (Gaston 1994; Gaston and Fuller 2008; Hanna and Cardillo 2013), and research on vertebrates supports this idea (*e.g.* Purvis *et al.* 2000; Jones *et al.* 2003; Murray and Hose 2005; Cardillo *et al.* 2005; Hanna and Cardillo 2013). Species with large ranges should have a reduced likelihood that a single environmental event will eliminate all individuals, and if local extinction occurs, then the species will persist in and potentially recolonize other areas (Brook *et al.* 2008). However, research predominately focuses on vertebrates and is less known for invertebrates (Korkeamäki and Suhonen 2002; Nylin and Bergström 2009; McCauley *et al.* 2013). With the world currently undergoing its sixth mass extinction (Barnosky *et al.* 2011), we need to understand whether geographic range currently affects extinction risk in other invertebrates, such as freshwater species.

The length of the flight period may be correlated with extinction risk in odonates as well as other flying insects for several reasons. First, length of the flight season likely correlates with dispersal ability in invertebrates; species with stronger dispersal abilities should be better at finding suitable habitat than those with weak dispersal abilities (Sullivan *et al.* 2000). Second, the length of flight season possibly reflects "fast-slow" life history patterns such as length of adult stage and voltinism (number of generations produced in a year). Species with longer flight periods should have longer adult stages (Mattila *et al.* 2008; Jeppsson and Forslund 2014), and as is the case in vertebrates (Webb *et al.* 2002; Morrison and Hero 2003) the length of the adult life stage should affect extinction risk in invertebrates because it is positively correlated with the number of reproduction events (Morrison and Hero 2003). Finally, length of flight period can also affect voltinism, with a longer flight season allowing more than one generation to reproduce and resulting in greater annual fecundity for multivoltine species. Multivoltinism is correlated with lower risk of extinction in longhorn beetles (Jeppsson and Forslund 2014). The length of the flight season correlates with extinction risk in several insect taxa with winged adults, including beetles (Jeppsson and Forslund 2014), hoverflies (Sullivan *et al.* 2000), and butterflies (Kotiaho *et al.* 2005) and moths (Mattila *et al.* 2008). Because odonates possess relatively strong dispersal capabilities and show interspecific variation in voltinism, length of flight season likely correlates with odonate extinction risk.

The number of habitats a species occupies has also been found to correlate with extinction risk (Fisher and Owens 2004). Species that occupy only a low number of habitat types are at a higher risk of extinction because the degradation or loss of any of these habitats can have a great impact on species persistence (Rabinowitz 1981). Conversely, a species occupying a large variety of habitats can still persist if one of those habitat types is destroyed. As with geographic range, vertebrates that occupy fewer habitat types are more at risk (*e.g.* Hutchings *et al.* 2005; Foufopoulos and Ives 1999; García *et al.* 2008). The number of habitats occupied is a measure of habitat specialization (Fisher and Owns 2004) and ultimately niche breadth (McKinney 1997), with the degree of habitat specialization increasing as the number of habitats occupied decreases. One would thus expect that the negative relationship between number of habitats occupied and extinction risk would also be seen across invertebrates. However, previous studies have not shown a clear pattern for invertebrate species. Extinction risk was not significantly affected by the number of habitats a species occupied in hoverflies (Sullivan *et al.* 2000) or butterflies (Nylin and Bergström 2009), but was affected by habitat specialization in beetles (Davies *et al.* 2004) and dragonflies (Korkeamäki and Suhonen 2002). One reason for this ambiguity may be due to the level at which habitat specialization is measured. In both studies in which habitat specialization was a significant predictor of extinction risk, habitat specialization was a qualitative measurement (*e.g.* habitat generalist versus specialist) rather a quantitative one, whereas in the studies in which specialization was not significant, the factor was measured as the number of habitats occupied.

I chose the order Odonata as my focal group because they are generally well-studied, and the group is relatively speciose and diverse. Further, odonates are considered bioindicators of ecosystem health (Corbet 1999) and are well studied in North America. These final two criteria make them excellent candidates for studying extinction threats (McKinney 1999). Two previous studies examined the relationship between odonate life-history traits and extinction risks, but at very different geographic scales. Clausnitzer *et al.* (2009) performed a global assessment of odonates and identified which geographic areas and broad habitat types (*e.g.* lentic or lotic, forest or shrubland) correlate with at-risk odonate species, and Korkeamäki and Suhonen (2002) found that geographic distribution and habitat specialization affect the local extinction of 20 odonate species in Finland. However, Nylin and Bergström (2009) found that extinction patterns among butterflies in Sweden differed from the patterns found among butterflies across all of Europe, cautioning that it may be difficult to generalize extinction patterns of a taxon at different geographical scales.

METHODS

Data Collection

Using a variety of sources ranging from books (Westfall and May 1996; Needham *et al.* 2000; Manolis 2003; Abbott 2005; Paulson 2009; Paulson and Dunkle 2009; Paulson 2011) to online databases (NatureServe Explorer 2009) I collected information regarding the extinction risk assessment, habitat specificity, geographic distribution, and flight seasons of all odonate species inhabiting the United States, with the exception of species endemic to Hawaii. I chose to obtain information from multiple sources to gain the most comprehensive and accurate list possible. Extinction risk in this study is ranked according to the global conservation status ranking system developed by NatureServe Explorer (2009). I used the global conservation status rather than the national conservation status because some of my species ranges included Canada and Mexico and some species with small ranges in the United States had large ranges in Mexico. Species are assigned by NatureServe to one of five global conservation statuses using a weighted, standardized calculator that takes into consideration rarity, trends in population size, and threats to species persistence (Faber-Langendoen *et al.* 2009). Conservation statuses are ranked from G1 to G5, with G1species considered critically imperiled and G5 species considered secure. Species given a status of two sequential ranks (*e.g.* G3G4) by NatureServe Explorer (2009) were adjusted to the lower rank for my analyses. Species given two non-sequential ranks were assigned the intermediate rank; for example, a species ranked as G1G3 would be given a G2 ranking. I excluded 26 species from this study because of missing or questionable information about them. Four species for which insufficient data were available were not given a conservation status by NatureServe (2009), and seventeen species were listed as inhabiting the United States in other sources but not by NatureServe (2009). The remaining five species I eliminated were listed as inhabiting the United States by NatureServe (2009) but not by any other source (and no information on habitat occupancy was provided by NatureServe or any other source).

As a measure of geographic distribution, I determined the number of American states, Canadian provinces (hereafter states), and Mexican states each species inhabits. I chose not to include Hawaii or island countries because of the inherently limited geographic distribution that may occur as a result of a species being endemic to an isolated island. I obtained geographic distributions within the United States and Canada via NatureServe Explorer (2009), and Mexican distributions were inferred from Paulson (2009, 2011). Distributions on NatureServe were cross-checked with Paulson (2009, 2011). Due to the wide range of size among the states included in my study, I combined certain small states and analyzed them as a single state. In Canada, I combined Prince Edward Island and Nova Scotia; in the United States, I combined Connecticut, Rhode Island, Massachusetts, Vermont, and New Hampshire into one state and Washington DC, Delaware, Maryland, and New Jersey into another. In Mexico, states were combined as follows: Mexico City, Mexico, and Hidalgo; Puebla, Tlaxcala, and Morelos; Guanajuato and Queretaro; Zacatecas and Aguascalientes; Colima and Jalisco. Thus, the maximum number of states and provinces across which a species could range is 81. NatureServe listed 3 species as having disconnected ranges, with sightings in Rhode Island but all other sightings more than 500 km distant. The Rhode Island occurrences for these species were disregarded as they were not also listed in Paulson (2009, 2011).

I determined the average flight season length (measured in months) per state of each species using information from Paulson (2009, 2011). These sources provided the most comprehensive information regarding flight season for each species of all the sources from which I obtained habitat occupancy information. However, these two field guides present flight seasons within the United States and Canada only. I did not factor flight seasons in Mexico into my analyses because this information was only rarely and sporadically given in any source and not included in Paulson (2009, 2011) at all. To remove the effect of latitudinal range on flight season, I calculated each species' average flight season length per state/province and used these values in my analyses.

To assess the habitat breadth of each species, I collected information on the types of aquatic systems each species inhabits (*e.g.* ponds, streams, rivers, lakes; Table 16) and the speed of the water body (still, slow, intermediate, fast). Lotic sites described as having “some current” were classified as having an intermediate flowing speed. I did not consider substrate type in my analyses because this information was not consistently provided for all species. To quantify the number of habitats occupied by each species, every descriptor was given a single point, and all points were summed together. I used this method to reflect the idea that a species can occupy a greater diversity of habitats both by occupying a larger number of habitat types, and in the case of lentic species, flow speeds.

Statistical Analyses

I performed statistical analyses separately for zygopterans (damselflies) and anisopterans (dragonflies). Due to a low number of G1 and G2 species, I combined G1 (if present), G2, and G3 species into a single group (“At-risk” group), resulting in three response categories: “At-risk”, G4, and G5. I performed an ordinal logistic regression because my response variable (global conservation status) was an ordered, discrete variable and my explanatory variables were a mixture of count data (habitat specificity and geographic distribution) and continuous data (average flight season per month). I first tested for heteroscedasticity among my variables using the gvlma function in the R package gvlma v. 1.0.02 (Pena and Slate 2006). I detected significant levels of heteroscedasticity between geographic distribution and both habitat occupancy and average flight season for anisopterans. To correct this, I used the MASS package v. 7.3-45 (Venables and Ripley 2002) to identify lambda from a Box-Cox transformation. Lambda values were similar to correct heteroscedasticity between geographic distribution and both habitat occupancy and average flight season (0.414 and 0.444, respectively), so I transformed geographic range values as $x^{0.43}$ to remove significant heteroscedasticity. All zygopteran predictor variables were heteroscedastic. I tested for collinearity among the variables and the interactions of the variables using the package car (v.2.0-20, Fox and Weisberg 2011). Because all variables and their interactions were highly collinear for both anisopterans and zygopterans, I performed a standardized transformation on each variable using the equation: $(\frac{1}{\sqrt{n-1}})\left(\frac{x-\overline{x}}{SD}\right)$. Because a one unit change in the original data is different than a one unit change in the transformed data (which is used in the interpretation of odds ratios), I then scaled the data using the R package plyr v. 1.8.3 (Wickham 2011) to ensure that the calculated values (*e.g.,* odds ratios) were at a relevant scale.

I used forward-selection ordinal logistic regressions (Allison 1999) using the polr function in the MASS package to determine which of the three explanatory variables and their interactions were associated with global conservation status within each suborder. I tested for overdispersion by dividing the residual deviance of the chosen model by the residual degrees of freedom and by a chi-square goodness-of-fit test. All statistical analyses were performed using the statistical software R v 3.1.1 (R Core Development Team 2015). All means were reported with standard deviation.

RESULTS

A total of 435 species (306 anisopteran and 129 zygopteran) from 12 families (seven anisopteran and five zygopteran) were documented and examined in this study. I found six G1 species (all anisopteran), 15 G2 species (11 anisopteran and four zygopteran), 34 G3 species (27 anisopteran and seven zygopteran), 104 G4 (73 anisopteran and 31 zygopteran), and 276 G5 species (189 anisopteran and 87 zygopteran). Table 17 lists the number of anisopterans and zygopterans found in each conservation rank. In anisopterans, geographic range size ranged from 1 to 76 states (19.44±13.04), average flight period ranged from 0.6 to 12 months (4.30±1.85), and habitat occupancy values ranged from 1 to 13 habitats (5.04±2.24). Zygopteran geographic range size ranged from 1 to 75 states (23.23±15.92), average flight season per state ranged from 1 to 12 months (5.87±2.26), and habitat breadth ranged from 1 to 12 habitats (5.45±2.35). Table 18 lists mean values for habitat specificity, geographic distribution, and average flight season for each conservation status within anisopterans and zygopterans.

Conservation statuses of anisopterans and zygopterans were differently affected by life history traits. For anisopterans, the best-fitting ordinal logistic regression model included geographic range, length of flight period, habitat breadth, geographic range x length of flight period, and habitat breadth x length of flight period (AIC: 346.16, residual deviance: 332.16, residual degrees of freedom: 299). All variables and interactions included in this model were significant (Table 19). Overdispersion was only moderate (1.15) and not significant (X^2 test, $p = 0.09$).

The odds ratios describe how a species' conservation status changes as a one-unit change in a predictor variable occurs (Table 20). The parameter value for the interaction between geographic range and length of flight period was negative, indicating that as the geographic range increased, the effect of length of flight season on extinction risk decreased. Because the odds ratio for the geographic range x average length of flight period interaction was 0.48, which was less than 1, the likelihood of a species transitioning from "At-risk" to G4 or G5 with a one unit increase in this interaction term decreased.

For zygopterans, the best-fitting model included geographic distribution and average length of the flight season (AIC: 135.90, residual deviance: 127.90, residual degrees of freedom: 125; Table 18). Over-dispersion was moderate and not significant (0.94, X^2 test, p=0.41). The odds ratios of both geographic distribution and length of flight season were both above a value of 1, indicating that a one unit change in either category increased the likelihood that a species moves from the "At-risk" rank to a G4 or G5 rank (Table 19). Increasing the geographic distribution of a species by one state increased the odds that the species was a G4 or G5 rank by 21.32 fold (Figure 1). Increasing the length of a species' flight period by one month increased the odds that the species was a G4 or G5 by 1.64 (Figure 2).

DISCUSSION

Geographic range and length of flight period affected assessed risk of extinction in both damselflies and dragonflies. In dragonflies, interactions between length of flight period with geographic range and with number of habitats occupied also affected extinction risk. These results show that ecological correlates can vary even among closely related taxa. More complex correlations with extinction risk exist in dragonflies than in damselflies. This research not only contributes to the growing support for the use of ecological correlates in identifying species most at risk of extinction but identifies a unique (length of flight season) ecological correlate with odonate extinction risk at the continental scale.

Geographic range size is driven by dispersal capability and is positively correlated with various measurements of wing size in damselflies (Rundle *et al.* 2007; Swaegers *et al.* 2014) and with odonate dispersal behavior (McCauley *et al.* 2014). Odonates possess strong dispersal abilities relative to other animals (Corbet 1999; Clausnitzer *et al.* 2009), but McCauley *et al.* (2013) found that of 15 North American dragonfly species, those with smaller ranges were less likely to recolonize an area after local extinction occurred. In general, species characterized as having strong dispersal capacities will be able to sample several habitats before selecting the one of highest quality (Pulliam and Danielson 1991). Thus, if a large geographic range indicates that a species avoids regions of unsuitable habitat and recolonizes areas where local extinction has occurred, then clearly the risk of extinction should decrease.

Length of flight period may also be positively correlated with dispersal capability (Grewe *et al.* 2012), although evidence is more equivocal. A short flight season may reflect low dispersal abilities in hoverflies (Sullivan *et al.* 2000), and butterflies with low dispersal abilities and shorter flight periods had higher risk of extinction (Kotiaho *et al.* 2005). However, Powney *et al.* (2015) found that the likelihood of persistence of odonates across Britain and Ireland over the past 30 years increased with shorter flight periods not longer periods, and they reasoned that length of flight period was not a suitable measure of dispersal ability.

Length of flight period could also be a surrogate measure of reproductive opportunities. A longer adult stage might indicate that individuals have more opportunities to mate and reproduce (Öckinger *et al.* 2010; Grewe *et al.* 2012), reducing the risk of population extinction (Henle *et al.* 2004). At the species level, length of the flight period also reflects the different adaptive strategies in species. Many odonate species are multivoltine Corbet *et al.* (2006), a trait that allows for resilience to environmental changes (Diaz *et al.* 2008). For example, climate change caused earlier than normal spring time emergence of odonates (Hassall *et al.* 2007), and for multivoltine species, only the first generation would be exposed to any detrimental effects of an early emergence time (Knell and Thackeray 2016), with subsequent generations of the same season potentially able produce enough offspring to counteract any population declines in the first generation (Knell and Thackeray 2016). If a longer flight season reflects more generations per year, as evidence suggests in lepidopterans (Kitahara and Fujii 1994; Roy and Sparks 2000; Nylin and Bergstrom 2009; Altermatt 2010), then multivoltine species may more quickly recover from changes or disturbances in the environment (Knell and Thackeray 2016). This same concept can be applied to univoltine species that have staggered emergence times, which would similarly lengthen the flight period (Zonneveld *et al.* 2003; Komonen *et al.* 2004). A population that has individuals overwintering at different instar stages will have staggered emergence times (Paulson and Jenner 1971); this temporal variation in emergence would allow for the utilization of optimal environmental conditions or avoidance of a catastrophic event (Neal *et al.* 1997) by at least some of a population.

I found a significant negative interaction between geographic range size and length of flight season in dragonflies but not in damselflies. Corser *et al.* (2015) found that damselflies with longer flight periods also had larger geographic ranges across the state of New York, and while I found that damselfly species with a low risk of becoming extinct had wider niche breadths and longer flight periods, the interaction between the two factors did not correlate with extinction risk assessment. In my study, I also found that increasing the geographic range of a species can mitigate the impact a short flight season has on a species' extinction risk, and vice versa. Because both geographic range size and length of flight period reflect dispersal capacities, strong dispersers would quickly reach other suitable habitat in a short amount of time or have plenty of time to reach suitable habitat that is far away. Or, a wide geographic range would decrease the likelihood that catastrophic event eliminated all adults of species with short flight seasons.

Habitat breadth significantly correlated with extinction risk assessment, but only in dragonflies. Habitat generalists had broader regional occurrences across Nevada and California across the past century (Ball-Damerow *et al.* 2014), so I expected to find this same pattern. However, the number of habitats occupied was not significantly correlated with extinction risk in damselflies, a pattern also found in hoverflies. For hoverflies, the number of habitats occupied may not accurately reflect niche breadth, and host plant type might be a more accurate correlate (Sullivan *et al.* 2000). Damselflies may be showing an analogous pattern with types of habitats occupied. Habitat type correlates with extinction risk (Korkeamäki and Suhonen 2002; Clausnitzer *et al.* 2009; Suhonen *et al.* 2014), and so habitat type may be a more accurate reflection of extinction risk across both dragonflies and damselflies. Surprisingly, Suhonen *et al.* (2014) found that odonate specialists had lower local extinction rates than generalists. Further studies are needed to better identify how habitat breadth affects odonate extinction risk.

Dragonfly extinction risk assessment significantly and positively correlated with the interaction between habitat breadth and the length of flight period. Komonen *et al.* (2004) found a significant correlation between length of flight period and habitat breadth in butterflies. They reasoned that habitat specialists would have shorter flight seasons due to habitat generalists being able to tolerate a wide variety of environmental conditions and thus able to tolerate changes in the environment. In my study, all 28 dragonfly species that utilize temporary habitats ranked as G5 species, and likely exhibit a multivoltine strategy because of the short generation time required to successfully inhabit temporary habitats (Corbet *et al.* 2006).

I found significant differences in how species' traits affect extinction risk in dragonflies and damselflies. Surprisingly, the differences were found despite the fact that there are no differences in the mean values of the three ecological correlates within each conservation rank between dragonflies and damselflies across ranks. These differences are possibly the result of the low number of at-risk damselflies found across North America. Increasing the number of damselflies included in this study could reveal ecological correlates with extinction that align more with those found in dragonflies. However, it is also possible that the differences I observed are true differences due to species-specific trait variations (McCauley *et al.* 2014).

The contrasting findings of my study versus those of other odonate studies suggest that geographical scale is also an important factor when identifying ecological correlates with extinction risk, as has been found in butterflies (Nylin and Bergstrom 2009). Corser *et al.* (2015) found a significant correlation between the length of flight period and geographic range size in damselflies in the state of New York, while my study was across the contiguous United States, Mexico, and Canada. Further, geographic distribution was found to be a significant predictor of regional extinction in Finland (Korkeamäki and Suhonen 2002), indicating that the use of geographic range is a correlate of extinction risk at larger landscape levels. McCauley *et al.* (2014) noted that geographic scale was a likely reason for the contrasting results between their study and others.

While the overall number of at-risk odonates across North America is fairly low, my study nonetheless contributes to the growing number of comparative studies that identify ecological correlates with extinction risk. The significant effects of flight period length in this study show that more studies of invertebrates need to be conducted in order to identify predictors of extinction risk that better reflect their life history traits and patterns.

Table 16. List of documented aquatic systems inhabited by odonates in my analyses.

System
Seep
Garden Pond
Pool
Stream
Spring Run
Rivulet
Brook
Stream Backwater
Irrigation Ditch
Slough
Bog
Ditch
Fen
Muskeg
Pond
Lagoon
Burrow Pit
Creek
Canal
Bayou
Marsh
Bay
Estuary
Lake
River

Table 17. Number of anisopterans and zygopterans found in each of NatureServe's global conservation ranks.

Conservation Status	Anisoptera	Zygoptera	Total
G1	6	0	6
G2	11	4	15
G3	27	7	34
G4	73	31	104
G5	189	87	276

Table 18. Mean (standard deviation) geographic range, length of flight period, and habitat breadth for each conservation status within Anisoptera and Zygoptera. Geographic range indicates number of American states, Mexican states, and Canadian provinces. Length of flight period is the average number of months adults are flying, and habitat breadth is the number of habitats a species occupies.

	Conservation Status	Geographic Range	Length of Flight Season	Habitat Breadth
Anisoptera	At-risk	6.20 (5.94)	2.73 (1.16)	4.05 (1.84)
	G4	13.37 (7.42)	3.49 (1.23)	3.73 (1.74)
	G5	24.86 (12.71)	4.98 (1.83)	5.77 (2.19)
Zygoptera	At-risk	6.09 (6.89)	5.40 (3.44)	4.81 (2.79)
	G4	9.52 (8.04)	5.92 (2.27)	4.62 (2.11)
	G5	30.29 (13.91)	5.98 (2.13)	5.79 (2.27)

Table 19. Values from ordinal logistic regression for anisopterans and zygopterans. For anisopterans, the best-fitting model included the variables and interactions listed below, and all were significant. For zygopterans, the best-fitting model included only geographic range and length of flight period. * indicate p-values less than 0.05; **, less than 0.01; ***, less than 0.0001.

	Ecological Correlate	Parameter	Standard Error	t value
Anisoptera	Geographic Range	1.71	0.21	8.00***
	Length of Flight Period	1.15	0.28	4.18**
	Habitat Breadth	0.65	0.22	2.96**
	Range x Flight Period	-0.74	0.26	-2.91**
	Habitat x Flight Period	0.68	0.29	2.36*
Zygoptera	Geographic Range	3.06	0.50	6.12***
	Length of Flight Period	0.50	0.23	2.15*

Table 20. Odds ratios and 95% confidence intervals of each significant variable for the ordinal logistic regression models with the lowest AIC values. In both Anisoptera and Zygoptera a 1-unit change in geographic range had the largest effect on conservation rank.

	Ecological Correlate	Odds Ratio	0.025	0.975
Anisoptera	Geographic Range	5.53	3.68	8.54
	Length of Flight Period	3.17	1.93	5.72
	Habitat Breadth	1.91	1.27	3.00
	Range x Flight Period	0.48	0.29	0.78
	Habitat x Flight Period	1.97	1.16	3.60
Zygoptera	Geographic Range	21.32	8.78	63.21
	Length of Flight Period	1.65	1.06	2.63

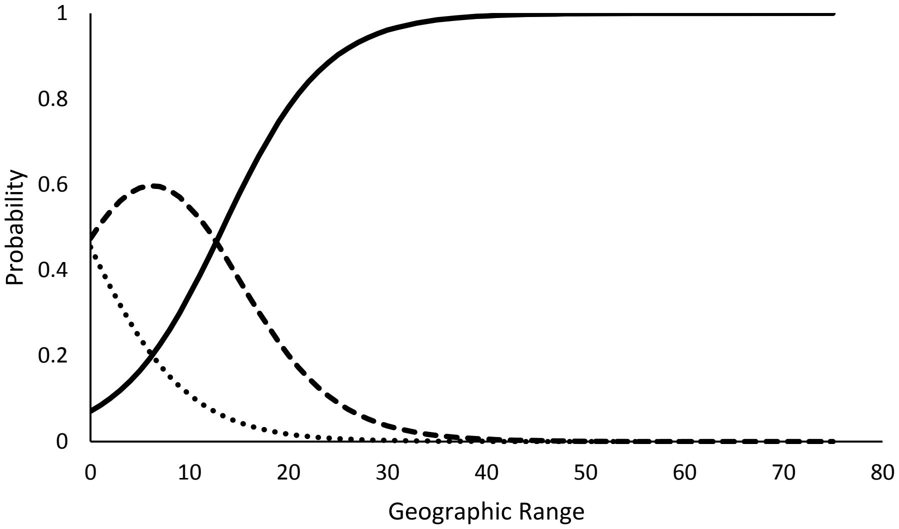

Figure 1. Prediction curves for predicting the probability of an odonate being a certain conservation status across geographic ranges. Increasing the geographic distribution of a species by one state increased the odds that the species was a G4 or G5 rank by 21.32 fold. Short-dashed line: “At-risk” conservation status; long-dashed line: G4 conservation status; solid line: G5 conservation status

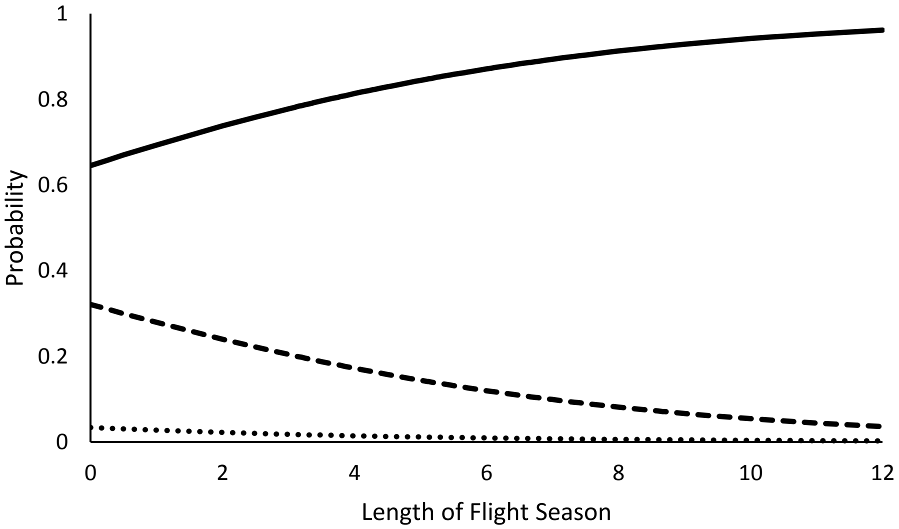

Figure 2. Prediction curves for determining a species' conservation status based on its flight period length. Increasing the length of a species' flight period by one month increased the odds that the species was a G4 or G5 by 1.64. Short-dashed line: "At-risk" conservation status; long-dashed line: G4 conservation status; solid line: G5 conservation status

CHAPTER V

CONCLUSION

Summary

I took three distinct approaches to studying arthropod conservation in North America. My research on wolf spiders shows that not all arthropods are negatively affected by urban development. Some species are able to tolerate and disperse through an inhospitable matrix caused by urbanization. Other taxa, such as odonates, are negatively affected by urban development. However, even among odonates, their responses to urbanization are variable, and these differences are likely due to variations in ecological and life-history patterns. My dissertation suggests that invertebrates have much more variation in their responses to urban development than do vertebrates.

Future Directions

Future studies need to develop a comprehensive theoretical framework to predict the responses of arthropod taxa to urbanization. Foundational data are necessary in order to identify the biological and environmental mechanisms that drive the differential responses of arthropod taxa to urban development. Biological factors (*e.g.* dispersal ability and voltinism) will certainly contribute to which species are resilient to extinction.

My research suggests that even passive forms of dispersal can help maintain gene flow so long as individuals successfully traverse large swaths of uninhabitable land and reach suitable habitat. Additionally, variations in dispersal abilities, as measured by geographic range size and length of flight period, correlate with extinction risk assessment in odonates. With such diverse modes of dispersal and variations in dispersal abilities, researchers need to investigate the ecological, behavioral, and morphological traits that enable some species to disperse successfully through inhospitable urban matrices while other species fail to do so. Direct measurements of long-distance dispersal are difficult to obtain (Nathan *et al.* 2003) and can be at least partially inferred from genetic analyses methods such as MIGRATE and BYESASS+, but more studies are needed to understand how different modes and patterns of dispersal contribute to species persistence in urban areas. Environmental mechanisms also need to be identified in order for invertebrates to be effectively conserved in urban areas (McDonnell and Hahs 2013). For example, I found that the amount of urban development surrounding a site affected pond communities but not stream communities. Future studies need to investigate why urban development affects odonate pond communities and not stream communities and if this pattern is found in other taxa as well.

In order to identify the mechanisms driving the urban biodiversity patterns that others and I have observed, I first need to better understand the basic ecology and distribution of invertebrates in general (D’Amen *et al.* 2013). In other words, in order for conservationists to effectively protect these taxa, I need to take a stronger interest in invertebrates and learn more about them. Sophisticated modeling techniques, which can inform conservation management practices, can only be effective if basic research has been conducted first (D'Amen *et al.* 2013) and researchers confidently know which environmental variables affect species persistence (Araujo and Guisan 2006).

Conclusion

The significance of urban areas in maintaining high levels of biodiversity is still being debated. Schwartz *et al.* (2014) concluded that the possibility of urban areas to contribute to animal conservation is low, but McDonnell and Hahs (2013) believe that cities can be important in conserving biodiversity. Certain species, such as *R. rabida*, may be able to tolerate urban areas, but study after study has shown that urban areas negatively affect biodiversity, especially those species that have narrow niches. If urban areas are to hold high levels of biodiversity, then society needs to take an active approach to making greener cities (Colding and Barthel 2013; McDonnell and Hahs 2013; Parker 2015) and conservationists need to put a stronger emphasis on learning more about the neglected 90% (Redak 2000) of an estimated 8.7 million extant invertebrate species (Mora *et al.* 2011).

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CURRICULUM VITA

Victoria A. Prescott

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Education

Doctoral Candidate-Biology PhD program
University of Louisville, Louisville, Kentucky
Anticipated Graduation Date: December 2016

Bachelor of Science in Biology, concentration: ecology
Baylor University, Waco, Texas
Graduation Date: May 2011
Baylor University Dean's List

RESEARCH EXPERIENCE

University of Louisville

2015-Present: **Correlating species attributes with extinction risk**

- Assembled information on three attributes of rarity for a single taxon
- Compiled data from resources databases such as NatureServe and International Union for Conservation of Nature
- Composed and managed extensive spreadsheets

2013-Present: **Conducted investigation of how habitat loss affects odonate diversity**

- Maintained compliance of permits with local and state governments
- Surveyed dragonflies at lentic and lotic water bodies
- Obtained water quality data using data sonde
- Conducted field surveys for over 8 hours each day throughout summer months
- Performed timed linear transects while visually identifying odonates
- Implemented novel odonate field survey technique
- Transported field equipment over rough terrain
- Quantified extent of perching and oviposition sites

- Communicated regularly with property owners
- Maintained highly organized data sheets
- Used ArcGIS software to quantify extent of urban land use surrounding around each site
- Analyzed data using R
- Identified which environmental factors affect odonate communities

2013-Present: **Examining how loss of habitat connectivity affects spider dispersal**

- Applied for permits with local and state governments
- Conducted nightly sampling of spiders
- Assessed genetic diversity among populations
- Quantified landscape resistance to dispersal using ArcGIS software and R
- Identified specific barriers to dispersal within the landscape
- Determined location and quality of wildlife corridors within the landscape
- Identified the most important corridors and core habitat areas for maintaining connectivity
- Discovered significant isolation-by-resistance among populations

Baylor University

2009: **Determined differential responses of odonate taxa to environmental stress**

- Participated in summer research fellowship
- Collected individuals at Lake Waco Wetlands
- Measured odonate wing areas and performed wing cell counts using Adobe Photoshop
- Analyzed levels of fluctuating asymmetry with Microsoft Excel

PRESENTATIONS

- Prescott, V.A., P.K. Eason. April 2016. Determinants of odonate diversity in ponds versus streams across an urban-rural gradient. Invited talk at Biology Department Awards Day, University of Louisville.
- Prescott, V.A, P.K. Eason. April 2016. Urbanization negatively affects dragonfly communities. Graduate Student Council Regional Conference.
- Prescott, V.A., P.K. Eason. November 2015. Dragonflies of pond and stream communities respond similarly to urbanization. Kentucky Academy of Science.
- Prescott, V.A., P.K. Eason. March, 2015. Pond and stream dragonfly communities respond differently to urban development. Midwest Ecology and Evolution Conference.
- Prescott, V.A., P.K. Eason. November, 2014. Odonate diversity across an urban-rural gradient: Odonates in ponds and streams respond differently to altered habitats. Kentucky Academy of Science.
- Prescott, V.A, D. Vodopich. August, 2009. Fluctuating asymmetry in damselflies of the Lake Waco Wetlands. Baylor University.

GRANTS RECEIVED

2015

- Effect of habitat destruction on odonate diversity
  - Horner Wildlife Refuge Grant ($1000)
  - Biology Graduate Student Association ($300)

2012-2014

- Effect of inhospitable matrix on wolf spider dispersal
  - Graduate Student Creative Activities Fund ($500)
  - Graduate Student Committee Research Fund ($300)
  - Graduate Student Committee Research Fund ($100)
  - Cornett Entomological Endowment Fund ($2000)

LEADERSHIP

2014-Present

- Senior Graduate Teaching Assistant
  - Taught laboratories for introductory biology to majors and nonmajors
  - Designed new lecture powerpoints used in all lab sections
  - Drafted homework assignments used in all lab sections
  - Mentor undergraduate teaching assistants
  - Corresponded with other teaching assistants on behalf of professor
  - Communicated clearly to students
  - Managed labs
  - Wrote and graded exams
  - Prepared equipment for laboratory experiments
  - Attended weekly meetings
  - Proctor exams

2011-Present

- Member, Biology Graduate Student Association

2015

- Guest Lecturer, *Principles of Ecology*

2015

- Third place, Oral presentation competition, Kentucky Academy of Science Conference

2014-2015

- President, Biology Graduate Student Association
  - Streamlined monthly meetings
  - Liaison between members and other associations
  - Coordinated fundraising events
  - Modified amendments and regulations of the association

    - Established new role entitled outreach coordinator

2014

- Judged undergraduate poster presentations at Kentucky Academy of Science conference

2013

- Guest Lecturer, *Invertebrate Zoology*

COMMUNITY INVOLVEMENT

2016

- Park Steward for Olmsted Parks Conservancy
    - Volunteer management
    - Community engagement
    - Pesticide management
    - Horticultural techniques
- Working with The Nature Conservancy to assess habitat needs of an endangered moth
- Entomologist for Lincoln Boyhood National Memorial Park BioBlitz
- Invited talk for the Sierra Club
- Invited talk for the Kentucky Society of Natural History
- Led nature walk for the Kentucky Society of Natural History

2014-2015

- Led nature walks for Kentucky Natural History Society
- Taught dragonfly biology to the public at Otter Creek Recreation Area and Blackacre State Nature Preserve

2014

- Hosted odonate booth at Bernheim Research Forest annual BugFest