

Evaluating the effects of landscape configuration on site occupancy and movement dynamics of odonates in Iowa

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Abstract

Odonates contribute highly to global biodiversity and are considered good indicators of environmental quality, but they are under-studied and quantitative information on their habitat associations is lacking. Our objective was to examine the effects of landscape configuration on site occupancy and movement dynamics of four odonate species in Iowa: *Tramea onusta*, *Epitheca princeps*, *Pantala flavescens*, and *Calopteryx maculata*. We conducted standardized visual encounter surveys for odonates at 233 public properties in Iowa from 2007-2011 and computed landscape variables within a 200 m, 600 m, and 1 km radius of each surveyed site. Using a robust design occupancy model in Program MARK, we estimated detection probability and site occupancy, site extinction, and site colonization probabilities for each species. We found few significant effects of landscape variables on site occupancy, extinction, or colonization, although landscape variables at 600 m were included in the best model for all species. Detection probability (SE) ranged from 0.30 (0.04) for *Pantala flavescens* to 0.49 (0.04) for *Calopteryx maculata*. Our study provides information to aid habitat restoration and management efforts on sites having suitable characteristics in the surrounding landscape and ultimately help conserve odonates.

Key words: damselfly, dragonfly, Iowa, landscape, occupancy, odonate

Introduction

The amount and spatial configuration of habitat on the landscape and how it affects the distribution and abundance or occupancy of a species is a commonly asked question in ecology. The magnitude of these effects depends highly on individual attributes of the species such as dispersal ability, body size, and degree of habitat specialization, as well as the species' demography (Morrison et al. 2006). Several studies have documented the influence of habitat configuration and other landscape factors on species density or richness, particularly with grassland birds (Ribic and Sample 2001; Fletcher and Koford 2002; Hamer et al. 2006), small mammals (Brady et al. 2011; Fischer et al. 2011), and herpetofauna (Joyal et al. 2002). The landscape variables affecting density or richness can be many and include amount of edge and habitat patch distribution (Hamer et al. 2006), habitat fragmentation (Herkert 1994; Pither and Taylor 1998) and amount of specific habitat type (Gibbons et al. 2002; Kadoya et al. 2008) among others. In addition, these factors can affect how individuals of a species move within the landscape, therefore potentially influencing metapopulation dynamics (Morrison et al. 2006 and citations therein). Knowing the degree to which landscape habitat variables affect species richness, abundance, and movement dynamics can inform future habitat

management and restoration decisions by providing guidance on habitat placement and the amount needed to benefit a species.

Odonates, or dragonflies and damselflies, are one taxon on which quantitative information on habitat use and site occupancy is lacking (Westfall and May 2006). Odonates occur on all continents except Antarctica. They spend the majority of their life as larvae in aquatic habitats. As adults, odonates will use a variety of habitats including aquatic for breeding and terrestrial for foraging and roosting. Dispersal of adult odonates depends largely on their ecological requirements. Species with narrow niches tend to disperse and colonize new areas poorly, whereas species that are habitat generalists tend to disperse long distances and colonize new habitats well (Clausnitzer et al. 2009). In addition to dispersal, some species will migrate from north to south to avoid harsh climatic conditions (Paulson 2011).

Along with other invertebrates, odonates contribute highly to global biodiversity and are considered good indicators of environmental quality, particularly for aquatic habitats (Corbet 1999; Cruden and Gode 2000; Roush and Anon 2003; Clausnitzer et al. 2009). Several populations of odonates are of conservation concern due primarily to habitat destruction and fragmentation (Paulson 2011). Currently, 85 odonates are listed as “endangered” and 55 as “critically endangered” on the IUCN Red List of Threatened Species (IUCN 2012). In Iowa, 28 of the 118 known odonates (24%) are currently listed as species of greatest conservation need (SGCN) in the Iowa Wildlife Action Plan (Zohrer 2006).

Because odonates utilize different habitat types during different life stages, landscape configuration can be a factor affecting presence or absence of a species at a particular site. Landscape-level habitat characteristics can affect the distribution of odonates, particularly dragonflies, because adults seek suitable habitat on the landscape, particularly when dispersing (Corbet 1999; Bilton et al. 2001; Dolný et al. 2013). For example, during the pre-reproductive phase, most adult odonates are strongly dependent on terrestrial habitats, such as woodlands and grasslands, for foraging and resting (Fincke 1992; Corbet 1999). Conversely, during the reproductive phase, odonates are tied to aquatic habitats for ovipositing (Corbet 1999). In addition, certain aspects of odonate behavior may require the utilization of different habitats on the landscape. Aeshnidae, for example, are typically seen patrolling for prey and will utilize open areas such as fields or prairies for doing so (Paulson 2011). Conversely, Gomphidae spend much of their time at rest and will commonly hunt from a woody perch, therefore being found

more often near woodlands (Paulson 2011). Knowing landscape-level habitat associations of odonate species will allow us to better focus habitat conservation and management efforts in areas more likely to host a diverse community of odonates or to support odonate species of conservation concern. The objective of our study was to evaluate the effects of landscape configuration on site occupancy and movement dynamics of four species of odonates in Iowa.

Methods

Study Area and Site Selection

Our study was conducted primarily on public properties in Iowa. A small number ($N = 18$) of private properties were included in our study that were surveyed to document SGCN on lands enrolled in the Landowner Incentive Program (see <http://wsfrprograms.fws.gov/subpages/grantprograms/lip/lip.htm>). Iowa covers approximately 145,000 square km and is described as an agriculturally-dominated landscape of low elevations (150 – 500 meters above sea level), numerous rivers, and fertile soils (Prior 1991). Iowa consists of seven distinct landform regions (Northwest Iowa Plains, Missouri Alluvial Plain, Western Loess Hills, Des Moines Lobe, Southern Iowa Drift Plain, Iowan Surface, Paleozoic Plateau, and Mississippi Alluvial Plain; Prior 1991) that give rise to a variety of habitat types. Approximately 74% of Iowa is agricultural land and 3.2% is developed, leaving forests, grasslands, and wetlands to 7.9%, 0.5%, and 13.7% of the land, respectively (Zohrer 2006). Approximately 2% of the land is in public ownership consisting of federal (U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, National Park Service), state (Iowa Department of Natural Resources), and county (county conservation boards) properties.

We considered all public properties >97 ha in size for selection in accordance with protocol for the Iowa Multiple Species Inventory and Monitoring (MSIM) program (<http://www.iowadnr.gov/Environment/WildlifeStewardship/NonGameWildlife/DiversityProjects/MSIM.aspx>). We then classified properties according to the 19 habitat types described in the Iowa Wildlife Action Plan (Zohrer 2006). Habitat classifications were determined using aerial imagery and 2002 land cover data in ArcGIS (ESRI 2012) and knowledge of the local land manager for each property. Each property could have received more than one habitat classification depending on the degree of habitat diversity on the property. Next, we divided Iowa into four equal management districts to allow for equal representation of all habitat types across the state. We utilized a stratified random sampling technique to select our properties to be surveyed. This technique

involved choosing properties from each habitat type (primary stratum) within each management district (secondary stratum), allowing us to obtain an equal representation of all habitat types within each management district. The number of properties with a particular habitat type was limited in some management districts. Therefore, we prioritized that habitat type within the respective management district to ensure it was represented. Once a property was chosen for a specific habitat type, it was excluded for future selection as a different habitat type. This procedure was repeated from 2007 to 2011 to obtain approximately 75 new properties each year. From those properties, we selected a subset of properties to be surveyed annually. Properties in this subset were selected by habitat type to obtain an equal representation of habitat types to be surveyed annually.

Odonate Surveys

We conducted standardized visual encounter surveys (VES) for odonates at properties each year from April to October in the period 2007–2011. Most properties were surveyed only during one year; however, some properties ($N = 42$) were surveyed during more than one year. Visual encounter surveys are a timed search for odonates within suitable habitat on the property. Suitable odonate habitats on each property were identified and mapped at the beginning of each year and subsequently surveyed upon each visit. We considered both terrestrial habitats (e.g., woodlands and grasslands) and aquatic habitats (e.g., wetlands, ponds, and streams) as suitable for odonates because several species will utilize both types of habitat during specific stages of their life cycle and for different behaviors (Fincke 1992; Corbet 1999). We divided each year into three survey seasons in order to minimize temporal variation in detection probability of different odonate species. Those seasons were spring (15 April–15 June), summer (16 June–15 August), and fall (16 August–15 October). Each property was surveyed for four person hours twice during each of the three survey seasons for a total of six visits per year. Surveys were conducted at least two weeks apart to ensure independence among visits and to allow wider coverage of species' flight times during each season. Surveys were conducted during warmer hours of the day, which was typically between 10 AM CST and 6 PM CST. All odonates observed were identified to species. If an individual could not be positively identified on the wing, we used aerial nets to capture the individual for identification. Any individuals not identified to species or which represented a potential county or state record were collected for a voucher specimen. Prior to conducting a survey, we recorded weather variables including starting temperature (°C), wind speed (km/h), and percent cloud

cover. We also recorded ending temperature (°C) at the end of the survey. Surveys were not conducted on cool days (< 10°C) or during periods of high winds (> 24 km/h°) or rain.

Habitat variables

Using ArcGIS (ver. 10.1; ESRI 2012), we measured various landscape habitat variables within three different radii of the surveyed sites to assess landscape configuration. We measured variables within a 600-m and 1-km radius of surveyed sites because odonates can disperse up to 1 km from a breeding site (Conrad et al. 1999). We also measured variables within 200-m radius of the surveyed site to assess local or on-site habitat configuration.

Using the buffer tool in ArcGIS toolbox (Analysis Tools, Proximity, Buffer; ESRI 2012), we placed a buffer around each of our surveyed sites. Next, we clipped the 2002 Iowa Landcover file (Kollasch 2004) to our site buffers using the “clipraster” command in the tools extension package Geospatial Modeling Environment (GME; Beyer 2012). The 2002 Iowa Landcover file provides information on the land use classification of the Iowa landscape in 2002 using satellite imagery and includes classifications such as “planted grassland”, “deciduous forest”, and “wetland” among others (Table 1). This is currently the most recent land use classification of Iowa. We repeated the above two steps for all three radii to obtain the land use description within the different radii of each of our surveyed sites. We focused our assessment of landscape configuration on five different habitat classes within the Landcover file we believed would be most utilized by odonates: water, wetland, woodland (consisting of both deciduous and coniferous types), planted grassland (i.e., restored grassland), and ungrazed grassland (i.e., native grassland). We added row-crop agriculture as a sixth habitat class to evaluate potential impacts of agriculture development on site occupancy and movement dynamics of odonates.

Using FRAGSTATS (ver. 3.4; McGarigal et al. 2002), we assessed landscape configuration within each of the three radii of our surveyed sites. For our analyses, we selected the area, landscape shape index (LSI), and interspersion-juxtaposition index (IJI) metrics. Area simply measures the area (ha) of the particular habitat class within the specified radius. LSI measures the perimeter-to-area ratio for the entire landscape, and quantifies the amount of edge present on the landscape relative to the amount of edge that would be on the landscape given that it was a simple geometric shape (e.g., circle or square; McGarigal et al. 2002). We applied this metric at the class level; it performed the above calculation on each habitat class and not on the landscape as a whole. IJI measures the

extent to which patch types are interspersed throughout the specified radius and the juxtapositioning of a focal patch type to all other patch types (McGarigal et al. 2002). One benefit of using IJI and not a contagion index is that IJI uses entire patches rather than raster cells to analyze adjacencies, thus making the result easier to interpret. For the agriculture habitat class, we only calculated the area and not LSI or IJI. Performing these three calculations on the six habitat classes (with the exception of agriculture) resulted in 16 landscape variables to be included as covariates in our models.

Occupancy Models

We utilized the robust design occupancy model framework (MacKenzie et al. 2003) in Program MARK (White and Burnham 1999) to evaluate site occupancy and movement dynamics of odonates in response to landscape characteristics. Robust design occupancy models relax the assumption of single-season occupancy models that sites are closed to changes in occupancy state during the sampling interval, therefore allowing the evaluation of site occupancy dynamics over time by assuming that changes in occupancy state may occur during primary sampling periods but remain static during secondary sampling periods (MacKenzie et al. 2002, 2003). In addition to site occupancy probability (ψ) and detection probability (p), robust-design occupancy models also estimate the probability of site colonization (γ) and the probability of site extinction (ϵ). Site colonization probability is defined as the probability a site becomes occupied at time $t + 1$ given it is not occupied at time t (MacKenzie et al. 2003). Conversely, site extinction probability is the probability a site becomes unoccupied at time $t + 1$ given it is occupied at time t (MacKenzie et al. 2003).

We modeled the effects of landscape characteristics on the above-mentioned parameters for four odonate species (three dragonflies and one damselfly): *Tramea onusta*, *Epithea princeps*, *Pantala flavescens*, and *Calopteryx maculata*. These species are commonly found throughout Iowa and have varying dispersal abilities. For example, the *P. flavescens* is a migratory species, whereas the *C. maculata* has the ability to disperse but may choose not to if it currently occupies suitable habitat (Conrad et al. 1999; Paulson 2011). The varying degrees of dispersal exhibited by these species make them good candidates for examining movement dynamics. In addition, these species vary in the types of habitats they prefer and the degree to which they utilize these habitat types (Iowa Odonata Survey 2013).

In our study, the primary sampling occasions were the years during which surveys were conducted (2007 – 2011) and the secondary sampling occasions were the visits (days) that occurred during each year (April to October). Site occupancy and detection probability were estimated annually and site colonization and extinction probabilities were estimated on the intervals between years. For each species, we truncated the data to the established flight times of each species according to the Iowa Odonata Survey (2013), which displays calendars of flight times for each species that are dynamically updated based on records entered by observers. These records are reviewed by experts and confirmed in the database. This is currently the best resource on flight times for odonates in Iowa.

Because little is known about the effects of landscape configuration on site occupancy and movement dynamics of odonates (but see Conrad et al. 1999; Jonsen and Taylor 2000; Kadoya et al. 2008), we treated our analyses as somewhat exploratory, meaning we modeled all landscape variables calculated above on site occupancy, site colonization, and site extinction. We utilized a step-wise modeling approach similar to that used by Olson et al. (2005) and evaluated models using Akaike's Information Criterion (AIC) adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). Prior to constructing our models, we examined correlation among landscape covariates and did not include covariates that were highly correlated ($r \geq 0.80$) as effects in the same model. First, we modeled environmental covariates on detection probability while keeping all other parameters constant. We modeled temperature (°C), wind speed (mph), and percent cloud cover on detection probability of all species. Using the best model from this exercise, we subsequently modeled site occupancy probability for each species. All 16 landscape covariates were modeled on site occupancy probability individually and then combined effects in competing models ($\Delta AIC_c \leq 2$; Burnham and Anderson 2002) as additive effects in the same model. We then selected the best model with effects on detection probability and site occupancy probability to use in examining effects on site colonization and extinction probabilities. The same model construction process was used for site colonization and extinction probabilities as that used for site occupancy probability. Finally, we selected the overall best model or models with effects on all parameters and used this as a basis for inference.

Results

Surveys were conducted on a total of 233 properties from 2007-2011: 28 in 2007, 40 in 2008, 54 in 2009, 51 in 2010, and 60 in 2011 (Figure 1). We detected *T. onusta* at 80 properties, *E. princeps* at 104 properties, *P. flavescens*

at 95 properties, and *C. maculata* at 121 properties. Below we present model results for each species individually along with effect sizes (β) and 95% confidence intervals (95% CI) for covariate effects and point estimates (\pm SE) for model parameters.

The best model for *T. onusta* included the effects of cloud cover on detection probability, area of water at 600 m on site occupancy probability, LSI of wetland at 1 km on site extinction probability, and LSI of woodland at 200 m on site colonization probability (Table 2). Competitive models ($\Delta\text{AIC}_c \leq 2$) included the above-mentioned effects on detection, site occupancy, and site extinction probabilities but also included the effects of IJI of wetland at 1 km, LSI of planted grassland at 200 m, IJI of planted grassland at 200 m, and IJI of woodland at 1 km individually on site colonization probability (Table 2). Cloud cover negatively affected detection probability ($\beta = -0.01$, 95% CI was -0.02 to -0.006). Area of water at 600 m positively affected site occupancy probability ($\beta = 0.05$, 95% CI was 0.001 to 0.11; Figure 2). All other covariates did not significantly affect the respective parameters because their 95% confidence intervals included zero.

The best model for *E. princeps* included the effect of temperature on detection probability and the effects of wetland IJI at 600 m, wetland area at 600 m, and LSI of ungrazed grassland at 600 m on site occupancy, site extinction, and site colonization probabilities, respectively (Table 2). The single competitive model ($\Delta\text{AIC}_c = 0.38$) included the effect of temperature on detection probability and the effects of wetland IJI at 600 m, wetland area at 600 m, and woodland area at 600 m on site occupancy, site extinction, and site colonization probabilities, respectively (Table 2). Temperature positively affected detection probability of *E. princeps* ($\beta = 0.06$, 95% CI was 0.03 to 0.09). Wetland area at 600 m negatively affected site extinction probability ($\beta = -0.08$, 95% CI was -0.14 to -0.02). All other effects were not significant because their respective 95% confidence limits included zero.

Cloud cover was included as an effect on detection probability in the best model for *P. flavescens* (Table 2). Also included in the best model were the effects of LSI of wetland at 600 m and wetland area at 600 m on site occupancy probability and site extinction probability, respectively (Table 2). Cloud cover had a weak negative effect on detection probability of *P. flavescens* ($\beta = -0.007$, 95% CI was -0.01 to -0.0007). LSI of wetland at 600 m positively affected site occupancy probability ($\beta = 0.85$, 95% CI was 0.16 to 1.54; Figure 3) and wetland area at 600 m positively affected site extinction probability ($\beta = 5.93$, 95% CI was 2.04 to 9.81). There was no effect on site colonization probability included in the best model.

For *C. maculata*, the best model included the effect of temperature on detection probability and the effects of wetland IJI at 600 m and woodland area at 600 m on site occupancy and site extinction probabilities, respectively (Table 2). There was no effect on site colonization probability included in the best model. The single competitive model ($\Delta AIC_c = 1.56$) included the effect of temperature on detection probability and the effects of wetland IJI at 600 m and ungrazed grassland IJI at 600 m on site occupancy and site extinction probabilities, respectively (Table 2). There was no effect on site colonization probability in the competitive model. Temperature positively affected detection probability of this species ($\beta = 0.08$, 95% CI was 0.05 to 0.11). None of the effects on site occupancy probability and site extinction probability were significant because their respective 95% confidence limits included zero.

Site extinction probability was estimated for *E. princeps* but was not estimated for the three other species. This could be the result of two scenarios: 1) lack of data, or too few data points to facilitate estimation of the parameter of interest, or 2) lack of opportunity, meaning sufficient data exists but occasions that result in the outcome (e.g., extinction or colonization) are few. Upon reviewing the data, we inferred that site extinction probabilities are not estimated due to lack of opportunity and not a lack of data. This demonstrates that extinction of a site rarely occurs in the time frame we studied once the site is occupied by three of our study species. This is likely due to unchanging characteristics on the surrounding landscape.

Discussion

Overall, we found area of wetland at 600 m was important for two of the four species and wetland IJI at 600 m was important for three of the four species. Other studies have found varying effects of the surrounding landscape on odonate probability of occurrence as well as dispersal abilities. Kadoya et al. (2008) found that occurrence of several dragonfly species was affected by landscape structure. However, the effect of landscape structure varied by species and by life history groups (short pre-reproductive phase versus long pre-reproductive phase). Gibbons et al. (2002) found three damselfly species associated with the number of ponds at various spatial scales. In addition, landscape connectivity and the distance between ponds influenced the probability of dispersal of odonates, particularly of smaller species (Angelibert and Giani 2003). Wetland area at 600 m negatively affected site extinction probability of *E. princeps* and positively affected site extinction probability for *P. flavescens*. *E. princeps* is known to associate with larger ponds and lakes across the northern part of their range (Paulson 2011) and this

same pattern is seen in Iowa (Iowa Odonata Survey 2013). Due to the small number and isolation of lakes and ponds in Iowa, we speculate that the increased amount of water associated with increased wetland habitat on the landscape serves as a suitable substitute for large lakes or ponds on the landscape. *P. flavescens* is often seen in open country and will utilize various ephemeral water bodies for breeding (Paulson 2011). The absence of fish seems to be a requirement for suitable breeding habitat for this species because their larvae are very conspicuous in water (Paulson 2011). Many of the wetlands remaining on the Iowa landscape are permanent or semi-permanent and are generally difficult to drain (Galatowitsch and Van Der Valk 1996), thus rendering them more suitable for harboring fish populations. The presence of fish in wetlands does have a detrimental effect on the abundance and taxon richness of aquatic invertebrates (Hanson and Riggs 1995). Therefore, increasing amount of wetland habitat at 600 m, particularly wetlands likely to harbor fish populations, could cause local extinction of *P. flavescens* due to increased predation risk.

Although we found few significant effects of landscape configuration on site occupancy or movement dynamics of odonates, landscape covariates at the intermediate scale (600 m) were included as effects on parameters in the top models for all species. This illustrates the potential importance of landscape configuration in predicting site occupancy, extinction, and colonization probabilities of odonates. We found some studies that evaluated the effects of landscape configuration and structure on odonate dispersal, taxon richness, and community composition, but few discuss the exact spatial extent at which landscape configuration most affects these measures. Jonsen and Taylor (2000) theorized that *Calopteryx aequabilis* and *C. maculata* choose not to venture away from natal habitats if significant forest cover is not detected within a 500-750 m radius. Our best model for this species included the area of woodland at 600 m on site extinction probability and though this effect was not significant, it did indicate that increased area of woodland at 600 m decreased site extinction probability. Knowing effects of the surrounding landscape configuration allows land managers to focus habitat restoration and management efforts for odonates on sites that have suitable characteristics on the surrounding landscape, thus maximizing the benefit of the on-site restoration and management.

Our estimates of site extinction and colonization probabilities lead us to believe that little movement exists between occupied and unoccupied sites for our study species. Therefore, once a site is occupied by one of our study species, the site remains occupied until a drastic change to habitat (e.g., habitat destruction) occurs that would render

the area unsuitable. However, it does appear that individuals of our study species are colonizing new sites at a moderate rate with the exception of *E. princeps*. There is some disagreement in the literature about the capability and likelihood of odonates to disperse from natal ponds or wetlands. In a study conducted in the United Kingdom, less than 40% of individuals of six species dispersed to a new pond, whereas >50% of one species dispersed to a new pond (Conrad et al. 1999). In another study, approximately 80% of adult *Sympetrum danae* were believed to be immigrants from sites of more than 1.75 km away (Michiels and Dhondt 1991). Despite the fact that most dragonflies and some damselflies are powerful fliers, the degree to which individuals disperse varies greatly both within and among species (Angelibert and Giani 2003). The decision to disperse involves a trade-off between potentially living longer at an already-occupied site with competition for limited resources or risking survival to disperse and colonize a new, unoccupied site (Angelibert and Giani 2003). Odonates are believed to be philopatric (McPeck 1989, Angelibert and Giani 2003), and individuals won't disperse if it is too risky (McCauley 2006) or if they currently occupy suitable breeding habitat (Corbet 1999). Distance to the nearest suitable habitat is the primary factor limiting odonate dispersal (Conrad et al. 1999; McCauley 2006). Iowa has lost >98% of its original wetland and grassland habitats to agricultural development resulting in an extremely fragmented landscape leaving remaining habitats highly isolated. Based on our results, we speculate that odonates remain at natal sites and disperse very little due to the increased risk, such as predation or the chance of not finding a suitable site, associated with moving into isolated habitats. In addition, odonates appear to be colonizing new sites and remain at these sites unless a drastic change in habitat occurs.

To our knowledge, this is the first study to estimate detection probabilities for odonates. Detection probability has been estimated for other taxa (e.g., birds, mammals, and amphibians) and is important to consider when conducting surveys for organisms because non-detection of a target organism at a site does not imply absence from the site (MacKenzie et al. 2002). Temperature and cloud cover were the two covariates affecting detection probability for all odonate species. It is intuitive that detection probabilities would be higher on days with warmer temperatures and decreased cloud cover because odonates are ectotherms and are most active on these days. The importance of considering detection probability is further emphasized when examining species-habitat relationships because ignoring detection probability could lead to over-estimation of a covariate effect on site occupancy (Gu and Swihart 2004). Detection probabilities of odonates also vary by species. For example, detection probability of *P. flavescens* may be relatively high because they are continuously patrolling and in flight. Estimating detection

probability provides an index of the effectiveness of surveys, and this can be valuable when conducting targeted surveys or when conducting surveys for multiple species.

Odonates are an under-studied group and are useful for monitoring biodiversity of aquatic habitats (Clausnitzer et al. 2009). Invertebrates currently face the highest extinction risk and the greatest loss to biodiversity (Thomas et al. 2004). Most odonates rely on vegetation structure and other habitat characteristics for foraging, reproduction, and to seek refuge from predators. Therefore, they respond very quickly to habitat change and are good indicators of habitat connectivity and environmental health (Corbet 1999; Clausnitzer et al. 2004; Lee Foote and Rice Hornung 2005). In the interest of conserving biodiversity, it is important to expend effort on restoring and managing habitat for invertebrates, including odonates. Our study provides valuable information on how landscape configuration affects site occupancy and movement dynamics of odonates. This information allows land managers to focus management and restoration efforts on sites that have suitable characteristics on the surrounding landscape in order to benefit odonates in Iowa.

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Table 1 List of all landcover types and corresponding descriptions included in the 2002 Iowa Landcover file (Kollasch 2004). * denotes landcover types used in analyses. Some landcover types (e.g., bottomland forest, coniferous forest, and deciduous forest) were combined into a single landcover type for analyses.

Landcover name	Description
Open water*	Areas of open water, generally without vegetation
Wetland*	Area of marsh land and areas of saturated soils
Bottomland forest*	Area of bottomland forest identified by presence of forest and water
Coniferous forest*	Area of forest consisting primarily of coniferous trees
Deciduous forest*	Area of broadleaf deciduous forest
Ungrazed grasslands*	Area of grasslands that appear unmanaged
Grazed grasslands	Area of grasslands that show healthy vegetative signature in spring indicative of grazing
Planted grasslands*	Area of grasslands that are unmanaged and appear to be planted
Alfalfa/hay	Area of lush vegetation, primarily alfalfa but could also include winter wheat
Corn*	Area of row-crop agriculture planted in corn
Soybeans*	Area of row-crop agriculture planted in soybeans
Other rowcrop*	Area of row-crop agriculture planted in a crop other than corn or soybeans
Roads	Area of traveled roadways
Commercial industrial	Area of urban development shown by broad expanses of impervious surfaces
Residential	Area of residential development identified by vegetation and impervious surfaces
Barren	Area of exposed rock or sand such as quarries or sandbars

Table 2 Model selection results for site occupancy (Ψ), site extinction (ϵ), site colonization (γ), and detection (p) probabilities of four species of Odonates in Iowa, 2007-2011. ΔAIC_c denotes the difference in Akaike's Information Criterion (AIC) units adjusted for small sample sizes (AIC_c) from the top model, K denotes the number of parameters in the model, w_i is the AIC_c weight, and Dev is the model deviance. Cloud denotes percent of cloud cover, Temp denotes ambient temperature ($^{\circ}C$), WaArea600 denotes the area of water at 600 m, WetLSI1km denotes landscape shape index of wetlands at 1 km, WoLSI200 denotes landscape shape index of woodlands at 200 m, WetIJI1km denotes interspersed-juxtaposition of wetlands at 1 km, PltLSI200 denotes landscape shape index of planted grasslands at 200 m, PltIJI200 denotes interspersed-juxtaposition of planted grasslands at 200 m, WoIJI1km denotes interspersed-juxtaposition of woodlands at 1 km, WetIJI600 denotes interspersed-juxtaposition of wetlands at 600 m, WetArea600 denotes area of wetlands at 600 m, UngrLSI600 denotes interspersed-juxtaposition of ungrazed grasslands at 600 m, WoArea600 denotes area of woodlands at 600 m, WetLSI600 denotes landscape shape index of wetlands at 600 m, “.” denotes no covariate effect on the parameter, and UngrIJI1km denotes interspersed-juxtaposition of ungrazed grasslands at 1 km.

Model	ΔAIC_c	K	w_i	Dev
<i>Tramea onusta</i>				
$p(\text{Cloud}) \psi(\text{WaArea600}) \epsilon(\text{WetLSI1km}) \gamma(\text{WoLSI200})$	0.00 ^a	6	0.12	624.01
$p(\text{Cloud}) \psi(\text{WaArea600}) \epsilon(\text{WetLSI1km}) \gamma(\text{WetIJI1km})$	0.40	6	0.10	624.41
$p(\text{Cloud}) \psi(\text{WaArea600}) \epsilon(\text{WetLSI1km}) \gamma(\text{PltLSI200})$	0.52	6	0.09	624.52
$p(\text{Cloud}) \psi(\text{WaArea600}) \epsilon(\text{WetLSI1km}) \gamma(\text{PltIJI200})$	0.78	6	0.08	624.79
$p(\text{Cloud}) \psi(\text{WaArea600}) \epsilon(\text{WetLSI1km}) \gamma(\text{WoIJI1km})$	0.86	6	0.07	624.87
<i>Epithea princeps</i>				
$p(\text{Temp}) \psi(\text{WetIJI600}) \epsilon(\text{WetArea600}) \gamma(\text{UngrLSI600})$	0.00 ^b	8	0.30	694.19
$p(\text{Temp}) \psi(\text{WetIJI600}) \epsilon(\text{WetArea600}) \gamma(\text{WoArea600})$	0.39	6	0.25	698.85
<i>Pantala flavescens</i>				
$p(\text{Cloud}) \psi(\text{WetLSI600}) \epsilon(\text{WetArea600}) \gamma(.)$	0.00 ^c	5	0.35	652.41
<i>Calopteryx maculata</i>				
$p(\text{Temp}) \psi(\text{WetIJI600}) \epsilon(\text{WoArea600}) \gamma(.)$	0.00 ^d	7	0.41	771.13
$p(\text{Temp}) \psi(\text{WetIJI600}) \epsilon(\text{UngrIJI1km}) \gamma(.)$	1.56	6	0.19	774.81

^a AIC_c for the best model for *T. onusta* was 636.38

^b AIC_c for the best model for *E. princeps* was 710.84

^c AIC_c for the best model for *P. flavescens* was 662.67

^hAIC_c for the best model for *C. maculata* was 785.63

Table 3 Parameter estimates (SE) from the best model for four species of odonates in Iowa, 2007-2011. p denotes detection probability, Ψ denotes site occupancy probability, ε denotes site extinction probability, and γ denotes site colonization probability. NE denotes parameters that were not estimated by the model.

Species	p	Ψ	ε	γ
<i>Tramea onusta</i>	0.31 (0.04) ^e	0.19 (0.08)	NE ^f	0.22 (0.05)
<i>Epitheca princeps</i>	0.44 (0.04)	0.76 (0.15)	0.79 (0.18)	0.97 (0.08)
<i>Pantala flavescens</i>	0.30 (0.04)	0.41 (0.14)	NE	0.27 (0.07)
<i>Calopteryx maculata</i>	0.49 (0.04)	0.48 (0.10)	NE	0.21 (0.07)

^eEstimates of detection probability were averaged across all years

Figure legends

Fig. 1 Location of public properties surveyed for Odonates in Iowa, 2007-2011. Each dot represents a single property

Fig. 2 Probability of site occupancy (ψ) of *Tramea onusta* in response to area (acres) of water habitat within a 600 m radius of surveyed sites in Iowa, 2007-2011

Fig. 3 Probability of site occupancy (ψ) of *Pantala flavescens* in response to landscape shape index (LSI) of wetland habitat within a 600 m radius of surveyed sites in Iowa, 2007-2011





