Odonata Richness and Abundance in Relation to Vegetation Structure in Restored and Native Wetlands of the Prairie Pothole Region, USA

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ABSTRACT

Over the past couple of decades, 2,200,000 ha of wetlands and grasslands have been restored in the prairie pothole region, USA. However, many restored and remnant wetlands in the region are dominated by two invasive plant species, reed canary grass (*Phalaris arundinacea*) and cattail (*Typha* spp.), which form dense monotypic stands. These restorations are usually evaluated as habitat for waterfowl and other birds; however, there is a need to evaluate their success for invertebrates. Odonata (dragonflies and damselflies) are ideal organisms to include in our evaluations of restored wetland habitat quality for both ecological and practical reasons. To examine the association between vegetation structure and odonate assemblages in shoreline vegetation of prairie pothole wetlands, we compared odonate richness and abundance in dense, monotypic stands to that of vegetation with diverse vertical structure. We also observed the use of these two different habitats by odonate species classified as "of conservation concern" in Iowa. Odonate species richness was substantially greater in the mixed-structure vegetation than in monotypic stands. A similar trend was found in odonate species with a "vulnerable" or "uncommon" conservation status. The number of occurrences of species of conservation concern was four times greater in mixed than in monotypic vegetation. A comparison of our data to those collected in the 1990s for one monotypic vegetation site further supported this conclusion. Many odonate species are targets for conservation and can readily benefit from wetland restoration and reconstruction if the sites are managed for proper vegetation structure.

Keywords: habitat structure, invasive species, odonates, prairie pothole region, wetland restoration

Before Euro-American settlement, the southern prairie pothole region of North America comprised an extensive prairie mosaic, characterized by depressions and swales that formed marshes and seasonal pothole wetlands interspersed among the upland prairies. Wetland drainage and conversion to row-crop agriculture started with Euro-American settlement of the region in the 1850s and 1860s, accelerated after 1900, and resulted in extensive wetland loss. For example, Iowa has lost 89% of its original wetlands and up to 99% of the shallow prairie pothole wetlands (Dahl 1990, Bishop et al. 1998). Other pothole states have had wetlands reduced any where from 27% to 49% (Dahl 1990). Pothole wetlands cumulatively supported nearly 350 plant species, and extensive efforts have been devoted to their restoration (Galatowitsch and van der Valk 1994). Over the past couple of decades, 2,200,000 ha of wetland and grassland habitats have been restored in the U.S portion of the pothole region through federal conservation programs (Gleason et al. 2008). Iowa, the state in the pothole region with the greatest wetland loss, has restored approximately 3,600 ha of wetlands, representing a small fraction (0.22%) of the original estimated 1,600,000 ha (Dahl 1990, Zohrer 2001).

Wetland restoration in the pothole region has largely focused on habitat for breeding birds (Van der Valk 1989, Delphey and Dinsmore 1993, VanRees-Siewert and Dinsmore 1996, Fairbairn and Dinsmore 2001). These efforts have been successful in increasing the breeding habitat for a wide range of birds that use the newly restored open-water areas as well as the emergent and upland vegetation zones (Delphey and Dinsmore 1993, VanRees-Siewert and Dinsmore 1996, Fairbairn and Dinsmore 2001). Since these restored wetlands have generally not been evaluated as habitat beyond waterfowl and other birds, invertebrate-focused studies are rare, especially for taxa other than butterflies and moths (Major 2009). In addition, there is a general need to better understand prairie pothole wetland invertebrates and their role in wetland ecosystems, particularly in response to human disturbance (Euliss et al. 1999).

Figure 1. A halloween pennant (*Celithemis eponina*), perching on a dead branch in the sedge meadow zone of a restored wetland at Camp Dodge, Johnston, Iowa, USA. Photo by Cathy Mabry

Odonata (dragonflies and damselflies) are ideal organisms to include in our evaluation of restored wetland habitat quality for both ecological and practical reasons. Degradation and loss of habitat have led to steep population declines for some species, making them targets of conservation concern (Cruden and Gode 2000, Roush and Anon 2003, Westfall and May 2006). At the same time, precise and quantitative habitat information is lacking for most North American species (Westfall and May 2006), placing a premium on quantitative studies of habitat use. Ecologically, odonates serve as important components of aquatic food chains (Thorp and Cothran 1984, Corbet 1999, Westfall and May 2006) and are associated with important attributes of wetland function and quality, including hydrological patterns and regimes (Clark and Samways 1996, Schindler et al. 2003), vegetation structure (Clark and Samways 1996, Chovanec and Raab 1997, Schindler et al. 2003, Bried and Ervin 2005, Foote and Rice Hornung 2005), and water quality (Carchini et al. 2005). They can respond quickly to changes in habitat quality (Chovanec and Raab 1997) and are sensitive to human disturbances to their habitat (Carchini et al. 2005, Foote and Rice Hornung 2005, Müller et al. 2003).

Practically, they also offer advantages for evaluating restored wetlands as habitat. The congruence between the distribution patterns of larvae and adults means that conservation assessments can be based on adult identification (Watson et al. 1982, Schmidt 1985, Hawking and New 1999), which can be readily learned for most species. As a result, these assessments are relatively easy to accomplish by managers. Finally, they are beautiful organisms with widespread public appeal and acceptance (Figure 1), often appearing in art and poetry (Kiauta 1986, Dunkle 2000).

Wetland restoration efforts generally consist of breaking drain tile and reflooding former low areas and depressions (Galatowitsch and van der Valk 1996). The focus is on reestablishing the hydrology, and the assumption is that seed bank and seed dispersal will be sufficient for revegetating the wetlands. However, these restored wetlands generally have little floristic resemblance to high-quality native wetlands, in large part because of the dominance of two invasive species, cattail (*Typha* spp.) and reed canary grass (*Phalaris arundinacea*) (Mulhouse and Galatowitsch 2003; for plant names, see GPFA 1986). Moreover, many of the remaining remnant prairie pothole wetlands have undergone similar extensive vegetation changes. Invasive cattail is a hybrid (*T.* × *glauca*) between the native broadleaf cattail (*T. latifolia*) and the non-native, invasive narrowleaf cattail (*T. angustifolia*), which may have arrived in eastern North America at the time of European settlement (Galatowitsch et al. 1999). However, it was not documented in the pothole region until 1949. Since then, it has proven to be an unwanted and aggressive invader of both native and restored wetlands, owing to its high tolerance of water-level fluctuations and eutrophication (Galatowitsch et al. 1999). Although less is understood about the sources of reed canary grass genotypes, it is similar to cattail in the causes and degree of its ability to invade aggressively (Galatowitsch et al. 1999). Both species grow in the wet prairie, sedge meadow, and shallow marsh zones of pothole wetlands, displacing native species and converting these formerly species- and structurally diverse zones, whether remnant or restored, into dense, often monotypic, stands (Galatowitsch and van der Valk 1994, Mulhouse and Galatowitsch 2003). The lack of wet meadow and sedge zone habitats associated with reed canary grass invasion may limit the use of these areas by some bird species (Delphey and Dinsmore 1993, Kirsch et al. 2007), but effects on odonates are largely unknown.

In this study we examined the association of odonate richness and abundance with two different wetland habitat structures: dense, nearly monotypic stands (also currently typical of many, if not most, restored wetlands in the region) versus assemblages with a diversity of plant life forms (a condition that typified many native wetlands in the region before Euro-American settlement). We also compared the use of these two different

habitat structures by odonate species that are classified as "of conservation concern" in the study region.

Field Site and Methods

The study was conducted at Camp Dodge, an Iowa Army National Guard base located in Johnston, Iowa, USA, near the southern border of the prairie pothole region (Figure 2). The climate of the study area is midcontinental, with average winter temperatures of –2°C and summer (June–August) temperatures of 28°C (National Weather Service 2008). The average frost-free growing season is 176 days (NCDC 2005). Total annual precipitation is 125.6 cm, 72% of which occurs from April to September (National Weather Service 2008). The total area of the base is approximately 1,780 ha, with 1,335 ha in a mosaic of mowed hay fields, restored prairie, riparian woodland, old fields in various stages of succession, wetlands, and row-crop agriculture. The wetlands include 66 ha of low prairie, seasonal emergent, and scrub-shrub wetlands that are the focus of this study (Madson et al. 2001).

Dragonflies and damselflies were extensively surveyed at Camp Dodge from 1995 to 1998 to develop lists of species using major habitat types on the base. The current Iowa list of dragonflies and damselflies contains 108 species (IOS 2005). During the early surveys, 53 of these species were recorded on the base (Cruden and Gode 1998).

We began quantitative surveys of Odonata in 2007, when nine transects were established across a range of restored and native wetland sites. The term "native" in this study refers to remnant wetlands that have not been intentionally managed or manipulated. Analyses of these data made it clear that vegetation structure was the source of variation in the odonate assemblages we recorded rather than the status of wetlands as native or restored.

Thus, based on these pilot observations, in 2008, we established eight transects in five sites to specifically quantify the relationship between wetland vegetation structure and odonate species richness and number of occurrences. Five of these transects were originally established and sampled in 2007. We established four transects in areas with diverse plant structure: one in a native sedge meadow, two in a wetland reconstructed in a former borrow site (representing a single transect in 2007), and one in a beaver pond. Four transects were in areas dominated by dense, nearly monotypic stands of graminoids or cattails: one in a stand dominated by soft-stemmed bulrush (*Scirpus validus* [= *Schoenoplectus tabernaemontani*]) and cattail near the native sedge meadow; one in a stand of reed canary grass in a native pothole, and two in reed canary grass in a wetland restored by removing tile lines. The site of the latter two transects was also heavily dominated by cattail in deeper water beyond the shoreline where sampling took place.

Transects ranged in length from 204 to 410 m and were oriented according to the layout of the vegetation. They were separated by a minimum of 200 m, a distance specified in other odonate surveys (Bried and Ervin 2005) and a minimum distance for surveys of birds, which are much more mobile (Hutto et al. 1986). In September 2008, we surveyed vegetation by establishing a vegetation sampling point every 30 m along each transect. The monotypic transects were uniform in cover and structure, and a single 1 m² quadrat placed on the transect line was sufficient to categorize the vegetation. The mixed-structure transects occasionally required two quadrats at each point to capture the structural variation. These were placed equidistant on opposite sides of the transect and about 2 m apart; the mean of these quadrats was then calculated for that sample point.

We categorized the vegetation into five structural classes that related in large part to plant life form. The structural classes were sedges, grasses, forbs, woody, and reed canary grass/

Figure 2. The prairie pothole region in the United States and Canada. Location of the study area is indicated by the black star.

cattail/bulrush. Each class present in the quadrats was assigned to one of eight modified Braun-Blanquet cover abundance classes (≤1%, 2–5%, 6–10%, 11–15%, 16–25%, 26–50%, 50–75%, and ≥76%). The midpoint of each cover class was used to calculate transect averages for each vegetation structural/life form class. We chose this method for characterizing the vegetation because odonate richness has been positively related to both vegetation cover and habitat structural diversity (Müller et al. 2003 and references therein). In addition, cover-abundance classes have gained widespread use and have been shown to be better than stem density for depicting species–environment relationships (Elzinga et al. 1998, Wikum and Shanholtzer 1978).

Transects were sampled for odonates three times during the breeding season (June, July, and August) between 9:00 a.m. and 4:00 p.m. using a modified Pollard method (Pollard 1977). We walked the transect at a steady pace to avoid double-counting, identified species, and recorded the number of occurrences of all dragonflies flying or perching within 10 m and all damselflies flying or perching within 5 m on either side of the individual walking the transect. Transect sampling order varied with each survey event in order

to avoid bias due to time of day for peak activity. The total time required to survey each transect was recorded, and the number of odonates was normalized to observations per hour. The clock was stopped during pauses to net and identify individuals. All surveys in 2007 and 2008 were conducted by both authors using identical methods.

Odonate species were classified according to conservation status (IOS 2005). Species were classified as vulnerable (S3) if they have a restricted range in the state or relatively few populations (often 80 or fewer), are undergoing population declines, or if there are other factors making it vulnerable to extirpation (Nature Serve 2009). Species were classified as apparently secure (S4) if they are uncommon but not rare in the state, or if there is some cause for long-term concern over their population trends (Nature Serve 2009).

Because results of single-year surveys are best verified over at least two years for assessment and monitoring of habitat conditions (Schmidt 1985), we evaluated whether the results obtained in the 2008 survey were consistent across the 2007 and 2008 seasons for the five transects surveyed in both years. For each species, we tabulated the maximum number of individuals counted at each transect across the three sampling periods during a given year. We then averaged this value across the two years of sampling to obtain a mean maximum count.

One of our monotypic transects traversed a native prairie pothole that was extensively sampled for damselfly and dragonfly species from 1995 to 1998 as part of a larger survey of Camp Dodge odonates. At the time of the first survey, the native pothole was classified as a high-quality sedge meadow remnant (Mary Jones, Iowa Army National Guard, pers. comm.). However, in the intervening 12–15 years, the wetland has been increasingly invaded by reed canary grass, and is currently a monoculture with nearly 90% cover of this species. We compared odonate composition of this site before and after the reed canary grass invasion, using data from the original survey, in order to compare those findings with the main portion of our study. This survey included three sample periods during breeding season in each year of the survey, and each sample period involved visiting three sites over the course of a single day, which likely makes the survey times comparable to ours.

Data Analysis

We used one-way ANOVA to test whether species richness and number of occurrences differed between the two vegetation zones sampled in 2008 and for the combined 2007–2008 data. Vegetation zone was the independent variable (fixed factor) and species richness and number of occurrences were the dependent variables. We also conducted a separate analysis that included only those species classified with conservation status in Iowa as vulnerable or uncommon, using the same ANOVA design to compare their richness and abundance between the two vegetation zones. All analyses were conducted with DataDesk (v. 6.0, Data Description, Ithaca NY).

Conducting exploratory studies in rare plant communities inherently limits the number of replicates, and one should be cautious about the probability of Type II errors that may lead to premature abandonment of lines of inquiry that may prove insightful and lead to further questions. Additionally, an overreliance on null-hypothesis testing leaves little margin of error for falsely accepting the conclusion of no effect (Fidler et al. 2006). For these reasons, we adopted a significance level of $\alpha = 0.10$.

Results

Results of vegetation sampling in 2008 documented the structural differences between transects (Table 1). The four mixed-vegetation transects were composed of a relatively balanced mixture of species in three groups: sedges (Cyperaceae), grasses, and forbs, all less than 0.5 meters in height, with some woody species also mixed in. In contrast, the monotypic transects had over 80% cover of species that are structurally similar in that they form dense stands, primarily reed canary grass and cattail, which grow to an average height of 2.1 m and 3 m, respectively. The transect dominated by bulrushes had similar cover to the other transects, with soft-stemmed and river bulrush (*Scirpus fluviatilis* [= *Schoenoplectus fluviatilis*]) growing to an average height of 3.9 m and 1.5 m, respectively (GPFA 1986). These stands also had very low forb and sedge cover and no grasses or woody species (Table 1).

We found that mean overall odonate species richness was nearly 30% greater in the mixed vegetation than in the monotypic transects, a trend that was consistent for both dragonflies and damselflies, although stronger for dragonflies (Tables 2 and 3). The overall number of occurrences was highly variable among both transect types, with no trends evident (Tables 2 and 3). Mean richness of species with S3

Table 1. Mean (± 1 SD) percent cover of five plant life-form classes in a 2008 wetland survey of structurally diverse mixed vegetation (*n* = 4) compared to dense monotypic vegetation (*n* = 4) consisting of reed canary grass (*Phalaris arundinacea*), cattails (*Typha* spp.), or bulrushes (*Schoenoplectus* spp.) at Camp Dodge, Johnston IA, USA.

Life-form class	% Cover	
	Mixed transects	Monotypic transects
Sedge	25.3 (26.0)	0.01 (.03)
Grass	20.6 (17.8)	0 (0.0)
Forb	18.1 (11.9)	4.8 (9.2)
Woody	14.3 (14.6)	0 (0.0)
Monotypic vegetation	2.6 (5.1)	82.6 (8.4)

Table 2. Maximum occurrence (individuals/transect) of damselfly and dragonfly species recorded at Camp Dodge, Johnston, Iowa, USA, wetland transects. Mixed transects were dominated by sedges (*Carex* spp.), grasses, and forbs. Monotypic transects were dominated by cattail (*Typha* spp.), reed canary grass (*Phalaris arundinacea*, RCG), or bulrush (*Schoenoplectus* spp.). CS = conservation status statewide: S3 = vulnerable to extirpation; S4 = uncommon, vulnerable to decline; S5 = common and secure. P = species recorded during vegetation surveys in 2007 or 2008, included in richness analyses but not in frequency of occurrence; asterisk indicates species recorded during pilot survey of transects in 2007, but not in 2008.

| | | | Mixed transects | | | | Bulrush stand | Monotypic transects | | |
| | | | | | | | | | | |
Species	Common name	CS	Borrow west	Borrow east	Native sedge	Beaver pond		RCG pothole	Restored east	Restored west
Damselflies										
Amphiagrion saucium	eastern red damsel	S3	*	0	*	0	0	0	0	0
Argia fumipennis	variable dancer	S5	0	0	3.6	0	2.0	0	0	0
Calopteryx maculata	ebony jewelwing	S5	0	0	0	0	2.3	0	0	0
Enallagma aspersum	azure bluet	S5	0	0	P	0	0	0	0	P
E. civile	familiar bluet	S5	13.1	137.5	0	0	P	0	0	0
Ischnura hastata	citrine forktail	S3	13.1	7.5	0	0	0	0	0	0
I. verticalis	eastern forktail	S5	55.9	20.0	64.9	62.9	48.0	9.0	165.9	250.0
Lestes unguiculatus	lyre-tipped spreadwing	S5	4.8	23.1	35.7	2.9	53.1	168.0	0	0
L. rectangularis	slender spreadwing	S4	31.4	32.3	56.8	12.5	20.8	15.0	0	0
Dragonflies										
Aeshna constricta	lance-tipped darner	S3	P	0	0	0	0	0	0	0
Anax junius	common green darner	S5	3.8	5.0	12.0	9.5	30.0	10.6	16.4	70.0
Celithemis elisa	calico pennant	S3	28.6	23.1	3.0	0	0	0	0	0
C. eponina	halloween pennant	S4	20.6	20.0	3.2	5.7	0	3.5	21.2	20.0
Erythemis simplicicollis	eastern pondhawk	S5	22.5	11.3	22.7	82.1	30.0	7.1	42.4	15.0
Leucorrhinia intacta	dot-tailed whiteface	S4	2.7	7.5	0	0	0	0	0	0
Libellula luctuosa	widow skimmer	S5	50.5	11.5	13.0	12.5	3.0	10.6	17.6	20.0
L. pulchella	twelve-spotted skimmer	S5	20.6	56.3	12.0	35.0	60.0	8.8	32.7	70.0
Pachydiplax longipennis	blue dasher	S5	63.8	65.0	60.0	53.7	34.6	0	109.1	248.6
Pantala flavescens	wandering glider	S4	0	3.8	0	0	0	1.8	0	0
Perithemis tenera	eastern amberwing	S5	*	0	0	0	0	*	0	0
Plathemis lydia	common whitetail	S5	4.1	7.5	1.6	31.6	0	0	3.5	5.0
Sympetrum corruptum	variegated meadowhawk	S5	0	*	*	0	0	0	0	0
S. costiferum	saffron-winged meadowhawk	S3	9.4	18.5	21.0	0	6.0	21.0	0	0
S. internum	cherry-faced meadowhawk	S4	*	*	*	0	0	*	0	0
S. obtrusum	white-faced meadowhawk	S5	0	0	9.0	7.5	6.0	24.7	0	0
S. rubicundulum	ruby meadowhawk	S5	0	0	0	0	0	3.5	0	0
S. semicinctum	band-winged meadowhawk	S4	0	P	6	0	0	1.8	0	0
S. vicinum	yellow-legged meadowhawk	S3	86.4	30.0	27.3	0	0	0	0	0
Tramea lacerata	black saddlebags	S5	11.3	9.2	3.0	10.0	3.0	7.1	10.9	15.0
T. onusta	red saddlebags	S5	0	6.9	0	3.2	0	0	3.2	4.3
Sum occurrences:	Damselfly		118.3	220.4	160.9	78.2	126.2	192.0	165.9	250.0
	Dragonfly		321.5	275.5	193.8	246.4	172.6	100.4	190.6	467.9
Species richness:	Damselfly		5	5	5	3	6	3	1	2
	Dragonfly		12	15	13	10	8	11	9	9
	Total		17	20	18	13	14	14	10	11

Table 3. Mean (± 1 SD) damselfly and dragonfly richness and abundance (individuals/transect) and ANOVA results from two vegetation zones at Camp Dodge, Johnston IA, USA. Conservation status species are those classified as vulnerable to extirpation or decline in the state of Iowa and include both damselflies and dragonflies. For each transect type, *n* = 4; for each *F*-test, df = 1,6.

| | | Transect type | | MS error | F | p |
		Mixed	Monotypic			
<u>All species</u>						
Richness:	Damselfly	4.5 (1.0)	3 (2.2)	2.8	1.6	0.2544
	Dragonfly	12.5 (2.1)	9.3 (1.3)	3.0	7.1	0.0369
	Overall	17 (2.9)	12.3 (2.1)	6.5	7.0	0.0384
Occurrences:	Damselfly	144.5 (60.8)	183.5 (51.9)	3200	0.95	0.3664
	Dragonfly	259.3 (53.5)	232.9 (161.5)	14,466	0.1	0.7665
<u>Conservation status species</u>						
	Richness	5.5 (2.5)	2 (2.0)	5.2	4.7	0.0723
	Occurrences	114.3 (68.9)	27.8 (10.6)	2,431	6.2	0.0477

and S4 status was 45% greater in the mixed versus monotypic vegetation, while the number of occurrences of these species was four times greater in the mixed than in monotypic vegetation (Tables 2 and 3).

The results of our other two analyses reinforced the above results. When the five transects sampled in both 2007 and 2008 were combined for analysis, overall richness was again notably higher in the mixed vegetation (approximately 35%), consistent for both dragonflies and damselflies (Table 4). Number of occurrences was also similar to the single-year results, with no differences in the number of occurrences evident among transects (Table 4).

Comparing odonate composition before and after reed canary grass invasion for one of our sites also reinforced the pattern we observed in our main study; monotypic dense vegetation in our study area did not support as rich an array of odonate species as did the diverse vegetation structure, particularly for damselfly species. Ten species of damselflies were recorded at the pothole site from 1995 to 1998 and only three from 2007 to 2008. Of the seven species that dropped out from the sample, five had S3 or S4 status (see Appendix 1). Nineteen dragonfly species were recorded from 1995 to 1998, eight of which were not recorded in 2007–2008. Five of these

eight had S3 or S4 status; however, three dragonfly S3 or S4 species were recorded in 2007–2008 that were not recorded earlier (Appendix 1).

There were two trends in species-specific differences between vegetation types. First, the high number of damselfly occurrences in the monotypic stands compared to the mixed vegetation stands in 2008 was driven by high numbers of only two common species, lyre-tipped spread wing (*Lestes unguiculatus*) and eastern forktail (*Ischnura verticalis*) (Table 2). Second, over the two years of study, the greater richness of the mixed vegetation included five odonate species of conservation or potential conservation concern (S3 or S4 status) not found in the structurally monotypic vegetation (Table 2): eastern red damsel (*Amphiagrion saucium*), citrine forktail (*Ischnura hastata*), lance-tipped darner (*Aeshna constricta*), dot-tailed whiteface (*Leucorrhinia intacta*), and yellow-legged meadowhawk (*Sympetrum vicinum*).

Discussion

Our results are the first that we know of to show the negative relationship between the two invasive plant species reed canary grass and cattail and odonate species richness, particularly for those species with more specialized habitat requirements. Our comparison of one monotypic transect site with

data collected in the 1990s before invasion by reed canary grass reinforces the observation of a negative relationship between monotypic structure and odonate species of statewide conservation concern or potential concern.

The monotypic vegetation we studied tended to have very high occurrences of generalist odonate species, particularly eastern forktail, lyre-tipped spreadwing, eastern pondhawk (*Erythemis simplicicollis*), twelve-spotted skimmer (*Libellula pulchella*) and blue dasher (*Pachydiplax longipennis*). Eastern forktails, for example, occur in every Iowa county and use a wide variety of aquatic habitats (Cruden and Gode 2000, IOS 2005, Westfall and May 2006). Similarly, eastern pondhawks and blue dashers occur in every Iowa county and also use a wide variety of wetland habitats with or without fish (Cruden and Gode 2000, Dunkle 2000, IOS 2005). These species also qualify as pioneering species, as one characteristic of pioneers is the wide range of habitats that are acceptable to them (Corbet 1999). In addition, pioneering species appear to lack preference for plant types or even prefer habitats that lack aquatic plants altogether (Corbet 1999).

In contrast, the species that were restricted to the mixed vegetation tended to have more exacting habitat requirements. These species also

Table 4. Mean (± 1 SD) damselfly and dragonfly richness and abundance (individuals/transect) and ANOVA results (df = 1,3 for all tests; *n* = 2 for mixed transects, *n* = 3 for the monotypic transects) from two vegetation zones averaged over two sampling years at Camp Dodge, Johnston IA, USA.

		Transect type		MS error	*F*	*p*
		Mixed	Monotypic			
Richness:	Damselfly	5.8 (0.35)	3.2 (0.77)	0.4	18.6	0.0230
	Dragonfly	13.5 (2.83)	9.2 (0.69)	3.0	7.4	0.0722
	Overall	19.3 (3.2)	12.4 (0.93)	4.0	14.4	0.0321
Occurrences:	Damselfly	232.5 (116.7)	140.3 (84.4)	9,287	1.1	0.3717
	Dragonfly	290.5 (128.0)	177.8 (58.3)	7,729	2.0	0.2550

tend to have a sparser distribution in the state than the generalist and pioneering species (IOS 2005). These included eastern red damsel, azure bluet (*Enallagma apsersum*), citrine forktail, lance-tipped darner, calico pennant (*Celithemis elisa*), dot-tailed whiteface, variegated meadowhawk (*Sympetrum corruptum*) and yellow-legged meadowhawk. For example, both the eastern red damsel and citrine forktail are uncommon in Iowa and require dense stands of bulrush or spike-rush (*Eleocharis* spp.) associated with seeps or still water (Cruden and Gode 2000, DuBois 2005, Westfall and May 2006). Similarly, calico pennants prefer edges with shallow water and emergent vegetation such as rushes (Mead 2003).

Other lines of evidence similarly point to the importance of structural complexity as an important component of odonate habitat. An early compilation and study of Iowa odonates notes the association between species and varied structural components of the habitat (Whedon 1912). For example, he writes that hundreds of yellow-legged meadowhawks "were found among the low shrubs and brush at the margins of woods" near the Little Sioux River, while "myriads of individuals" of lyre-tipped spreadwings were found at " a small marshy pond grown up to Cattails, Sedges and Bulrushes . . . every Bulrush stem was covered from ground to tip" (Whedon 1912). A study in Ohio showed that restored wetland complexes can support odonate species with specialized habitat requirements, such as the eastern red damselfly, calico pennant,

band-winged meadowhawk (*Sympetrum semicinctum*), and yellow-legged meadowhawk, if they include a range of native wetland habitats (sedge meadows, fens, marshes, and ponds) that are not associated with monotypic shoreline vegetation dominated by a single species (Roush and Anon 2003).

The importance of the physical structure of odonate habitat has been established across many other habitat types and regions (Westfall and May 2006), including bottomland hardwoods in North America (Bried and Ervin 2005), riverine habitats in South Africa (Clark and Samways 1996), mountain ponds in Italy (Carchini et al. 2005), and shallow lakes and newly created wetlands in Austria (Chovanec and Raab 1997, Schindler et al. 2003).

Varied physical structure appears to promote odonate species richness for a number of possible reasons. Dense stands may impair flight and reduce the growth of submerged and floating vegetation (Moore 1991). This is congruent with the very low cover of forbs we observed in the monotypic stands. Diversity in physical structure provides a diversity of oviposition sites (Westfall and May 2006). For example, three species of dancers (*Argia* spp.) in Oklahoma coexisted by differing their oviposition sites, one ovipositing on a floating aquatic species and two other ovipositing at two different depths on roots of willow (*Salix* spp.) (Bick and Bick 1972). Habitat can be partitioned both temporally and structurally in other ways. For example, spreadwing (*Lestes*) species have been shown to coexist, with

common spreadwing (*L. disjunctus*) perching in full sun on low grassy vegetation and emerald spreadwing (*Lestes dryas*) found in areas dominated by shrubs (McKay and Herman 2008). A single species may also use distinct structural components of the habitat, for example, meadows for nocturnal roosting and reeds and bushes for mating, seeking, and pairing (Corbet 1999). Opening up dense vegetation and creating structurally diverse shoreline vegetation are both key to habitat management for threatened dragonflies in central Europe (Schmidt 1995).

Our study was not designed to separate plant structure from plant species richness or other measures of diversity. However, both our monotypic and mixed structural sites included transects that ranged from high to low plant species richness. This suggests that, irrespective of the number of species present, it was structural diversity rather than plant species richness that was associated with higher odonate species richness. However, plant species composition and overall diversity metrics may still be important, and these relationships deserves further study. For example, the presence of specific aquatic plant species has been associated with the successful colonization of some odonate species in newly created habitat (Voshell and Simmons 1978), and, as noted above, some odonate species oviposit on specific plant species (Gibbons et al. 2002).

The importance of structure does not preclude the importance of other habitat variables, however. Other

factors may also be important components of habitat, including hydrology, water flow, larval substrate, oxygen content and other water chemistry, predators (especially fish), and terrestrial vegetation (Corbet 1999, Westfall and May 2006). Odonates are among a group of wetland macroinvertebrates that appear to be especially sensitive to turbidity as larvae in Midwestern wetlands (Stewart and Downing 2008), although the wetlands included in our study Camp Dodge study are surrounded by perennial grasslands and shrublands and are generally not subject to agricultural and urban runoff associated with turbidity.

Landscape-level factors, particularly habitat connectivity and dispersal limitation, are also important in governing odonate diversity and the composition of species assemblages (Pither and Taylor 1998, McCauley 2006, 2007). A useful distinction may exist between overall habitat and microhabitat (Corbet 1995). Habitat is considered the total ecosystem and microhabitat the portion of the habitat needed by a specific life stage at a specific time (Corbet 1995), and where the structure of the habitat serves as the cue for initial habitat recognition (Corbet 1999). The interplay of all these factors deserves greater attention, particularly for restoration sites.

In conclusion, this research is highly relevant to management of prairie pothole wetlands as wildlife habitat, particularly newly restored pothole wetlands. Dense stands of invasive reed canary grass and cattail are major causes of wetland homogenization throughout the prairie pothole region. Our study suggests that without active vegetation management, these wetlands also may not provide suitable habitat for many species of odonates, particularly those of conservation concern. Recent research suggests that, until effective and affordable control methods are developed for reed canary grass, priority may best be given to controlling it at sites with less than 25% reed canary grass cover (Annen

et al. 2008). In contrast, cattail control methods are well-developed and can be undertaken at a reasonable cost and effort in restored and native wetlands (Beule 1979, Grace and Harrison 1986). Moreover, success of wetland restorations and management of native remnants will be better evaluated if their use by birds and invertebrates is monitored regularly. Odonates, because of their sensitivity to habitat structure and ease of identification, appear to be ideal taxa for this purpose.

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Appendix 1. Comparison of damselfly and dragonfly species recorded during two sample periods over ten years at a native prairie pothole site at Camp Dodge, Johnston, Iowa, USA. Vegetation consisted of diverse sedge meadow in 1995–1998 but converted largely to reed canary grass (*Phalaris arundinacea*) by the second survey in 2007–2008. CS = conservation status statewide: S3 = vulnerable to extirpation; S4 = uncommon, vulnerable to decline; S5 = common and secure.

Scientific Name	Common name	CS	1995	1996	1997	1998	2007	2008
Damselflies								
Coenagrion resolutum	taiga bluet	S3			X	X		
Enallagma aspersum	azure bluet	S3/S4				X		
E. civile	familiar bluet	S5	X	X		X		
E. geminatum	skimming bluet	S4				X		
E. hageni	Hagen's bluet	S5		X		X		
Ischnura verticalis	eastern forktail	S5	X	X	X	X	X	X
Lestes disjunctus	common spreadwing	S3				X		
L. rectangularis	slender spreadwing	S4		X	X		X	X
L. unguiculatus	lyre-tipped spreadwing	S5	X	X	X	X	X	X
Nehalennia irene	sedge sprite	S3				X		
Dragonflies								
Aeshna constricta	lance-tipped darner	S3	X	X				
Aeshna interrupta lineata	variable darner	S2			X			
Anax junius	common green darner	S5	X	X	X	X	X	X
Celithemis elisa	calico pennant	S3					X	
Celithemis eponina	halloween pennant	S4						X
Epitheca cynosura	common baskettail	S4		X				
Erythemis simplicicollis	eastern pondhawk	S5	X	X	X	X	X	X
Leucorrhinia intacta	dot-tailed whiteface	S4		X	X	X		
Libellula luctuosa	widow skimmer	S5	X	X	X	X	X	X
L. pulchella	twelve-spotted skimmer	S5	X	X	X	X	X	X
Pachydiplax longipennis	blue dasher	S5		X	X	X		
Pantala flavescens	wandering glider	S4						X
Perithemis tenera	eastern amberwing	S5				X	X	
Plathemis lydia	common whitetail	S5	X	X	X	X		
S. costiferum	saffron-winged meadowhawk	S3	X		X	X	X	X
S. internum	cherry-faced meadowhawk	S4	X	X	X		X	X
S. obtrusum	white-faced meadowhawk	S5		X	X	X	X	X
S. semicinctum	band-winged meadowhawk	S3/S4				X		X
S. rubicundulum	ruby meadowhawk	S5	X	X	X	X	X	
S. vicinum	yellow-legged meadowhawk	S3				X		
Tramea lacerata	black saddlebags	S5	X	X	X	X	X	X
T. onusta	red saddlebags	S5			X			