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Odonata species diversity, distributions, and status in a rare sand prairie-savanna wetscape

https://doi.org/10.23797/2159-6719 24 15

Received: 4 January 2021 - Accepted: 6 April 2021 - Published: 15 November 2021

Abstract: Inland sand areas scattered across the North American eastern deciduous forest and western tallgrass prairie ecotone are known for supporting pyrogenic early-successional vegetation and specially adapted terrestrial faunas. Many of these globally and regionally rare systems contain functionally connected wetland networks ("wetscapes") potentially important for aquatic insects. Sampling adults, nymphs, and exuviae in a remnant sand prairie-savanna wetscape in Illinois, USA, I assessed odonate species diversity (alpha, gamma, beta), distributions (spatial, temporal, abundance), and rarity status. In one field season (12 sites, 12 visits) I found more than a third of Illinois odonate species and close to half of the state's lentic breeding odonates, including a new state record (Ervthemis vesiculosa). Richness averaged 25.8 species per site, reducing to 12.4 species with removal of nonbreeding occurrences. Three sites including a shrub swamp, beaver pond, and forested vernal depressions complex made significant contributions to beta diversity, dependent on general versus breeding occurrences. Majorities of Anisoptera species (70%) and Zygoptera species (53%) bred at three or fewer sites. Eight species flew during all or most of the study period (late May to early Oc-tober) whereas 14 species were detected on a single survey. Status classification derived from the observed spatial, temporal, and abundance distributions resulted in 24 common or very common species, 20 uncommon or rare species, and 10 vagrants across the wetscape. These context-specific classifications may be combined with diversity and breeding patterns and other information in wetscape prioritization schemes.

Keywords: conservation; dragonfly; North America; rarity; species distributions; species diversity; wetlands

Introduction

Inland sand areas commonly referred to as pine barrens, oak savannas, and sand prairies are found scattered across the eastern deciduous forest and western tallgrass prairie ecotone of the U.S. northeast, northern Great Lakes, and upper Midwest. They are typically characterized as pyrogenic earlysuccessional vegetation communities threatened by fire suppression (Nowacki & Abrams, 2008). Collectively the sand areas, some of which are protected and managed, contribute unique prairie, savanna, and shrubland plant diversity across the region (Latham, 2003; Leach & Givnish, 1999). The vegetation composition and structure in turn promotes a specially adapted terrestrial insect fauna dependent on open canopies, exposed sandy areas, and specific floral resources (Barber, 2015; Lettow et al., 2018; Panzer & Schwartz, 1998; Schlesinger & Novak, 2011; Wagner et al., 2003; Wallner et al., 2013).

There is comparatively scarce knowledge of the aquatic insects of inland sand areas across the region. Long-term insect surveys of prairies and savannas in the Chicago region comprehensively documented many terrestrial groups but largely missed the aquatic taxa (Panzer et al., 2010). In postglacial sand areas, abundant and distinctive wetlands may form in the swales amid rolling dune topography (Bried & Edinger, 2009; Phillippe et al., 2011). Often the wetlands are closely clustered and separated by open landcover, creating functionally connected waterscapes (or "wetscapes" referring

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specifically to wetlands) important for aquatic insect conservation (Samways, 2020). Odonata were surveyed in a northwest Indiana oak savanna (Smolka et al., 1999) and at several pine-oak barrens in New York State (Bried et al., 2015), but otherwise there seems to be scarce systematic inventory of odonates in sand area wetscapes of the U.S. post-glacial region.

I had the opportunity in 2020 to survey odonates in one of the best quality sand area remnants in Illinois (Phillippe et al., 2008). Historically this area had sporadic odonate records from general entomological inventories (by R. Panzer, the Illinois Natural History Survey, and amateur enthusiasts) but no standardized targeted searches. My objective was to document odonate species diversity, distribution, and rarity status across the inland sand prairie-savanna wetscape. Sampling adults, nymphs, and exuviae, I assessed gamma, alpha, and beta taxonomic diversity and used the observed spatial, temporal, and abundance distributions to estimate rarity status of each species for the study area. I conclude by discussing how diversity and breeding patterns and context-specific rarity status may be used to prioritize sites for protection and conservation management.

Materials and methods

Study area

Braidwood Sands Area (BSA) is found in the southwestern corner of Will County (Figure 1, 41.261°N, -88.179°W) in northeastern Illinois near the western terminus of the Kankakee River watershed and sand deposits (Phillippe et al., 2011). The BSA encompasses the 125-ha Braidwood Dunes and Savanna Nature Preserve (BDN or 'Braidwood Dunes'), the 220-ha Sand Ridge Savanna Nature Preserve (SRN or 'Sand Ridge'), and the 225-ha Kankakee Sands Preserve (KSP or 'Kankakee Sands') owned and managed by the Forest Preserve District of Will County (Figure 1). These preserves contain remnants of dry to dry-mesic sand savanna and dry, mesic, and wet-mesic sand prairie, along with sedge meadows, marshes, shrub swamps, and shallow depressions. Examples of characteristic plants of the BSA include black oak (*Quercus velutina*) and white oak (*Q. alba*) in the savanna-woodland overstory, little bluestem (*Schizachyrium scoparium*) and gray goldenrod (*Solidago nemoralis*) in the sand prairies, and tussock sedge (*Carex stricta*), woolgrass (*Scirpus cyperinus*), and Virginia iris (*Iris virginica*) in the wetlands (Phillippe et al., 2008).

Although much of the BSA waterscape was drained for agriculture by the late 1800s, many potential Odonata sites exist among the post-glacially formed interdunal swales and the shallow ponds created by beavers or humans. Major aquatic features immediately adjacent to BSA include the Kankakee river to the northeast (visible in Figure 1), abandoned strip-mining ponds just north of BDN and west of KSP (visible in Figure 1), and a series of fishing lakes and industrial cooling ponds to the south-southwest; farther southwest lies a large system of water impoundments associated with the Mazon river and the Mazonia-Braidwood State Fish and Wildlife Area.

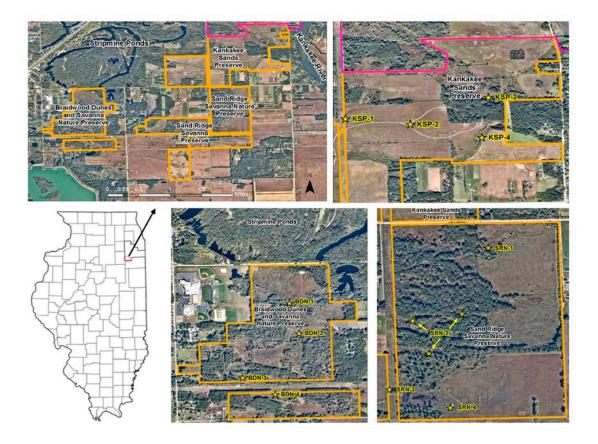


Figure 1. Study sites in the 2020 Odonata survey of the Braidwood Sands Area, located in the southwest corner of Will County in northeastern Illinois, USA. See text and Table 1 for study site information.

Study sites

I concentrated searches on a dozen wetland sites (Figure 1), four in each preserve representing the major wetland types and available breeding habitat across the BSA. I classified sites as marsh, sedge meadow, wetland pond, wet meadow/shrubland mix, shrub swamp, or forested vernal depression (Table 1) based primarily on hydrology, geomorphic position, and characteristic vegetation, as described in the Illinois natural community classification system (White, 1978, pp. 310–405) and applied by the Illinois Natural History Survey Wetland Science Program. In 2020, northeastern Illinois and Will County received above-average rainfall through June changing to below-normal rainfall or moderate drought from late July through August (U.S. Drought Monitor, https://droughtmonitor.unl.edu/).

Table 1. Braidwood Sands Area study site information. Hydroperiod: 'short' – early season (June/July) inundation only, 'long' – early to late season (August/September) inundation, 'permanent' – inundation throughout the 2020 survey. Surface water pH and salinity (ppt): means (SD) of three location measurements (PC60 Premium Multi-Parameter Tester, Apera Instruments, LLC, Columbus, Ohio, www.aperainst.com) repeated 14–17 June and 28–31 July 2020.

Preserve	Site	Wetland type	Hydroperiod	pН	Salinity
Braidwood Dunes	BDN-1	shrub swamp	permanent	6.93 (0.25)	0.07 (0.02)
	BDN-2	wet meadow/ shrubland	short	6.63 (0.25)	0.06 (0.02)
	BDN-3	sedge meadow	permanent	7.25 (0.76)	0.09 (0.01)
	BDN-4	sedge meadow	long	6.35 (0.19)	0.04 (0.01)
Kankakee Sands	KSP-1	marsh	short	7.80 (1.35)	0.06 (0.02)
	KSP-2	wetland pond	long	8.55 (1.18)	0.04 (0.01)
	KSP-3	sedge meadow	long	6.45 (0.14)	0.05 (0.01)
	KSP-4	wetland pond	permanent	7.68 (0.34)	0.22 (0.01)
Sand Ridge	SRN-1	marsh	long	7.08 (0.24)	0.14 (0.02)
	SRN-2	vernal depressions	short	no water	no water
	SRN-3	wetland pond	permanent	7.40 (0.60)	0.08 (0.01)
	SRN-4	marsh	long	7.39 (0.42)	0.12 (0.03)

Marshes and sedge meadows were densely vegetated but varied in their dominant species including sedges (Bolboschoenus fluviatilis, Carex lacustris, C. pellita, C. stricta, Eleocharis obtusa, Scirpus cyperinus, S. tabernaemontanii), grasses (Calamagrostis canadensis, Glyceria septentrionalis), other monocots (Iris virginica, Juncus effusus, Sparganium eurycarpum), and herbaceous dicots (Persicaria amphibia, P. punctata, Ranunculus flabellaris, Sagittaria latifolia). Most marshes and sedge meadows experienced major drawdown starting late July, and by mid August most sites had dried; two refilled partially in September. The wetland ponds contained sparse vegetation cover (during high water) except at the edges (e.g. Carex spp., Eleocharis obtusa, Leersia oryzoides, Persicaria hydropiper) and in localized patches of true aquatic plants (e.g. Lemna sp., Potamogeton foliosus). These ponds were created by humans (KSP-2), beavers (KSP-4), or both influences (SRN-4); KSP-2 included four small dugouts intersected by the main preserve trail. The shrub swamp (BDN-1) was thicketed by buttonbush (Cephalanthus occidentalis) and remained flooded throughout the study. The wet meadow/shrubland (BDN-2) contained a roughly even mix of buttonbush and herbaceous dominants (Leersia oryzoides, Persicaria hydropiperoides, Scirpus cyperinus) and was mostly drained by mid July. The vernal depressions complex (SRN-2) contained abundant steeplebush (Spiraea tomentosa) and woolgrass and became dry by the first larval collection (see below) in mid June.

Fish, water pH, and salinity factors can strongly influence odonate diversity and distributions (Arrowsmith et al., 2018; Crumrine et al., 2008; Uboni et al., 2020). All sites were fishless except KSP-4 where beavers dammed a stream flowing into the nearby Kankakee river (Figure 1). Five sites were circumneutral (pH 6.5–7.5), three leaned more alkaline, and two more acidic (Table 1). Salinities were generally similar across sites but relatively high at KSP-4 and to lesser extents at SRN-1 and SRN-4 (Table 1).



Odonata survey

Adult and exuviae surveys began May 22 and 24 returning weekly over the first month and then biweekly (±3 d) through mid September, finishing October 6–7 after recording few species, low numbers, and no tenerals. Each survey event required two days, visiting about half the sites each day on a rotating basis over the study. At each site visit I spent 30 min observing adults and 30 min searching for exuviae (in emergent vegetation) between 0930–1700 hr along fixed meandering routes through major vegetation zones. Adult surveys captured from ~50% to 100% of the wetland area (including edges) depending on size; exuviae searches covered a much more limited area. I additionally noted species in the uplands while travelling to and from sites. I enumerated adults by species using categories of 1, 2–5, 6–20, 21–50, and >50 individuals, with full tallies at three sites (BDN-3, KSP-3, SRN-4) to assess total and relative abundance distributions. Adult counts along with the presence of exuviae, nymphs, tenerals, pairing, and oviposition attempts were used to distinguish breeding occurrences across sites following Bried et al. (2015). I identified adults by sight or in hand, referring to Paulson (2011) and taking specimens/photos as needed. I identified dragonfly exuviae to species (using Needham et al., 2014; Tennessen, 2019) in the field or lab and damselfly exuviae to genus or species (using Westfall & May, 2006) in the lab, keeping specimens of most taxa.

I collected nymphs June 14–17 and July 28–31. Each site had five collecting stations spread at least 10 m apart and stratified by open water and major vegetation zones. At each station I performed five 1-m sweeps of a D-frame dipnet (1 mm mesh). I sorted odonates onsite and deposited all identifiable (late instar) nymphs into water-filled 50-mL Falcon® tubes or Whirl-Pak® bags, transferring to 70% ethanol for storage. I relied on the same taxonomic keys as for exuviae. I did not collect at the vernal depressions (SRN-2), because surface water disappeared before the first event. Also, drawdowns limited the second collection to three stations at KSP-1 and four stations at KSP-2.

Diversity, distributions, and rarity status

I compared the BSA odonate checklist to the Illinois odonate checklist on Odonata Central before and after removing lotic and quasi-lotic species due to scarcity of lotic habitat at BSA. The mean and range alpha richness for Anisoptera, Zygoptera, and Odonata (suborders combined) is reported based on breeding occurrences and general (breeding + nonbreeding) occurrences. I noted any singleton (unique) species occurrences and computed local contributions to beta diversity (LCBD) following Legendre and De Cáceres (2013). Each site's LCBD was calculated on Ochiai-transformed incidence data using the beta.div function in the adespatial package (Dray et al., 2020). The LCBD values equaled row (sites) sums of squared deviations from species means in the incidence matrix, divided by the total sum of squares (Legendre & De Cáceres, 2013). Larger and significant (tested using 999 permutations) LCBD values indicate sites with relatively unique community composition.

Spatial distributions were summarized from the general and breeding incidence matrix, and temporal distributions by showing the detection history of each species. I plotted total and relative abundance distributions for nymphs, exuviae, and adults of species shared across the abundance focal sites (BDN-3, KSP-3, SRN-4), and additionally plotted each focal site's total adult count across surveys. Counts of males and females were combined unless otherwise noted.

I used the distribution results to classify the BSA rarity status of each species as very common, common, uncommon, rare, or vagrant. Very common species had high incidence rates (general and breeding) and were abundant in one or more life stages at many sites and during all or most of the study period. Common species were generally abundant as adults at multiple sites but were often scarce as nymphs and exuviae and tended to be more ecologically specialized than very common species. Uncommon species were never found as nymphs and typically in low adult numbers, scattered among sites and over surveys, although some received a high count at one site or visit. Rare species were seldom observed and always scarce as adults (no nymphs or exuviae collected), in many cases sighting just a lone individual. Vagrant species were like rare species except could not be presumed as resident due to lack of breeding habitat and breeding occurrences.

Results

Diversity

I observed 30 dragonfly species and 24 damselfly species across the Braidwood Sands Area in 2020, including eight dragonflies and 16 damselflies that had not been reported previously at BSA (Table 2). This total represents more than a third (36%) of the odonate fauna known throughout Illinois (Odonata Central, https://www.odonatacentral.org/, accessed 06-Dec-2020), and jumps to almost half the fauna if we ignore lotic and quasi-lotic species given the primarily lentic wetscape.

Table 2. Odonata checklist (nomenclature follows Paulson, 2018) for the Braidwood Sands Area (BSA) in 2020. All species were observed as adults; those additionally observed as exuviae and/or nymphs are indicated by an 'X'. Species in bold font were not previously documented at BSA (*Erythemis vesiculosa* is new for Illinois). See text for detailed information on BSA rarity status.

Taxonomy	Exuvia	Nymph	BSA status
Anisoptera			
Aeshnidae			
Aeshna constricta Say, 1839			rare
Aeshna verticalis Hagen, 1861			rare
Anax junius (Drury, 1773)	X	X	very common
Epiaeschna heros (Fabricius, 1798)	X		uncommon
Gomphidae			
Dromogomphus spinosus Selys, 1854			vagrant
Gomphurus vastus Walsh, 1862			vagrant
Corduliidae			
Epitheca costalis (Selys, 1871)			uncommon
Epitheca princeps Hagen, 1861			rare
Libellulidae			
Celithemis elisa (Hagen, 1861)			vagrant
Celithemis eponina (Drury, 1773)	X		common
Erythemis simplicicolis (Say, 1839)	X	X	very common
Erythemis vesiculosa (Fabricius, 1775)			vagrant
Leucorrhinia intacta (Hagen, 1861)	X		uncommon
Libellula incesta Hagen, 1861			rare
Libellula luctuosa Burmeister, 1839		X	common
Libellula pulchella Drury, 1773	X		very common
Libellula semifasciata Burmeister, 1839	X		uncommon
Pachydiplax longipennis (Burmeister, 1839)	X	X	very common

Taxonomy	Exuvia	Nymph	BSA status
Pantala flavescens (Fabricius, 1798)			uncommon
Pantala hymenaea (Say, 1839)			vagrant
Perithemis tenera (Say, 1839)			common
Plathemis lydia (Drury, 1773)			common
Sympetrum ambiguum (Rambur, 1842)	X		uncommon
Sympetrum internum Montgomery, 1943			rare
Sympetrum obtrusum (Hagen, 1867)			uncommon
Sympetrum rubicundulum (Say, 1839)	X		common
Sympetrum vicinum (Hagen, 1861)	X	X	very common
Tramea carolina (Linnaeus, 1763)	X		common
Tramea lacerata Hagen, 1861	X	X	common
Tramea onusta Hagen, 1861			rare
Zygoptera			
Calopterygidae			
Calopteryx maculata (Beauvois, 1805)			uncommon
Hetaerina americana (Fabricius, 1798)			vagrant
Coenagrionidae			
Argia apicalis (Say, 1839)			vagrant
Argia fumipennis (Burmeister, 1839)			uncommon
Argia moesta (Hagen, 1861)			vagrant
Enallagma antennatum (Say, 1839)			vagrant
Enallagma aspersum (Hagen, 1861)			common
Enallagma basidens Calvert, 1902			uncommon
Enallagma civile (Hagen, 1861)			common
Enallagma exsulans (Hagen, 1861)			uncommon
Enallagma geminatum Kellicott, 1895			common
Enallagma signatum (Hagen, 1861)			uncommon
Ischnura hastata (Say, 1839)		X	common
Ischnura posita (Hagen, 1861)	X	X	very common
Ischnura ramburii (Selys, 1850)			uncommon
Ischnura verticalis (Say, 1839)	X	X	very common
Nehalennia irene (Hagen, 1861)			common

Taxonomy	Exuvia	Nymph	BSA status
Lestidae			
Lestes australis Walker, 1952	X		rare
Lestes congener Hagen, 1861		X	common
Lestes dryas Kirby, 1890	X		common
Lestes eurinus Say, 1839			vagrant
Lestes forcipatus Rambur, 1842	X		common
Lestes rectangularis Say, 1839	X	X	very common
Lestes unguiculatus Hagen, 1861			common

Alpha richness based on general species occurrences (breeding + nonbreeding) averaged 25.8 species per site (15.8 dragonflies, 10.0 damselflies) in a range of 19 to 33 species (12 to 19 dragonflies, 6 to 14 damselflies). Across sites, breeding occurrences comprised fewer than half ($\bar{x} \pm SD = 47.8\% \pm 10.0\%$) of the general occurrences for odonates; damselflies had a higher percentage (54.9% \pm 14.0%) than dragonflies (43.5% \pm 12.1%). Retaining only breeding occurrences, the richness levels dropped to 12.4 species per site (6.8 dragonflies, 5.6 damselflies) in a range of 7 to 19 species (4 to 10 dragonflies, 3 to 9 damselflies). The maximum alpha richness from breeding occurrences (19 species at KSP-3) equaled the minimum richness from general occurrences (19 species at BDN-1). These results indicate that reported species richness levels may reduce drastically if general occurrences are filtered to breeding occurrences.

Singleton occurrences came from BDN-3 (Erythemis vesiculosa, Tramea onusta), BDN-4 (Lestes eurinus), KSP-2 (Pantala hymenaea), KSP-4 (Calopteryx maculata), and SRN-3 (Sympetrum internum). Of these only Calopteryx maculata provided a definite breeding occurrence. Four other damselflies (Hetaerina americana, Argia fumipennis, Enallagma antennatum, E. exsulans) were seen exclusively at the KSP-4 stream outlet. Argia apicalis and A. moesta, although not observed at the study sites, were documented from single locations in Braidwood Dunes and Kankakee Sands, respectively. Similarly, Celithemis elisa and Dromogomphus spinosus were recorded offsite exclusively in Sand Ridge.

Three sites (BDN-1, KSP-4, SRN-2) showed relatively unique species composition and greater contributions to overall beta diversity (Table 3). The forested vernal depressions complex (SRN-2) contained among the fewest species but also a distinctive breeding assemblage of *Sympetrum* and *Lestes* adapted to short hydroperiods, including the only breeding occurrence for *S. obtrusum*. This site was also unique for lacking the most common BSA species (see below), including the only absences of *Anax junius* and *Libellula pulchella* and the only non-breeding occurrences of *Erythemis simplicicolis*, *Pachydiplax longipennis*, *Ischnura posita*, and *I. verticalis*. The BDN-1 shrub swamp was distinguished by a paucity of *Lestes* and damselflies in general, and the KSP-4 beaver pond by the only breeding occurrences of *Calopteryx maculata* and *Enallagma signatum* and the only nonbreeding occurrence of *Lestes rectangularis*.

Table 3. Local contributions to beta diversity (row sums of squared deviations from the species means in the incidence matrix, divided by the total sum of squares) and their significance (*P < 0.05, **P \leq 0.001) indicating sites with relatively unique community composition, repeated for general and breeding occurrences of dragonflies and damselflies.

Site	Anisopter	a	Zygoptera	Zygoptera		
	General	Breeding	General	Breeding		
BDN-1	0.101	0.035	0.130*	0.053		
BDN-2	0.089	0.054	0.072	0.049		
BDN-3	0.101	0.049	0.055	0.071		
BDN-4	0.040	0.073	0.051	0.060		
KSP-1	0.040	0.053	0.081	0.053		
KSP-2	0.077	0.098	0.119	0.103		
KSP-3	0.074	0.074	0.057	0.069		
KSP-4	0.085	0.127	0.113	0.171*		
SRN-1	0.108	0.035	0.085	0.062		
SRN-2	0.127*	0.248**	0.107	0.172*		
SRN-3	0.067	0.107	0.063	0.079		
SRN-4	0.092	0.049	0.066	0.057		

Distributions

Anisoptera species were detected at 6.8 sites (3.9 SD) and Zygoptera species at 6.7 sites (3.5 SD) on average. Removal of nonbreeding occurrences drops these rates to 3.0 sites (3.7 SD) for Anisoptera and 3.7 sites (3.8 SD) for Zygoptera. The site-species matrix was more than half filled by Anisoptera (56.3% occupied cells) and Zygoptera (55.6%) general occurrences, reducing to 35.0% and 37.2% respectively for Anisoptera and Zygoptera breeding occurrences (Figure 2). Eight Anisoptera and three Zygoptera lacked breeding occurrences. The relatively balanced distributions of general occurrences shifted to low-biased distributions of breeding occurrences, with 70% of Anisoptera species and 53% of Zygoptera species found to breed at just 1–3 sites (Figure 2).

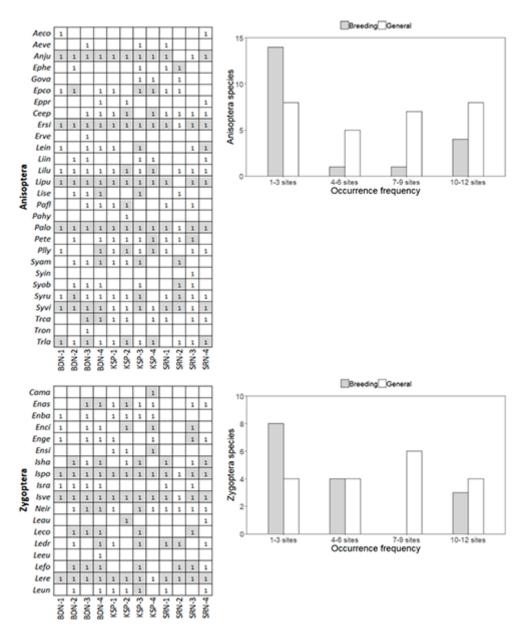


Figure 2. Incidence matrix and frequency distribution for dragonflies (Anisoptera) and damselflies (Zygoptera). "1" indicates presence and gray shading indicates breeding occurrence. Site names correspond with Table 1 and Figure 1. Species are listed by the first two letters of their genus and specific epithet (e.g. "Aeco" for Aeshna constricta), in the same order shown in Table 2. Eight of the 54 total species are excluded because they were never seen at the sites.

Adults of *Anax junius*, *Ischnura posita*, and *I. verticalis* were found over the entire survey period (Figure 3). Four species (*Enallagma aspersum*, *Erythemis simplicicolis*, *Libellula pulchella*, *Pachydiplax longipennis*) were seen flying on all but the final survey and *Lestes rectangularis* on all but the first survey. At the other extreme, 14 species (9 Anisoptera, 5 Zygoptera) were detected on a single survey. Several species (*Epiaeschna heros*, *Leucorrhinia intacta*, *Lestes dryas*) were observed exclusively during the early surveys whereas others first appeared, or suddenly became common, during the mid to late period (*Sympetrum ambiguum*, *S. obtrusum*, *S. vicinum*, *Lestes congener*, *L. unguiculatus*).

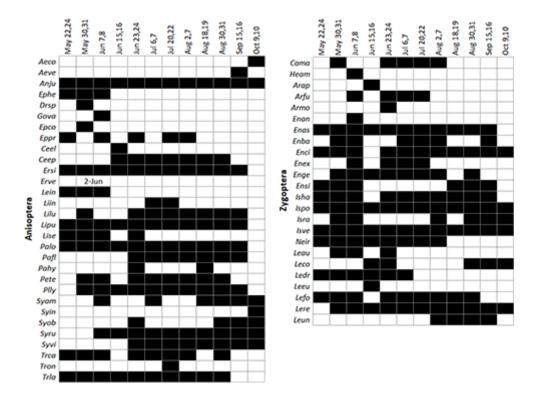


Figure 3. Detection histories (black cells) of all 30 dragonfly (Anisoptera) species and 24 damselfly (Zygoptera) species observed (combining adults, nymphs, and exuviae) throughout the Braidwood Sands Area in 2020. Species are listed by the first two letters of their genus and specific epithet, in the same order shown in Table 2. Erythemis vesiculosa (Erve) was detected between the second and third surveys (on June 2nd) as indicated.

Using shared species across three abundance focal sites, total counts for adults, nymphs, and exuviae were highest at BDN-3 (Figure 4). This site contained the adult peak count (06-Jul in Figure 4A) and the highest adult count of a species (*Pachydiplax longipennis* in Figure 4B); SRN-4 contained the second highest adult count of a species (*Ischnura posita*, males only). Total counts of exuviae and nymphs were similar between KSP-3 and SRN-4, but the relative counts of species differed. More *Anax junius* exuviae and nymphs, *Pachydiplax longipennis* nymphs, and *Sympetrum vicinum* exuviae were collected at KSP-3 than SRN-4, whereas more *Erythemis simplicicolis* exuviae and nymphs, *Ischnura* nymphs, and *P. longipennis* exuviae were collected at SRN-4 than KSP-3 (Figure 4C, 4D).

I used the distribution results (Figures 2–4) to classify the BSA rarity status of all 54 species observed, resulting in 8 very common, 16 common, 13 uncommon, 7 rare, and 10 vagrant species (Table 2). Details are given in the following accounts.

Very common species

The most common odonates at BSA in 2020 were *Pachydiplax longipennis*, *Erythemis simplicicolis*, *Ischnura posita*, and *I. verticalis*. I found these species at every site and confirmed their successful reproduction everywhere except SRN-2 (Figure 2). These species flew during all or most of the survey period (Figure 3) and were generally abundant in multiple life stages (Figure 4). *Lestes rectangularis*, the most common spreadwing, appeared at every site and across all surveys except the first (Figures 2, 3). The remaining very common species included large-bodied migratory *Anax junius* and *Libellula pulchella* showing broad spatial and temporal distributions (Figures 2, 3). *Anax junius*

was most abundant in pre-adult stages (Figure 4), possibly a function of its migratory behavior. *Libellula pulchella* adults were prevalent at most sites and appeared to increase during August and September as *P. longipennis* and *E. simplicicolis* adult numbers subsided. *Sympetrum vicinum* occurred at every site and accumulated high numbers of adults and exuviae (e.g. Figure 4) within a truncated flight/emergence period (Figure 3); I did not find mature adults of *S. vicinum* until August.

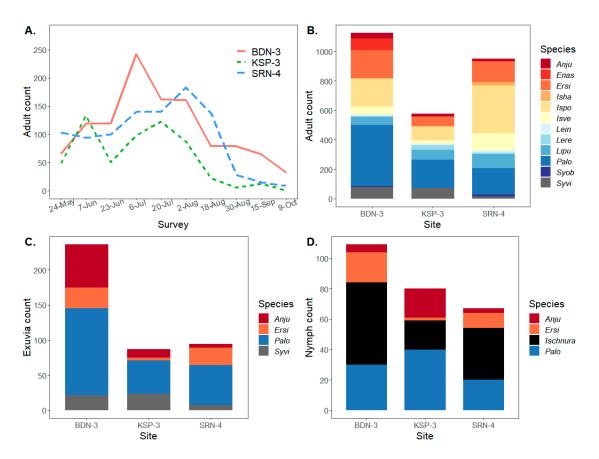
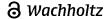


Figure 4. Total and relative abundance distributions for species shared at three focal sites, including counts of adults by sites and surveys (A) and by sites and species (B), and counts of exuviae (C) and nymphs (D) by sites and species. Species are listed by the first two letters of their genus and specific epithet. Adult males and females were combined; females of *Ispo* and *Isve* were not always separable and were therefore counted only when found in tandem with males. *Ischnura* nymphs consisted mostly of *I. posita* and *I. verticalis*; I collected only a couple *I. hastata* nymphs and no *I. ramburii* nymphs.

Common species

Although I did not conduct standardized surveys in the uplands, adults of *Celithemis eponina*, *Libellula luctuosa*, and *Plathemis lydia* seemed more common in the upland prairies than the aquatic and wetland areas. *Celithemis eponina* appeared particularly abundant away from water, often perching on the tallest substrates such as dead shoots of peachleaf willow (*Salix amygdaloides*) and the "turkey-foot" inflorescence of big bluestem (*Andropogon gerardii*). Some species were common for most of the survey (*Enallagma aspersum*, *E. civile*, *E. geminatum*, *Sympetrum rubicundulum*, *Tramea lacerata*) whereas others were common earlier (*Lestes dryas*, *Nehalennia irene*) or later (*Lestes congener*, *L. unguiculatus*, *Perithemis tenera*) in the season. Unlike the very common species, *Libellula pulchella* excluded, I rarely or never detected exuviae and nymphs in the common species except



T. lacerata. Many of these species showed apparent ecological specialization, such as *Ischnura hastata* and *Nehalennia irene* adults frequently co-occurring amid patches of blunt spikerush (*Eleocharis obtusa*).

Uncommon species

The uncommon anisopterans included four earlier flying species (Epiaeschna heros, Epitheca costalis, Leucorrhinia intacta, Libellula semifasciata) and three later flying species (Pantala flavescens, Sympetrum ambiguum, S. obtrusum). Epitheca costalis appeared in high numbers at many sites during just one early survey. The cosmopolitan migrant P. flavescens was seen sporadically at multiple sites but never as exuviae or nymphs. The uncommon zygopterans included species in high numbers at one site (Argia fumipennis, Calopteryx maculata, Enallagma exsulans), low numbers at many sites (Enallagma basidens, Ischnura ramburii), or low to moderate numbers at several sites (Enallama signatum). The exclusive breeding occurrences of C. maculata and E. signatum combined with the only non-breeding record of Lestes rectangularis at the KSP-4 beaver wetland (Figure 2) helps explain that site's significant contribution to breeding zygopteran beta diversity (Table 3).

Rare species

The rare species were found in very limited numbers, often at a single site or on a single occasion, or both (Figures 2, 3). Their breeding status at BSA was either confirmed or could be reasonably assumed based on known habitat requirements. Lestes australis had a clear resident population at KSP-2, a cluster of small dugouts created during trail construction. The other rare species were detected either multiple times in early or mid season (Epitheca princeps, Libellula incesta) or once later in the season (Aeshna constricta, A. verticalis, Sympetrum internum, Tramea onusta). Sympetrum internum looks very similar to S. rubicundulum, which was common, but I examined the frons, hamules, and subgenital plates on hundreds of individuals and could not confirm S. internum until the last survey. Body size, frons color, and degree of S8 black marking allowed confident separation of T. onusta and T. carolina, but I often did not get an in-hand or close-up view and so T. onusta may have been more common than my data suggest.

Vagrant species

The vagrant species were represented by a single individual (Argia apicalis, A. moesta, Dromogomphus spinosus, Erythemis vesiculosa, Hetaerina americana, Lestes eurinus, Pantala hymenaea) or by several immigrants detected once (Enallagma antennatum, Gomphurus vastus). Three of these species (A. apicalis, A. moesta, D. spinosus) were spotted far from water. Two (E. antennatum, H. americana) were seen only along the stream below the KSP-4 beaver dam. It is highly probable that A. moesta, D. spinosus, E. antennatum, H. americana, and G. vastus flew in temporarily from the Kankakee river, the nearest major lotic feature to BSA. Argia apicalis may have arrived from the industrial ponds or recreation impoundments just south of Braidwood Dunes preserve. The 02-Jun sight record of E. vesiculosa (OC#1509333) appears to be the first reporting for Illinois and a distribution outlier.

Discussion

In one field season at the Braidwood Sands Area (BSA) I found more than a third of the statewide species total and nearly half of the lentic-breeding fauna. I added 24 species, including a new state record (*Erythemis vesiculosa*), to the BSA checklist. Many damselflies had not previously been re-



corded, including *Ischnura posita* and *Lestes rectangularis* which I rated as 'very common' across the study sites. There were four historically documented species (*Dromogomphus spoliatus*, *Epitheca cynosura*, *Gomphurus fraternus*, *Sympetrum semicinctum*) that I did not observe. Two of these (*D. spoliatus*, *G. fraternus*) associate with rivers and therefore may have been temporarily visiting from the adjacent Kankakee river, just like several of the putative vagrants I observed. Other species are possible or expected based on surrounding habitats and proximity of distribution records, and because many odonate species are ephemeral or transient, appearing one year and not the next (Schilling et al., 2019; Shiffer & White, 2014; White & Moore, 2018).

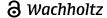
Currently, Aeshna verticalis and Ischnura ramburii are on the Illinois Watch List for species in greatest conservation need (SGCN), and Lestes eurinus, Nehalennia irene, and Sympetrum internum have NatureServe 'imperiled' or 'vulnerable' rankings in Illinois. I could not confirm any breeding localities for A. verticalis, but it occurred at two prime examples of sedge meadow wetlands (BDN-3 and KSP-3) which align with the known breeding habitats for this species (Paulson, 2011). Ischnura ramburii (Odonata Central #1500958) is noteworthy for being disjunct from its more southerly and easterly distribution. This species was not reported in Illinois until October 2018 (OC#491395) when it was collected about 5 km south of the Braidwood Dunes preserve; it was found again a year later in that same vicinity. Further surveys are needed to verify the breeding status of A. verticalis and I. ramburii at BSA.

There were other records of interest at BSA, most notably *Erythemis vesiculosa*. This species' BSA occurrence is one of only a handful of records (OC#1358205, OC#1405111, OC#1557671), all recent (since 2018), found disjunct from its central distribution in the U.S. midsouth, and presence of disjunct populations is one of the vulnerability criteria for selecting SGCN (Bried & Mazzacano, 2010). Taxa specialist teams of the Midwest Landscape Initiative recently identified regional SGCN for the 13-state jurisdiction, and although *E. vesiculosa* has not made the current list it could become a future candidate depending on its climate vulnerability and potential northward range shift.

Standardized odonate-targeted surveys are almost nonexistent in globally significant sand areas that closely resemble the BSA. Over a five-year period in the 1990s, Smolka et al. (1999) documented 60 odonate species across the interdunal wetlands and surroundings of a nationally protected oak savanna-woodland in northwest Indiana. Several historically recorded species missing from their survey have been documented at BSA, including *Argia fumipennis*, *Haeterina americana*, *Nehalennia irene*, and *Sympetrum semicinctum*. Since 2013 the Illinois Odonata Survey has documented about 50 odonate species, including 38 shared with BSA, at The Nature Conservancy's Nachusa Grasslands located ~120 km northwest of BSA, however the prevailing geology (karst terrane, loess drift) differs and consequently so does the wetscape. In 2011, two colleagues and I recorded about 50 odonate species across three pine-oak sand barrens in the northeastern U.S., searching 32 wetlands on eight biweekly visits (Bried et al., 2015). Approximately two-thirds of those species overlap with the BSA checklist. From these studies and the diversity at BSA it seems reasonable to expect 50 to 60 odonate species across an inland sand area wetscape of the region.

Protected areas with a diversity of potential breeding sites may attract and support high odonate diversities (e.g. White et al., 2020). Many of the ponds and wetlands at BSA are fishless and seasonally flooded, important factors structuring odonate assemblages (Stoks & McPeek, 2003; Crumrine et al., 2008; Van Allen et al., 2017). The variety and abundance of fishless seasonal waters explains why a species like *Enallagma aspersum*, which deviates from the *Enallagma* ancestral state of occupying permanent fish-filled waters (Siepielski & Beaulieu, 2017), appears widespread and abundant in BSA. For such species the BSA wetscape may offer refuge from the dominant surroundings of permanent fish-filled deeper waters.

The mosaic of dry-mesic sand woodlands, savannas, and prairies bordering or surrounding the breeding areas may be just as important to maintain for foraging, sheltering, roosting, maturation, and dispersal (e.g. Harabiš, 2016; Hykel et al., 2018; Leite et al., 2021). For example, I found *Sympetrum rubicundulum* only at sites with extensive forest border, and forest specialist *Epiaeschna heros* breeding only at the woodland-surrounded vernal pools. Species like *Celithemis eponina* were far more common in the prairies than at the breeding areas, and the extensive BSA prairie matrix may



facilitate metacommunity dynamics better than the forest matrix by allowing more dispersal among breeding areas (French & McCauley, 2019).

Wetscape prioritization for odonates

With only one field season it is difficult to fully prioritize BSA wetlands for protection and conservation management aimed at odonates, but here I will briefly discuss how the information may eventually be applied. Generally for odonates I recommend combining a coarse-filter diversity screen with breeding patterns and context-specific rarity status (Table 2).

Taxonomic diversity patterns can suggest the initial site ranking. At BSA the collective sedge meadows, Kankakee Sands wetland ponds, and Sand Ridge vernal depressions all appear to be priority candidates because they added to gamma richness, supported high breeding diversity, and contributed significantly to beta diversity. The shrub swamp (BDN-1) also contributed to beta diversity, but this was driven by observing uniquely few damselflies (especially *Lestes*), indicating that significant local contributions to beta diversity (Legendre & De Cáceres, 2013) can be positive or negative and need careful interpretation. Breeding diversity is especially relevant to prioritization because successful recruitment (sensu Bried et al., 2015) indicates population source localities. Breeding occurrences also drastically reduced the general richness levels (see 'Diversity' results) and altered the spatial distributions (Fig. 2) linked to BSA rarity status.

Rarity status specific to the wetscape context can be used to modify initial site rankings. Presumably sites with higher proportions of rare and uncommon species would take precedent over sites with more common and very common species. The three sedge meadow wetlands, for example, contained larger numbers of uncommon species which could justify prioritizing those sites over the Kankakee Sands wetland ponds. Other factors to consider include abundance levels (at multiple stages; Fig. 4) and whether the site is recruiting a given species (breeding occurrence) or merely attracting it (non-breeding occurrence). Locally high counts of rare and uncommon species, relative to other sites and species, could be an important modifying factor in the prioritization. Of course, any species ranked with broader conservation status (e.g. state-listed, federally listed, state or regional SGCN, Nature-Serve rank, IUCN rank) may override the wetscape-level status in prioritizations.

Other factors such as vulnerability traits (Rocha-Ortega et al., 2020) and species relatedness (Campbell & Novelo-Gutiérrez, 2007) could be useful to scoring and ranking sites in practice. Furthermore, the wetscape dispersal network brings useful metacommunity concepts into play, such as multispecies source-sink relations implied by dispersal mass effects (Leibold & Chase, 2018). For species distributed by mass effects, breeding sites may be prioritized as favorable (source) habitats whereas nonbreeding occurrences may reflect population sinks, and frameworks are emerging to identify mass effect species assembly (Leboucher et al., 2020; Bried & Vilmi, in revision). A goal moving forward is to develop and leverage all these ideas and tools into a more concrete prioritization scheme applicable to wetscapes.

Acknowledgements

This survey was made possible by funding from the Forest Preserve District of Will County. Special thanks to Floyd Catchpole for his enthusiastic support, sharing his in-depth knowledge of the study area, and for creating the map figure. Thanks also to Suneeti Jog for assisting with plant identifications and to two reviewers for comments and edits that helped to improve the final manuscript.

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