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Travis J. Schepker[1,2] · Ted LaGrange[3] · Elisabeth B. Webb[4]

Abstract

Accurate bioenergetic carrying capacity estimates of wetlands on public and private lands, as well as those managed for crop production are important for managing waterfowl populations and habitats. Given the importance of wetlands in the Rainwater Basin region of Nebraska for spring migrating waterfowl, we quantified and compared seed and aquatic invertebrate biomass and true metabolizable energy (TME) at three wetland types; public wetlands, wetlands enrolled in the Wetlands Reserve Program (WRP), and cropped wetlands. Median seed biomass estimates at public, WRP, and cropped wetlands were 593 kg/ha, 561 kg/ha, and 419 kg/ha respectively. Cumulative TME varied among wetland type, with greater TME at cropped wetlands (2431 kcal/kg) than public (1740 kcal/kg) and WRP wetlands (1781 kcal/kg). Seed biomass estimates from this study were statistically greater than those currently used for management planning in the RWB, however, TME estimates were statistically lower than estimates currently assumed for WRP and public wetlands. Our estimates for aquatic invertebrate biomass were approximately 40-fold less than seed biomass estimates. Based on spring ponding frequency at wetlands in Nebraska's Rainwater Basin, and the caloric estimates derived for each wetland type, we concluded that the regions wetlands meet the energetic demand of spring migrating waterfowl during 10% of years.

Keywords Wetlands restoration program · WRP · Food resource availability · Spring migration ecology · True Metabolizable energy · Waterfowl · Dabbling duck · Carrying capacity · Nebraska Rainwater Basin · Annual plant seed · Perennial plant seed · Aquatic invertebrate · Foraging threshold

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Introduction

The spring condition hypothesis acknowledges the potential relationship between food availability at migration stopover sites and subsequent reproductive success on breeding grounds (Afton and Anderson 2001; Anteau and Afton 2009). During spring, female waterfowl seek aquatic invertebrates and plant foods to accumulate the energy and protein needed to complete migration and initiate egg production (LaGrange and Dinsmore 1989; Pearse et al. 2011; Tidwell et al. 2013). When demand for quality food resources is unmet, waterfowl may arrive at nesting grounds with insufficient energy and lipid reserves, and consequently become less likely to reproduce (Heitmeyer and Fredrickson 1981; Devries et al. 2008). Given the importance of food resource acquisition at mid-latitude migration stopover sites and subsequent potential effects on migration and arrival at nesting areas, waterfowl

Springer

managers have adopted a bioenergetics approach to guide habitat conservation planning for remaining wetlands at spring staging areas (North American Waterfowl Management Plan 2012; Straub et al. 2012; Rainwater Basin Joint Venture (RWBJV) 2013; Williams et al. 2014). This approach requires accurate estimates of: 1) habitat-specific food resource biomass (dry weight/unit area), 2) habitat-specific estimates of true metabolizable energy (TME; kcal/dry weight), 3) habitat-specific availability (ha of foraging habitat), 4) species-specific daily energy expenditure (kcal), and 5) species-specific population goals (Williams et al. 2014). Thus the goal of this strategy is to assess a regions ability to sustain the bioenergetic demand of migratory birds. However, regional conservation planning using a bioenergetics approach is likely hindered by variation and uncertainty in daily ration model parameters, particularly the need for more accurate habitat-specific estimates of food resource biomass and corresponding TME values (Straub et al. 2012; Williams et al. 2014; Livolsi et al. 2015).

The Rainwater Basin Joint Venture (RWBJV) is responsible for developing long-term conservation strategies and delivery of wetland habitats for migratory waterfowl in Nebraska's Rainwater Basin (RWB) region. Currently the RWBJV is tasked with providing habitat, and food resources sufficient to support ~10 million spring migrants in a region that has experienced a 90% reduction in wetland area (Schildman and Hurt 1984; LaGrange 2005; Bishop and Vrtiska 2008). Reduction of quality wetland habitat can promote intense competition among birds for wetland resources during this critical period (Webb et al. 2010, Bishop et al. 2016). One strategy for providing additional wetland resources within the region involves restoring function for a portion of those wetlands previously converted to agricultural use (Bishop and Vrtiska 2008). The Natural Resources Conservation Service (NRCS) offers several voluntary conservation easement programs that provide private landowners financial and technical assistance to retire farmlands from agricultural production, and restore historic wetland hydrology (King et al. 2006). Although NRCS programs such as the Wetlands Reserve Program (WRP; enrollment expired in 2014) and Agricultural Conservation Easement Program (ACEP; established in 2014) offer financial incentives and technical support for initial habitat restoration, program participants have no contractual obligation to provide continued management to promote ecosystem function (Tapp and Webb 2015; Natural Resources Conservation Service 2017a). Cattle grazing and a variety of mechanical soil disturbance treatments are commonly used to manage wetland vegetation throughout the RWB, with the intended goal of increasing seed production by promoting early successional plant communities (LaGrange 2005; Bishop and Vrtiska 2008; RWBJV 2013). Without sporadic disturbance, annual vegetative communities may transition to dense stands of perennial

monocultures, such as river bulrush (*Scirpus fluviatilis*) or reed canary grass (*Phalaris arundinacea*), that offer minimal food resources or energetic value to migratory birds (Haukos and Smith 1993; Bowyer et al. 2005; Strader and Stinson 2005; Kross et al. 2008). An alternative conservation easement strategy within ACEP is the Agricultural Land Easement option (ACEP-ALE), that involves restoring the hydrology of non-functional cropped wetlands and encouraging private landowners to continue crop production (Natural Resources Conservation Service 2017b). This strategy provides agricultural producers an additional program for flood-prone cropland, where crops can be harvested during dry years, while maximizing foraging opportunities for migrating birds during years with sufficient precipitation (Nugent et al. 2015). Although conservation easement programs have become an integral tool for developing long-term wetland management strategies, their energetic contribution for waterfowl in the RWB has not been assessed.

The current bioenergetic model used for wetland conservation planning in the RWB assumes seed biomass and TME estimates derived from actively managed wetlands in Southern United States during autumn (Kaminski et al. 2003; Bishop and Vrtiska 2008). There is likely a spatial bias associated with these estimates as vegetative communities and seed production can vary across regions resulting from length of growing season at different latitudes (Olmstead et al. 2013; Tapp et al. 2017), annual precipitation (Casanova and Brock 2000), soil type (Reed 1988), and interactions with exotic or endemic species (Houlahan and Findlay 2004). In addition, seed biomass estimates developed during autumn would likely overestimate actual seed availability during spring, resulting depletion by autumn migrants and decomposition (Greer et al. 2007; Brasher et al. 2007; Hagy and Kaminski 2012; Williams et al. 2014). Brasher et al. (2007) acknowledged an 80% decrease in food resource availability between autumn and spring migration at actively and passively managed wetlands in Ohio, suggesting spring is the most food-limited season for non-breeding waterfowl. Drahota and Reichart (2015) assessed seed biomass at the most productive public wetlands in the RWB, and reported seed biomass as much as four times greater than current estimates used for spring conservation planning in the RWB. Although these estimates are useful for assessing seed biomass in actively managed public wetlands, they may not represent seed biomass at conservation easements and cropped wetlands, which account for greater than 30% of ponded wetland area in the RWB during years with average precipitation (RWBJV 2013).

Energetic contributions recognized by the RWBJV for developing bioenergetics models focus exclusively on seed biomass estimates (Bishop and Vrtiska 2008; Nugent et al. 2015). While plant seeds are consistently the primary wetland food resource consumed by most dabbling ducks during spring migration, aquatic invertebrates are likely also an essential

food resource given their high protein content and the shift in waterfowl diets to contain a greater proportion of invertebrates during spring (Anderson and Smith 1998; Hitchcock 2008; Pearse et al. 2011; Tidwell et al. 2013). Although the exact phenology of shift in dabbling duck diets from high-calorie to high-protein food sources is unclear, and is likely influenced by a number of factors (e.g., food availability, use of exogenous nutrients in egg formation, annual weather), the shift is thought to be a requirement for optimal reproduction to occur (Swanson et al. 1985; Euliss and Harris 1987; Ankney and Alisauskas 1991).

Waterfowl food resources are potentially limited during spring migration (Brasher et al. 2007; Straub et al. 2012) and given the reduction in wetland habitat in the RWB, it is critical to determine the region's bioenergetic carrying capacity for spring migrating dabbling ducks. Therefore, we conducted a regional study to: 1) estimate plant seed biomass and associated TME at public, conservation easement, and cropped wetlands, 2) estimate the potential energetic contribution of aquatic invertebrates to water birds, and 3) conduct an energetic assessment to evaluate the potential spring caloric value of wetland habitats in the RWB to determine if the energetic demands of migrating waterfowl are being met.

Methods

Wetland Selection

Our study was conducted in the RWB of Nebraska from 18 February – 24 April, 2014 and 11 February – 13 April, 2015. The RWB spans 21 counties in south-central Nebraska, adjacent to the southern border of the Platte River (Fig. 1). Most wetlands within the region are classified as playas, which are small depressional wetlands, lined with a clay layer with low permeability and located at the low spot of closed basin watersheds (Smith 2003). Playas in the RWB are seasonally or ephemerally inundated, with historic hydrologic processes driven by surface runoff following precipitation events and accumulated snowmelt (Bolen et al. 1989; Cariveau et al. 2011). Historically, the RWB included >11,000 playas that would have provided approximately 80,000 ha of wetland habitat (Bishop and Vrtiska 2008). However, drainage ditches, irrigation pits, culturally-accelerated sedimentation, and agricultural expansion resulted in a long-term decline of up to 90% of wetland area within the region (Raines et al. 1990; Bishop and Vrtiska 2008). Wetland loss in the RWB is magnified during drought years, when a large portion of the remaining wetlands fail to pond water. Ground water pumping is available for some public wetlands to offset drought conditions, however the high cost associated with installation and maintenance of pumping infrastructure leaves most private

wetlands without such capabilities (personal communication with landowners).

Study sites were located on public lands managed by the Nebraska Game and Parks Commission and the U.S. Fish and Wildlife Service, on private conservation easement lands enrolled in the WRP, and on private lands managed for agricultural crop production. The WRP expired in 2014, and has since been replaced by the ACEP. All conservation easements included in this study were enrolled under WRP, thus we refer to all conservation easements as such hereafter. Private lands managed for crop production pond water following intense precipitation events in areas where functional playa wetlands historically occurred (Personal communication, J. Drahota, USFWS). Although native moist-soil wetland plant communities are not management objectives at cropped fields, low densities of dormant seeds in remnant seed banks can germinate and mature given appropriate conditions (i.e. moist-soil). Albeit highly modified, hereafter we hereafter refer to privately owned, ephemeral wetlands managed for crop production as cropped wetlands.

Study sites were limited by minimal precipitation leading into and during springs 2014 and 2015. We stratified potential study sites by county, identified the six counties containing the greatest number of public wetlands that ponded water (Nebraska Game and Park Spring Habitat Conditions Summary 2014 and 2015) and randomly selected public wetlands within these counties (Stafford et al. 2006; Tapp et al. 2017). Inclusion of WRP and cropped wetlands was conditional based on proximity to public wetlands, inundation frequency, and landowner participation. In 2014, we selected 12 public, 10 WRP, and 10 cropped wetlands. In 2015 we selected 12 public, 11 WRP, and 10 cropped wetlands. In February 2014 all public wetlands ponded water; however only three WRP, and three cropped wetlands ponded water. In February 2015 all public and WRP wetlands ponded water, however no cropped wetlands ponded water. During both years we sampled 18 public, 17 WRP, and 13 cropped wetlands, thus some, but not all wetlands were sampled during both years. We acknowledge that assessing foraging conditions at private sites not ponding water was not ideal, however minimal precipitation leading into springs 2014 and 2015 provided limited alternatives. Regardless, all WRP sites exhibited some levels of ponding during the previous two years and all cropped wetlands had been inundated during the previous five years (personal communication with landowners and annual inundation surveys provided by the RWBJV). Cattle grazing and mowing were the primary management strategies used at public and WRP wetlands. All public and 81% of WRP wetlands had received some level of management during the previous three years (personal communication with private and public land managers). Maize (*Zea* spp.), sorghum (*Sorghum bicolor*), and soybeans (*Glycine max*) were the only crops observed at cropped wetlands.

Fig. 1 Locations of study sites within the Nebraska Rainwater Basin, USA where food resources were estimated during spring 2014–2015
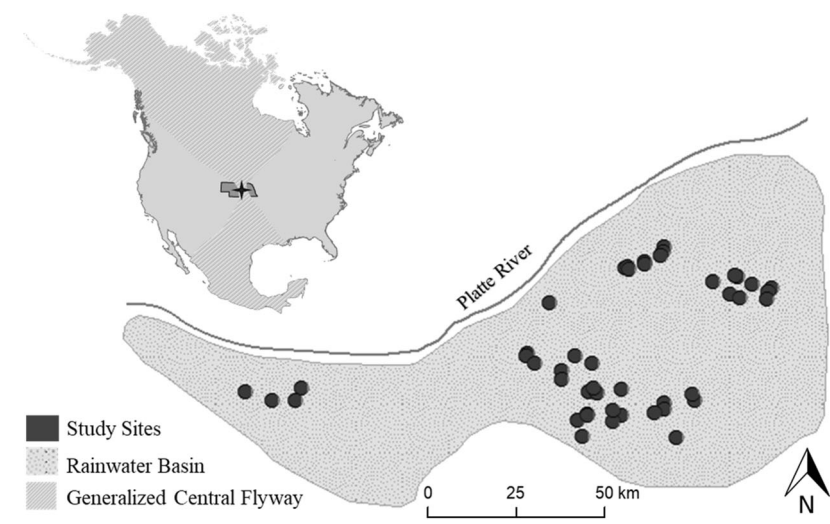
Quantification of Plant Seed Biomass and Caloric Value for Waterfowl

We collected plant seed biomass, consisting of moist-soil seeds and waste grains, during two sampling events each spring. Initial seed samples were collected at all sites prior to arrival of most spring migrating waterfowl (mid-February through the first week of March), regardless of inundation status, and a second time when we considered the majority of spring migrants had departed the region (last two weeks of April; Drahota and Reichart 2015). We collected 10–20 soil cores (dependent on wetland area) during each sampling event at random locations along a transect positioned across the widest portion of each wetland (Greer et al. 2007; Olmstead et al. 2013; Behney et al. 2014). For sites not ponding water at the time of seed collection, we used aerial imagery from previous years of above average precipitation to identify areas where ponding frequently occurred and established sampling transects accordingly. Soil core samples measured 10 cm in diameter ($78.54 cm^2$) and we removed from the top 5 cm of substrate (Evans-Peters et al. 2012; Olmstead et al. 2013).

Soil cores were deflocculated in a hydrogen peroxide and baking soda solution to separate fine clay sediments (Hagy and Kaminski 2012). We rinsed soil samples through a series of two graduated sieves (#10[250 μm], and #50 [500 μm]) to remove small clay particles, and isolate remaining materials into coarse and fine samples (Greer et al. 2007). Samples were dried to constant dry-mass at 60 °C for 48 h in a convection oven and weighed to the nearest 0.1 mg. Seeds were removed from the coarse and fine debris samples, identified to genus, weighed to the nearest 0.1 mg, and converted to biomass estimates (kg/ha; Kross et al. 2008, Straub et al. 2012). Previous studies have suggested that ~16% of seed biomass is lost during processing (destroyed during sieving or not identified while sorting), thus we corrected for potential seed loss in this study by multiplying all raw biomass measurements by 1.16 (Hagy et al. 2011; Drahota and Reichart 2015). We determined available energy (kcal/ha) by multiplying mean biomass of an individual seed taxa by the corresponding published value of true metabolizable energy (gross energy in kilocalories of food consumed minus the gross energy of excreta; Schepker 2017; Appendix A). We were unable to identify TME values for *Marsilea* spp. sporocarps, a genus from the family Marsileaceae, thus we used methods described by Straub (2008) to estimate TME based on crude fiber estimates observed in collected *Marsilea* sporocarps. Finally, we estimated cumulative TME across all plant genera present at a wetland by summing the products of genus biomass (percentage of total biomass for all genera) and the corresponding TME value, and dividing by the sum of weights (Williams et al. 2014);

$$\bar{x} = \frac{\sum_{i=1}^{n} w_i {}^* x_i}{\sum_{i=1}^{n} w_i}$$

where,

$\bar{x}$ The weighted average of TME (kcal/kg) across all genera present at a single wetland

w_i The weight or percentage of a genus seed biomass contributed to the overall seed biomass of all genera

x_i The TME value of an individual species/genus

Quantification of Aquatic Invertebrates Biomass and Caloric Value

We assessed aquatic invertebrate biomass in alternating weeks at 17 wetlands in 2014 and 24 wetlands in 2015. At each wetland, we established 3–5 (dependent on wetland area) randomly located 3 m × 3 m sample plots at water depths <30 cm (preferred range of foraging depths for dabbling ducks;

Fredrickson 1991) and where vegetative cover was <50%. Within each plot, we collected two nektonic samples using a 500 μm rectangular sweep net (Murkin et al. 1994; Tapp and Webb 2015). The net was lowered vertically into the water column, pressed firmly against the substrate, and bounced through the water column for a distance of 1.1 m ($0.5m^2$; Klemm et al. 1990; Davis and Bidwell 2008). We also collected two benthic samples using a 10-cm diameter × 5-cm deep benthic core sampler in an undisturbed area adjacent to the corresponding nektonic sampling location (Swanson 1983). Benthic and nektonic samples were preserved in 70% ethanol to prevent deterioration (Murkin and Kadlec 1986a) and shipped to the University of Missouri for processing.

To increase efficiency for invertebrate sorting and identification, we stained samples with rose bengal for 24 h prior to sorting (Sherfy et al. 2000; Tapp and Webb 2015). We rinsed invertebrate samples through a series of two graduated sieves (#50 [500 μm] and #10[250 μm]) to remove small clay particles and partition remaining materials into coarse and fine samples (Tapp and Webb 2015). We used a Folsom wheel sample splitter (Aquatic Research Instruments) to subsample (1/4 volumes) material retained by the 250 μm and 500 μm sieve (Meyer et al. 2011; Whiting et al. 2011; Tapp and Webb 2015). Aquatic invertebrates were removed from remaining debris, adults and larvae were identified to the lowest taxonomic level practical, measured to the nearest millimeter, and catalogued (Kaminski and Prince 1981; Straub et al. 2012). Biomass estimates for individual taxa were obtained using published dry length-mass regressions (Duffy and LaBar 1994; Benke et al. 1999). When a length-mass regression was not available for specific taxa, we used estimates from similar species observed in comparable habitats (Benke and Huryn 2006). We were unable to identify published length-mass regression models for taxon similar to phylum Nematoda and class Hirudinea. Further, we were unable to obtain published length-mass regression models for taxa within the order Gastropoda that did not include shell mass. Using a subset of specimens collected from our study, we developed dry length-mass regressions for Nematoda and Hirudinea, and length-mass regressions that excluded the shells of families Planorbidae, Physidae, and Bithyniidae following methods by Benke et al. 1999 (Supplementary Material A). Biomass estimates were pooled and averaged for all taxa collected at a wetland for each sampling event and converted to biomass estimates (kg/ha). We determined available energy (kcal/ha) by multiplying the mean biomass of all invertebrate taxa by a factor of 580 kcal/kg (Hohman et al. 1988; Straub et al. 2012).

Statistical Analysis

During both years, seed biomass values were not normally distributed and contained outliers that we believed to be ecologically relevant for our analysis. Thus, we applied the wilcox.test function in program R (Wilcoxon 1945; R Development Core Team 2017) to compare paired samples when evaluating seed depletion. We also applied the one-tailed wilcox.test function in Program R (Wilcoxon 1945; R Development Core Team 2017) to test whether seed biomass exceeded a foraging threshold of 200 kg/ha. Foraging thresholds can occur when biomass falls below a level at which time the energetic cost of foraging exceeds the energetic benefit (Reinecke et al. 1989; Hagy and Kaminski 2015; Williams et al. 2014). Although there has been debate as to what an appropriate foraging threshold should be for dabbling ducks foraging on moist-soil seeds, 200 kg/ha is regarded as a relatively conservative threshold (Williams et al. 2014; Hagy et al. 2017).

We compared plant seed biomass, TME, and energy produced for each wetland type using measures of central tendency (e.g., median), as each metric followed a non-normal distribution, and there is considerable uncertainty whether spring-migrating waterfowl distribute themselves in an ideal free manner relative to energy available in wetlands (Straub et al. 2012). We used a non-parametric Kruskal-Wallis H test in program R (R Development Core Team 2017) to test for differences in seed biomass, TME, and energy among wetland types (Kruskal and Wallis 1952). Proceeding each Kruskal-Wallis H test, we tested data for general Kruskal-Wallis H test assumptions including homogeneity of distributions. Raw distributions were not homologous (Levene 1960; Fox et al. 2016) and were thus log transformed. Following a statistically significant result, we conducted Dunn's multiple comparison test to assess differences between independent wetland types (Dinno 2015).

Total area (based on hydrologic footprint) for public, WRP, and cropped wetlands was approximately 11,582 ha, 2117 ha, and 65,874 ha respectively (Bishop et al. 2016). However actual wetland area available to waterfowl is dependent upon a hydrologic footprint ponding water. We corrected for actual wetland area available for duck use by multiplying potential wetland area by an annual spring inundation frequency factor specific to each wetland type (refer to Bishop et al. 2016 for methods used to determine annual spring inundation frequency). To determine the overall caloric contribution of each wetland type, we multiplied ponded wetland area by the corresponding bioenergetic estimate (kcal/ha). Finally, total energetic carrying capacity for spring migrating waterfowl was estimated by summing available energy for each wetland type (Supplementary Materials B).

Results

Plant Seed Composition

We collected and processed 1202 soil core samples from 24 public, 21 WRP, and 20 cropped wetlands during springs

2014 and 2015. We identified seeds from 42 native, exotic, and agricultural plant genera. *Polygonum* spp., *Echinochloa* spp., *Sparganium* spp., *Potamogeton* spp., and *Scirpus* spp. were the most common native plant genera observed, and accounted for 73% of the total native seed biomass in both years (Schepker 2017). *Glycine* spp. and *Zea* spp. were the most common agriculture plant genera observed and accounted for 97% of the total agricultural seed biomass observed in both years (Schepker 2017). Our Wilcoxon Ranks Test indicated that pre and post-migration seed biomass estimates were not statistically different in 2014 ($Z = 94$, $p = 0.42$) or 2015 ($Z = 207$, $p = 0.24$), indicating minimal seed depletion.

Seed biomass estimates (kg/ha) did not differ among wetland type in 2014 ($H_{2,30,0.05} = 5.76$; Table 1). Among wetlands sampled in 2014, median seed biomass was significantly greater than 200 kg/ha at public ($Z = 74$, $p = 0.002$) and WRP wetlands ($Z = 52$, $p = 0.005$), but did not exceed the 200 kg/ha threshold in cropped wetlands ($Z = 41$, $p = 0.097$). Wetland-specific estimates of mean seed biomass in 2014 were greater than the 200 kg/ha threshold at 83% of public sites, 90% of WRP sites, and 70% of cropped sites (Fig. 2). Mean ranks of TME (kcal/kg) for seeds collected in 2014 varied among wetland type ($H_{2,30,0.05} = 7.38$). Overall TME was greater in cropped fields (median = 2405 kcal/kg) than public wetlands (median = 1750 kcal/kg: $Z_{21,0.05} = 2.64$), but TME did not differ among other pairwise comparisons ($p > 0.05$; Fig. 3). Energy produced by seeds collected in 2014 did not vary among wetland type ($H_{2,30,0.05} = 2.68$).

Seed biomass estimates did not differ among wetland types in 2015 ($H_{2,31,0.05} = 1.60$ (Table 1). Wetland-specific estimates of mean seed biomass in 2015 were greater than the 200 kg/ha threshold at 100% of public sites, 90% cropped sites, and 91% WRP sites (Fig. 2). Overall, median seed biomass exceeded the 200 kg/ha threshold at all wetland types ($p < 0.05$). Mean ranks of TME for seeds collected in 2015 varied among wetland types ($H_{2,31,0.05} = 11.83$). Overall TME was greater in

cropped fields (median = 2587 kcal/kg) than public (median = 1714 kcal/kg: $Z_{21,0.05} = 3.23$) and WRP wetlands (median = 1804 kcal/kg: $Z_{20,0.05} = 2.73$), however TME did not differ between WRP and public wetlands ($Z_{22,0.05} = 0.46$; Fig. 3). Energy produced by seeds collected in 2015 did not vary among wetland types ($H_{2,31,0.05} = 2.80$).

Macroinvertebrate Composition

We collected and processed 1524 invertebrate samples from 41 wetlands during springs 2014 and 2015. Given the limited number of ponded WRP and cropped wetlands, we combined data from both years and all wetland types when summarizing aquatic invertebrates. Forty-five invertebrate families were identified from nektonic and benthic communities (Schepker 2017). Among the most frequently observed taxonomic orders during both years were *Diptera, Gastropoda, Odonata, Copepoda*, and *Anostraca*. During both years, invertebrate biomass (kg/ha) was greater in benthic communities, however taxonomic richness was greater in nektonic communities. Mean aquatic invertebrate biomass observed in benthic samples during 2014 and 2015 was 8.45 kg/ha (SE = 1.62), and 9.88 kg/ha (SE = 1.79) respectively (Table 2). Mean aquatic invertebrate biomass observed in nektonic samples was 1.81 kg/ha (SE = 0.55), and 6.29 kg/ha (SE = 0.84) during 2014 and 2015, respectively. Plant seed biomass estimates exceeded aquatic invertebrate biomass at all sites ($n = 41$) in 2014 and 2015. We estimated the caloric value of aquatic invertebrates at playa wetlands in the RWB as 7958 kcal/ha.

From 2006 to 2015, we estimated annual mean energy at ponded wetlands in the RWB to be 1.2 billion kcal (Supplementary Material B). During the 10-year period, estimated mean annual energy produced varied among wetland types ($F_{2,27,0.05} = 3.35$). Ponded area was greatest for public wetlands, and consequently public wetlands represented the greatest caloric contribution to energetic carrying capacity in the RWB. Although ponded area was greater at cropped

Table 1 Estimates of median, mean, standard error (SE), and 95% confidence intervals (CI) for seed biomass (kg/ha dry mass), TME (kcal/kg), and Energy (kcal/ha) collected in public, Wetlands Reserve Program WRP) and cropped wetlands during springs 2014 and 2015

| Year	Metric	Public Wetlands			WRP Wetlands			Cropped Wetlands		
		Biomass	TME	Energy	Biomass	TME	Energy	Biomass	TME	Energy
2014	Median	582	1750	768,020	569	1776	1,112,588	310	2405	632,648
	Mean	546	1652	898,015	594	1832	1,013,186	281	2256	613,029
	SE	104	78	191,492	133	112	183,466	55	137	127,309
	CI	229	172	421,471	300	253	415,028	125	311	287,992
2015	Median	651	1714	892,954	560	1804	1,090,553	637	2587	1,413,891
	Mean	695	1665	1,192,197	540	1741	964,815	934	2511	2,448,435
	SE	93	97	226,274	91	86	195,223	243	207	727,825
	CI	204	213	498,024	203	192	434,983	550	469	1,646,454

a

b
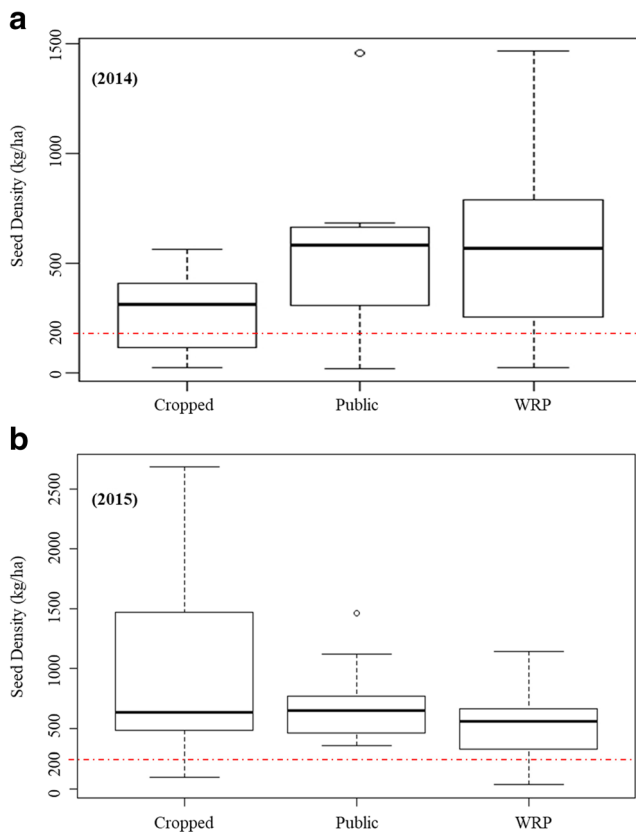
Fig. 2 Seed biomass at cropped, public, and Wetlands Reserve Program (WRP) wetlands during springs 2014 (**a**) and 2015 (**b**). The horizontal line (200 kg/ha) represents a foraging threshold which recognizes the point at which a wetland would have little to no forage value to dabbling ducks. The foraging threshold was exceeded at 70% of cropped, 83% of public, and 90% of WRP wetlands sampled in 2014 and 90% of cropped, 100% of public, and 91% of WRP wetlands sampled in 2015

a

b

Fig. 3 True Metabolizable Energy (TME) at cropped, public, and Wetlands Reserve Program (WRP) wetlands during springs 2014 (**a**) and 2015 (**b**). The horizontal line at 2470 kcal/kg represents a TME estimate commonly when constructing bioenergetic models throughout North America. TME values observed at public and WRP wetlands were significantly less than 2470 kcal/kg in the Rainwater Basin

wetlands than WRP wetlands, there was no difference in available caloric production between the two wetland types ($t_{18, 0.05} = 0.08$). Based on these projections and estimates, the RWBJVs annual objective for providing 4.4 billion kilocalories to spring migratory waterfowl was achieved in one year over the 10-year period of assessment.

Discussion

Food resources for migrating waterfowl are often considered limited during spring migration, as a result of seed depletion by fall migrants and decomposition (Nelms and Twedt 1996; Greer et al. 2007; Barney 2008; Foster et al. 2010). Nevertheless, our estimates for spring biomass were similar to estimates reported by studies conducted prior to, or during autumn migration (Kross et al. 2008; Evans-Peters et al. 2012; Olmstead et al. 2013). Over 90% of the public and WRP wetlands included in this study had seed biomass exceeding 200 kg/ha, suggesting that the vast majority of wetlands in the
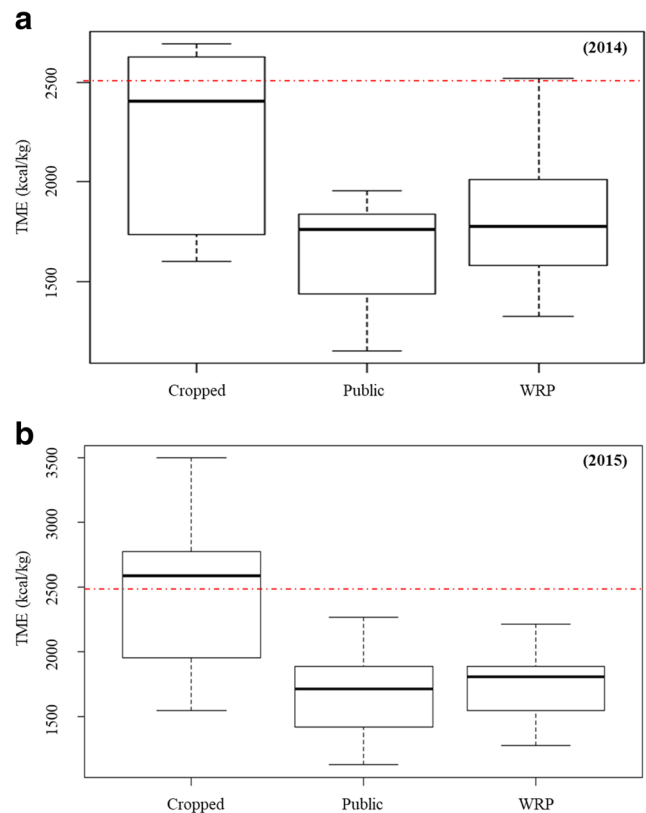
RWB offer beneficial spring foraging opportunities. Although seed biomass at wetlands in the RWB appears to be sufficient at the local level, concerns are likely warranted when assessing seed availability at the regional level. Specifically, during dry years when seed biomass at wetlands is substantial, however only a small percentage of those wetlands is available to foraging dabbling ducks resulting from minimal precipitation.

The Wetlands Reserve Program appears to be a viable conservation strategy for increasing suitable waterfowl foraging habitat in the RWB. Our estimate for seed biomass at WRP sites was 566 kg/ha, which was similar to seed estimates for public wetlands (621 kg/ha). In addition to quantity, the nutritional quality of seeds, in terms of TME, was also comparable between the two wetland types. Although incidental, active management techniques used among the two wetland types may explain comparable plant communities (Olmstead et al. 2013; Tapp et al. 2017). Vegetative disturbance techniques such as prescribed burning, disking, and mowing are commonly associated with moist-soil management, with the objective of maintaining plant communities in early-successional stages (Fredrickson and Taylor 1982). The cost and labor required to implement these disturbance techniques

Table 2 Estimates of mean, standard error (SE), median, and 95% confidence intervals (CI) for invertebrate biomass (kg/ha dry mass) at wetlands in Nebraska's Rainwater Basin during springs 2014 (n = 17) and 2015 (n = 24)

Metric	2014 Invertebrate Biomass		2015 Invertebrate Biomass		Average Biomass	
	Benthic	Nektonic	Benthic	Nektonic	Benthic	Nektonic
Mean	8.45	1.81	9.88	6.29	9.29	4.43
SE	1.62	0.55	1.79	0.84	1.24	0.64
Median	6.80	0.93	6.42	5.04	6.66	3.58
Lower CI	5.02	0.63	6.18	4.54	6.79	3.13
Upper CI	11.88	2.98	13.59	8.03	11.79	5.73

are a concern for landowners with no perpetual obligation to manage waterfowl foraging habitats on WRP easements (King et al. 2006; Tapp and Webb 2015). Consecutive years of passive or no management can promote dense stands of late-successional plant species that often produce fewer seeds and are associated with less desirable TME values (Fredrickson and Taylor 1982; Olmstead et al. 2013). Conversely, WRP enrollees in the RWB also have the option of cattle grazing during certain months of the year, which mimics a natural vegetative disturbance (Stutheit et al. 2004; LaGrange 2005; Marty 2005). Among the private landowners who permitted us access to their WRP wetlands, approximately 80% used cattle grazing as an indirect management tool to control persistent emergent vegetation and promote early successional plant communities.

Although less common and still in initial implementation phase, the Agricultural Land Easement (ALE) option within the Agricultural Conservation Easement Program could serve as an alternative to, or, complement the WRP (Nugent et al. 2015). Although we did not collect samples from ALEs, seed biomass estimates derived from cropped wetlands are likely equivalent and may offer some guidance when assessing the program's potential for meeting waterfowl foraging habitat goals. Site-specific seed biomass at cropped wetlands were highly variable, ranging from 23 to 2680 kg/ha over both years (Fig. 2), and the majority of this variation was explained by harvest during the preceding autumn. Over both years, mean seed biomass at harvested sites (n = 15) was 480 kg/ha, compared to 991 kg/ha at sites (n = 5) that went unharvested during the preceding fall (Table 3). In addition to biomass, the caloric value of waste grains commonly produced in the RWB (*Zea mays* and *Glycine max*) are estimated to be twice that of annual smartweed (*Polygonum* spp.), which was the most frequently observed native seed in this study (Reinecke et al. 1989; Ballard et al. 2004). Despite the caloric benefit waste grains offer, they can fail to provide dabbling ducks with the range of nutrients necessary to complete life history requirements and maintain optimal body condition (Baldassarre et al. 1983; Loesch and Kaminski 1989; Miller et al. 2000). Still, estimated median biomass for native moist-soil seeds at cropped wetlands was 333 kg/ha, which is above the proposed foraging threshold of 200 kg/ha, indicating that

cropped fields ponding water have potential to provide waterfowl with meaningful energetic foraging opportunities from both waste grains and/or recruitment moist-soil seeds.

Mean TME provided by a gram of seed across all moist-soil plant species is generally estimated as 2470 kcal/kg (Kaminski et al. 2003; Bowyer et al. 2005; Kross et al. 2008; RWBJV 2013); however, variation in seed composition resulting from differences in plant community, vegetative manipulations, and geographic location may influence exact estimates (Dugger et al. 2007; Williams et al. 2014). For instance, a late-successional stand dominated by bulrush (*Scirpus* spp.) and spike rush (*Eleocharis* spp.) would likely have an overall TME less than 1000 kcal/kg, whereas an early-successional stand of smartweed (*Polygonum* spp.) and barnyard grass (*Echinochloa* spp.) would be associated with an overall TME of ~2000 kcal/kg (Sherfy 1999; Ballard et al. 2004; Dugger et al. 2007; Straub 2008). Further, TME may exceed 3000 kcal/kg when assessing agricultural waste grains in cropped wetlands (Reinecke et al. 1989). For public and WRP wetlands assessed in this study, we estimated TME to be significantly less than the 2470 kcal/kg used as an average in other studies (Bowyer et al. 2005; Kross et al. 2008). Thus, continuing to use 2470 kcal/g when modeling energetics in the RWB, or other regions where the plant community has not been assessed, will likely substantially overestimate actual accessible energy to waterfowl when all other metrics (seed biomass and ponded area) remain

Table 3 Seed composition observed at cropped wetlands where row crops were not harvested during the previous fall (n = 5)

	Agricultural Waste Grains			Moist-Soil Seeds		
	Biomass	TME	Energy	Biomass	TME	Energy
Mean	653	3058	1,996,874	339	2045	693,255
Median	497	2650	1,317,050	340	2422	823,480
SE	230	559	128,570	22	313	6886
Upper CI	1291	3751	4,843,547	399	2914	1,162,686
Lower CI	15	2365	34,841	279	1176	328,104

Crops went unharvested when land managers were unable to operate equipment in the wet soils. Estimates of mean, standard error (SE), median, and 95% confidence intervals (CI) for seed biomass (kg/ha dry mass), TME (kcal/kg), and energy (kcal/ha)

constant. Based on our findings, future seed biomass assessments may also consider accounting for species composition of plant seeds collected, as associated TME values can reduce uncertainty and variation a when constructing effective bioenergetic models for a region (Livolsi et al. 2015).

The relatively low abundance and patchy distributions of aquatic invertebrates during spring migration likely presents a challenge for waterfowl biologists to identify appropriate target aquatic invertebrates biomass (Murkin and Kadlec 1986a; Drahota and Reichart 2015; Stafford et al. 2016). Our study estimates of mean aquatic invertebrate biomass were approximately 40-fold less than estimates for mean seed biomass. Davis and Bidwell (2008) observed similar densities of aquatic invertebrates during spring in the RWB, however our estimates were considerably lower than those reported by studies outside the RWB (Hohman et al. 1988; Johnson 2007; Straub et al. 2012). In an effort to evaluate the role of invertebrates in influencing waterfowl habitat use, Schepker (2017) explained dabbling duck densities in the RWB using several metrics of food resource availability and reported a significant relationship between dabbling duck density and seed biomass, however no relationship was observed between dabbling duck density and aquatic invertebrate biomass. Tapp (2013) observed similar results when assessing dabbling duck abundance in the Lower Mississippi Alluvial Valley during autumn and winter, although Murkin and Kadlec (1986b) observed a strong positive relationship between dabbling duck density and invertebrate biomass during late spring/early summer on Manitoba breeding grounds. Despite lack of consistent evidence that invertebrate biomass influence dabbling duck habitat use during the non-breeding season, diet studies have emphasized the importance of invertebrates during spring migration (Hitchcock 2008; Tidwell et al. 2013). Given that invertebrate biomass is generally not incorporated into energetic carrying capacity models, there is rarely a standardized or well defined target for invertebrate abundance or biomass, which would likely vary across space and time.

Management Implications

Our bioenergetics assessment indicated that available energy for spring-migrating waterfowl in wetlands exceeded the RWBJVs energetic objective of 4.4 billion kilocalories in only one year from 2006 to 2015 (Supplementary Material B). Based on our observations at seasonally flooded wetlands in the RWB, seed biomass appears sufficient to achieve this energetic objective on a more consistent basis, provided sufficient wetlands are inundated to make these food resources available to dabbling ducks. Although TME was far below expectations in moist-soil units, its potential to increase in the RWB is improbable considering most wetlands already receive management for early-successional plant communities. Increasing

ponded area of unharvested cropped fields would likely be the most efficient method for increasing available energy during spring; however, the utility of this approach may not benefit all wetland-dependent wildlife (Gray et al. 2004; Riens et al. 2013; Casanova and Casanova 2016). Although beyond the scope of this study, developing methods to increase inundation frequency during years with minimal precipitation would likely increase accessible food resources for waterfowl. Despite the potential for WRP sites to provide waterfowl with optimal foraging opportunities, only 3 and 5% of WRP wetland area ponded water in 2014 and 2015 (Bishop et al. 2016). Fully restoring wetland hydrology and the surrounding watershed (e.g. removing culturally-accelerated sediment, plugging surface drains, and filling pits within the wetlands) will help improve inundation frequency. Installing additional groundwater-pumping capabilities at public and WRP wetlands could potentially offset unfavorable conditions during years with low precipitation and limited inundated wetland area, thus making more food biomass available to waterfowl. Additional opportunities to increase natural inundation frequencies at wetlands within closed basin systems (e.g. playas) will require addressing hydrological modifications within the watersheds of the wetlands (Bishop and Vrtiska 2008). Regardless of temporal and spatial considerations, increasing inundation frequency of ephemeral wetlands in semi-arid regions will increase the probability that adequate wetland-derived energy is consistently available to spring-migrating waterfowl (RWBJV 2013; Nugent et al. 2015; Petrie et al. 2016).

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1 **Supplementary Material A**: Length-mass regression equations based on methods from Benke et al. 1999. The power equation of the
2 form $DM = aL^b$ was used to explain biomass where DM = dry mass (mg), L = body length (mm), and a and b are fitted constants.
3 Measurement = the method of measurement used to determine length, n = the number of specimens included in regression model, and
4 range = range of body lengths (mm) and mass (mg) of individuals included. A shell measurement was used to determine the length of
5 families in class Gastropoda, however the shell was discarded when determining an individual's mass.

Taxon	Measurement	n	Range (mm)	Range (mg)	a $\pm$ SE	b $\pm$ SE	R^2
Gastropoda							
Physidae/Bithyniidae	Shell Length	133	3 - 33	0.20 - 47.40	0.05 $\pm$ <0.01	2.03 $\pm$ 0.08	0.94
Planorbidae	Shell Length	61	3 - 23	0.85 - 67.60	0.07 $\pm$ <0.01	2.21 $\pm$ 0.10	0.91
Hirudinea	Body Length	91	3 - 28	0.11 - 17.70	0.01 $\pm$ <0.01	2.04 $\pm$ 0.11	0.89
Nematoda	Body Length	166	2 - 5	0.01 - 0.03	0.01 $\pm$ <0.01	0.96 $\pm$ 0.09	0.78

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Supplementary Material B. Wetland habitat summary and energetic production in the Rainwater Basin from 2006-2015. Inundation frequency, potential habitat, and ponded area were all derived from annual habitat surveys conducted by the Rainwater Basin Joint Venture. Available energy at each wetland type was calculated by multiplying ponded area by median energetic biomass (kcal/ha) for each wetland type from 2014 and 2015. Wetland type listed as "other" in table was not assessed in this study.

Inundation Frequency

Wetland Type	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	10yr Avg
Public	0.0520	0.2246	0.1363	0.1404	0.2681	0.0629	0.0589	0.0296	0.0460	0.0617	0.1080
WRP	0.0666	0.3043	0.2282	0.1878	0.3946	0.0583	0.0444	0.0177	0.0296	0.0560	0.1388
Cropped	0.0006	0.0183	0.0071	0.0028	0.0210	0.0009	0.0009	0.0003	0.0001	0.0001	0.0052
Other	0.0051	0.0169	0.0136	0.0114	0.0235	0.0048	0.0057	0.0035	0.0035	0.0050	0.0093

Potential Wetland Area (ha)

Wetland Type	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	10yr Avg
Public	11,634	11,540	11,549	11,476	11,672	11,626	11,631	11,610	11,542	11,534	11,582
WRP	1,712	1,907	1,893	1,985	2,031	2,363	2,325	2,246	2,345	2,363	2,117
Crop/Other	66,169	66,067	66,073	66,055	65,918	65,632	65,665	65,745	65,715	65,704	65,874
Total	79,515	79,515	79,515	79,516	79,622	79,622	79,622	79,601	79,601	79,601	79,573

Ponded Area (ha)

Wetland Type	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	10yr Avg
Public	605	2,591	1,575	1,611	3,130	732	685	343	531	711	1,251
WRP	114	580	432	373	802	138	103	40	69	132	278
Cropped	38	1,206	472	188	1,382	58	61	18	8	4	344
Other	340	1,119	900	750	1,549	318	376	231	227	330	614
Total	1,097	5,497	3,379	2,923	6,863	1,246	1,225	632	836	1,177	2,487

Available Energy (kcals in THOUSANDS)

Wetland Type	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	10yr Avg
Public	510,314	2,185,006	1,327,580	1,358,528	2,638,816	617,044	577,327	289,585	447,395	599,608	1,055,120
WRP	124,321	634,945	471,068	406,591	874,217	150,315	112,581	43,294	75,775	144,224	303,533
Cropped	32,464	1,017,516	397,865	158,804	1,166,080	48,918	51,342	15,020	7,135	3,243	289,839
Other	-	-	-	-	-	-	-	-	-	-	-
Total	667,098	3,835,467	2,196,512	1,923,922	4,679,111	816,276	741,251	347,899	530,304	747,076	1,648,942

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