



Illinois Natural History Survey  
PRAIRIE RESEARCH INSTITUTE

University of Illinois  
Prairie Research Institute  
Mark R. Ryan, Executive Director

Illinois Natural History Survey  
Eric Schaubert, Director  
Forbes Natural History Building  
1816 South Oak Street  
Champaign, IL 61820  
(217) 333-6830

## **True Metabolizable Energy of Submersed Aquatic Vegetation in Semi-permanent Marshes for Dabbling Ducks in the Upper Midwest**

### **Final Report**

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*Prepared by:*

Joseph D. Lancaster<sup>1</sup>, Aaron P. Yetter, Heath M. Hagy, Margaret C. Gross, Sarah E. McClain, Christopher S. Hine, John W. Simpson, and Christopher N. Jacques

Forbes Biological Station  
Frank C. Bellrose Waterfowl Research Center  
20003 CR 1770 E, Havana, IL 62644  
Phone (217) 332-3825

<sup>1</sup>Email: [lancastj@illinois.edu](mailto:lancastj@illinois.edu)

*Prepared for:*

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U.S. Fish and Wildlife Service, Region 3  
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Bloomington, MN 55437  
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## Executive Summary

Wetlands provide important foraging habitat for waterfowl, but many wetlands in the United States have been lost or degraded in the last two centuries. Wetland managers are tasked with retaining, restoring, and enhancing remaining wetlands to meet energetic and other needs of continental waterfowl and other waterbird populations. However, paucity of information needed to describe the energy availability (i.e., true metabolizable energy [TME] and biomass) of natural wetland foods, including submersed aquatic vegetation, prevent wetland managers and conservation planners from evaluating the consequences of these losses on landscape energetic carrying capacity for waterfowl. Moreover, an understanding of bird response to wetland composition and energy density among historic and contemporary periods would allow wetland managers and conservation planners to envision how changing conditions or tradeoffs in wetland management practices may translate to cumulative waterfowl density in the region. Therefore we quantified: 1) true metabolizable energy of submersed aquatic vegetation shoots (i.e., Canadian waterweed [*Elodea canadensis*], coontail [*Ceratophyllum demersum*], Eurasian watermilfoil [*Myriophyllum spicatum*], sago pondweed [*Stuckenia pectinata*], southern naiad [*Najas guadalupensis*], and wild celery [*Vallisneria americana*]) fed to mallards (*Anas platyrhynchos*) and gadwall (*Mareca strepera*); 2) energy density (energetic use days per hectare [EUD/ha]) of 20 important semi-permanent wetlands used by dabbling ducks in the Upper Midwest; 3) energy density at important stopover sites within the Illinois River Valley between contemporary (2005–2006) and early (1939–1942) and late (1943–1959) historic periods using updated information; and 4) correlation between estimated energy densities and waterfowl use days measured during long-term aerial surveys conducted by the Illinois Natural History Survey (INHS).

We completed 186 TME assays with mallards ( $n = 72$ ) and gadwall ( $n = 114$ ) between 2015 and 2018. Bioavailable energy (i.e., TME) of submersed aquatic vegetation was highly variable among duck and vegetation species as supported by their interaction in the most parsimonious model ( $w_i = 0.42$ ;  $R^2_m = 0.33$ ,  $R^2_c = 0.47$ ). For gadwall, mean TME ( $\pm$  SE; kcal/g[dry]) was greatest for Eurasian watermilfoil ( $0.77 \pm 0.32$ ,  $n = 19$ ), followed by Canadian waterweed ( $0.70 \pm 0.31$ ,  $n = 20$ ), coontail ( $0.55 \pm 0.28$ ,  $n = 18$ ), southern naiad ( $-0.61 \pm 0.34$ ,  $n = 17$ ), wild celery ( $-0.98 \pm 0.39$ ,  $n = 20$ ), sago pondweed ( $-1.07 \pm 0.33$ ,  $n = 20$ ). Mallards assimilated greatest energy from Canadian waterweed ( $1.66 \pm 0.26$ ,  $n = 13$ ), followed by coontail ( $1.51 \pm 0.28$ ,  $n = 8$ ), southern naiad ( $1.37 \pm 0.39$ ,  $n = 14$ ), sago pondweed ( $0.50 \pm 0.22$ ,  $n = 14$ ), wild celery ( $0.05 \pm 0.42$ ,  $n = 11$ ), and Eurasian watermilfoil ( $-0.13 \pm 0.26$ ,  $n = 12$ ). There was evidence from a competing model ( $w_i = 0.11$ ;  $R^2_m = 0.34$ ,  $R^2_c = 0.47$ ) that females acquired 0.52 kcal/g ( $\pm 0.34$ ) more energy from vegetation than males and that TME declined 0.20 kcal/g ( $\pm 0.16$ ) for every 100 g increase in initial mass.

We estimated energetic carrying capacity at 318 random points within 20 wetlands across three years (2015–2017) in the Midwest, USA (Simpson et al. 2017). Across all points, *Ceratophyllum* spp. was the most commonly encountered genera ( $n = 188$ ) of submersed aquatic vegetation, followed by *Myriophyllum* spp. ( $n = 64$ ), *Najas* spp. ( $n = 47$ ), *Elodea* spp. ( $n = 41$ ), and *Stuckenia* spp. ( $n = 36$ ). These five genera comprised 91.5% of the total energy density across all points and years. Extrapolated energy density estimated at sample points ranged from 0 to 5,624 EUD/ha ( $\bar{x} = 426 \pm 52$ ) and biomass estimates ranged from 0 to 2,340 kg/ha (dry) ( $\bar{x} = 204 \pm 22$ ). Evidenced from the best supported model ( $w_i = 0.68$ ;  $R^2_m = 0.19$ ,  $R^2_c = 0.27$ ), energy density was 195 EUD/ha (85% CI = 39 – 964) greater at managed points than unmanaged points, decreased 2 EUD/ha (85% CI = 1 – 3) for every 100 cm increase in water depth, increased 9

EUD/ha (85% CI = 6 – 12) for every 100 cm increase in Secchi depth, and increased 3 EUD/ha (85% CI = 0 – 11) if emergent vegetation was present.

The best supported model ( $w_i = 0.96$ ;  $R^2_m = 0.46$ ,  $R^2_c = 0.63$ ) accounting for variability in energy density at 16 surveyed wetlands in the Illinois River Valley included the proportion of non-persistent emergent wetland and time period. Energy density (EUD/ha) increased 21.1% (85% CI = 17.2 – 25.2) for every 10% increase in the proportion of non-persistent emergent (i.e., moist-soil) wetland at a site. Relative to the early historic period (1938–1942), energy density was 7.8% (85% CI = –2.6 – 17.2) and 30.0% (85% CI = 18.6 – 39.8) less in the late historic (1943–1959) and contemporary (2005–2006) periods, respectively. Moreover, energy density was 24.1% (85% CI = 12.2 – 34.3) less in the contemporary period than the late historic period.

There were two competing models explaining variation in mallard use days between 1 October and 15 December 1950–1959; the first ( $w_i = 0.43$ ,  $R^2_m = 0.71$ ,  $R^2_c = 0.87$ ) included refuge, total wetland area, interspersion-juxtaposition index, and proportion of the site containing aquatic bed, whereas, the second ( $w_i = 0.22$ ,  $R^2_m = 0.69$ ,  $R^2_c = 0.86$ ) included refuge, total wetland area, interspersion-juxtaposition index, and total energetic use days. Model averaged estimates indicated that mallard use days decreased 20,593 (95% CI = 4,774 – 36,412) for every 1% increase in the proportion of aquatic bed and 9,244 (95% CI = 864 – 17,624) for every increase of 10,000 energetic use days. Moreover, for every hectare increase in total area, mallard use days increased 4,596 (95% CI = 2,658 – 6,534). Mallard use days increased 279,397 (95% CI = –294,588 – 853,382) for every increase in the classification of refuge (i.e., 25% range) and 46,781 (95% CI = 19,943 – 73,618) for every point increase in the interspersion-juxtaposition index. The best supported model ( $w_i = 0.32$ ,  $R^2_m = 0.27$ ,  $R^2_c = 0.43$ ) explaining variation in diving duck use days included total wetland area. An increased in 1 ha of wetland area resulted

in 77 (95% CI = 28 – 127) additional diving duck use days. The best supported model ( $w_i = 0.44$ ,  $R^2 = 0.36$ ) indicated mallard use during the contemporary period (2005–2006) was positively related to the proportion of refuge, and they increased 226,264 (95% CI = 36,266 – 416,262) use days for every increase in the classification of refuge (i.e., 25% range).

Our results suggest that contemporary EUD/ha has declined since Bellrose and the INHS (Bellrose 1941, Bellrose et al. 1979) surveyed wetlands in the Illinois River Valley in the mid-20<sup>th</sup> Century. This decline in energy availability is surprising despite a near 3-fold increase (12.4% early to 32.5% contemporary; Stafford et al. 2010) in the coverage of non-persistent wetland class which contained the greatest energy density among classes (i.e., 2.14 Million kcal/ha). However, the substantial loss of alternate wetland classes such as aquatic bed (i.e., persistent emergent, aquatic bed, and floating-leaved aquatic classes) and an overall increase in forested wetland classes (i.e., bottomland and scrub-shrub) seem to counteract the non-persistent increase. Specifically, the proportion of total EUDs available from the aquatic bed wetland class declined from 44–54% historically to ~5% contemporarily. Reasons for wetland changes are discussed extensively in Stafford et al. (2010), but alteration of the Illinois River system leading to disconnected backwaters, sedimentation, and introduction of non-native species are prevailing foundations. Substantial gains in energy density following restoration of former floodplain wetlands in the IRV (i.e., Emiquon Preserve and Hennepin and Hopper Lakes) are not reflected in our contemporary estimates, and could net an additional 13.3 million EUD not available in the mid-20<sup>th</sup> century (Bajer et al. 2009, McClain et al. 2018).

We suggest conservation planners use our TME values of submersed aquatic vegetation and biomass to update energetic carrying capacity estimates of aquatic macrophytes in aquatic bed wetland classes. Our results suggest that energetic carrying capacity alone does not govern

the quality of wetlands to waterfowl in the Illinois River Valley during fall. Both historically and contemporarily, large wetland area, a complexity of wetland classes, and some degree of waterfowl sanctuary were important attributes of wetlands used by large concentrations of non-breeding waterfowl in the Illinois River Valley.

## Introduction

Aquatic systems in the Midwest have been highly modified since the beginning of the 20<sup>th</sup> century, including channelization, damming, and dredging of most large rivers (e.g., Illinois, Mississippi, Ohio, Missouri) and disconnection from their natural floodplains with networks of levees (Bellrose et al. 1983, Sparks 1995). Increased water levels, sedimentation, and variation in stage heights have contributed to near extirpation of aquatic macrophytes in some areas important to waterfowl, such as the Illinois River Valley (IRV). Stafford et al. (2010) showed that coverage of submersed and floating-leaved aquatic plants in backwater lakes and wetlands of the IRV declined from >25% during 1939–1942 to <0.2% during 2005–2006. Moore et al. (2010) examined trends in aquatic vegetation occurrence using long-term resource monitoring data within the Mississippi River watershed and noted that few areas of aquatic vegetation persisted below Pool 13 of the Mississippi River, specifically noting that areas connected to the Illinois River were particularly devoid of vegetation. Highly modified rivers and tributaries carry increased sediment loads, harbor species such as common (*Cyprinus carpio*) and grass carp (*Ctenopharyngodon idella*), and subject riverine and connected floodplain areas to unnatural hydrologic regimes which prevent re-establishment of rooted aquatic vegetation (Moore et al. 2010).

In highly modified aquatic systems, successful restoration and management may include maintaining disconnected floodplains and wetlands from rivers or large lakes due to detrimental effects associated with connectivity (Jackson and Pringle 2010). While the loss of submersed aquatic vegetation (SAV) from hydrologically-connected wetlands and backwater lakes along the Illinois and Mississippi rivers is well-documented (Bellrose et al. 1983, Moore et al. 2010, Stafford et al. 2010), information is unavailable to determine the implications of these losses on



energetic carrying capacity for waterfowl, especially dabbling ducks. A few notable restoration projects have demonstrated that floodplain lakes and wetlands disconnected from these degraded river systems can sustain aquatic vegetation communities (Bajer et al. 2009, Hine et al. 2017, J. Simpson, unpublished data), but without information on the density and nutritional value of SAV in semi-permanent marshes, conservation planners cannot reliably estimate the effects on habitat objectives or effectively assess the tradeoffs in future restoration projects (e.g., restoring moist-soil wetlands versus semi-permanent marshes; Sparks et al. 2017). Information is needed on the density and forage value of SAV and other aquatic plants in semi-permanent marshes throughout the Upper Mississippi River and Great Lakes Region Joint Venture Region (hereafter, Joint Venture Region) before carrying capacity models can be updated and wetland restoration practices can be fully understood relative to value for dabbling ducks.

Therefore, we estimated TME of submersed aquatic vegetation in semi-permanent marsh habitats of the Upper Midwest for mallards (*Anas platyrhynchos*) and gadwall (*Mareca strepera*). Moreover, we sought to use contemporary and historic estimates of wetland communities during autumn within the IRV to understand the net change in energetic carrying capacity for dabbling ducks and to compare waterfowl use to wetland characteristics including energy density. Specifically, we quantified: 1) TME of submersed aquatic vegetation shoots (i.e., Canadian waterweed [*Elodea Canadensis*], coontail [*Ceratophyllum demersum*], Eurasian watermilfoil [*Myriophyllum spicatum*], sago pondweed [*Stuckenia pectinata*], southern naiad [*Najas guadalupensis*], and wild celery [*Vallisneria americana*]); 2) energy density (energetic use days [EUD/ha]) of 20 important semi-permanent wetlands used by dabbling ducks in the Midwest; 3) energy density estimates at important stopover sites within the IRV between contemporary (2005–2006) and early (1939–1942) and late (1943–1959) historic periods using

updated energy density estimates; and 4) correlation between estimated energy densities and waterfowl use days measured during long-term aerial surveys conducted by the Illinois Natural History Survey (INHS). Our results will provide novel TME energy and biomass estimates for use in estimating the energetic carrying capacity of semi-permanent marshlands and provide managers and conservation planners a basis to make informed decisions regarding the tradeoffs in wetland management for waterfowl and other waterbirds in the Upper Midwest.

## **Methods**

For detailed descriptions of methods pertaining to TME estimation see McClain (2017) and Gross (2018), and for detailed methodology regarding submersed aquatic vegetation biomass estimation see Simpson et al. (2017) and Gross (2018).

### ***Updated Energy Density of Wetland Classes***

Following true metabolizable energy and biomass estimation, we sought to update energetic carrying capacity estimates for predominate wetland classes outlined by Soulliere et al. (2017:65). We made the following changes to Table 14 in Soulliere et al. (2017): 1) updated McClain (2017) reference to McClain et al. (2018), 2) updated McClanahan (2015) reference to Osborn et al. (2017) and included a value of 0 kJ/ha and 1,741,318 kJ/ha for unconsolidated wetlands and mudflat, respectively, 3) updated Simpson and Hagy (unpublished) reference to Gross (2018) and calculated aquatic bed estimates using genera specific TME estimates, 4) added estimates of energy availability in mudflat from Smith et al. (2012), 5) calculated the weighted average for the unconsolidated wetland class across fall periods only, and 6) updated the formula for calculation of weighted fall average in the emergent wetland class.

### ***Historic vs. Contemporary Energy Density***

We used data of historic (1939–1959) and contemporary (2005–2006) wetland class availability at 16 wetland sites organized by Stafford et al. (2007b, 2010) to update the estimated energy available to migrating and wintering waterfowl in the Illinois River Valley. We combined several of the nine wetland classes of Stafford et al. (2007b, 2010) to align with the six classes in our updated version of the Soulliere et al. (2017) energy density table. Specifically, we combined persistent emergent, aquatic bed, and floating-leaved-aquatic wetland classes into the inclusive aquatic bed wetland class and we combined scrub-shrub and bottomland forest into a single forested wetland class.

We estimated the amount of energy within each wetland class by multiplying the combined area of each wetland class within a wetland site by its associated energetic availability (Stafford et al. 2007b, Table 1). We then computed the overall energy content (kJ) for a wetland site by summation across wetland classes and calculated total energetic use days (EUDs) by dividing the sum by 1410 kJ (i.e., 337 kcal/EUD; Gross 2018). Lastly, we calculated the energy density (EUD/ha) for the entire wetland site by dividing the total EUDs by the overall wetland area.

We included wetland energy density (EUD/ha) as the dependent variable in a general linear mixed model (*lme4* package; Bates et al. 2015) and tested for influences of the proportion of non-persistent vegetation, the proportion of aquatic bed, and period. We included wetland site as a random effect in models to account for inherent variation among sites. We ranked models using second order Akaike's Information Criterion ( $AIC_c$ ) and model averaged beta estimates from competing models within  $2 \Delta AIC_c$  of the best supported model (Burnham and Anderson 2002).

### ***Waterfowl Use in Relation to Wetland Characteristics***

We used cumulative annual use days between 1 October – 15 December derived from aerial surveys conducted from 1950–1959 (mallard and diving duck use days) and 2005–2006 (mallard use days) from Stafford et al. (2007a,b) to investigate whether energy density at a wetland impacted wetland use by ducks during fall. We included covariates used by Stafford et al. (2007a,b) for comparison including refuge class (proportion of the site where hunting and other disturbance was prohibited; 0–25%, 26–50%, 51–75%,  $\geq 76\%$ ), total wetland area, an interspersed-juxtaposition index, and the proportion of individual wetland classes. However, because we truncated wetland classes from Stafford et al. (2010) to match our energy density estimates (Gross 2018), our proportion of total wetland area estimates included: 1) nonpersistent emergent; 2) open water; 3) aquatic bed; 4) mudflat; 5) forested; and 6) cropland. For the contemporary data, we used a simple linear model (*stats* package; R Core Team 2017) and avoided overparameterizing by running limited covariate combinations. In separate analyses for cumulative mallard use days and diving duck use days during the historic period (1950–1959), we used a general linear mixed model (*lme4* package; Bates et al. 2015) using year and location as random effects. In each analysis, we ranked models using second order Akaike's Information Criterion ( $AIC_c$ ) and model averaged beta estimates from competing models within  $2 \Delta AIC_c$  of the best supported model (Burnham and Anderson 2002).

## Results

We completed 186 true metabolizable energy assays with mallards ( $n = 72$ ) and gadwall ( $n = 114$ ) during 2015–2018. Bioavailable energy (i.e., TME) of submersed aquatic vegetation was highly variable among duck and vegetation combinations as supported by their interaction in the most parsimonious model ( $w_i = 0.42$ ;  $R^2_m = 0.33$ ,  $R^2_c = 0.47$ ; Gross 2018:97). For gadwall, mean TME ( $\pm$  SE; kcal/g[dry]) was greatest for Eurasian watermilfoil ( $0.77 \pm 0.32$ ,  $n = 19$ ), followed by Canadian waterweed ( $0.70 \pm 0.31$ ,  $n = 20$ ), coontail ( $0.55 \pm 0.28$ ,  $n = 18$ ), southern

naiad ( $-0.61 \pm 0.34$ ,  $n = 17$ ), wild celery ( $-0.98 \pm 0.39$ ,  $n = 20$ ), sago pondweed ( $-1.07 \pm 0.33$ ,  $n = 20$ ). Mallards assimilated greatest energy from Canadian waterweed ( $1.66 \pm 0.26$ ,  $n = 13$ ), followed by coontail ( $1.51 \pm 0.28$ ,  $n = 8$ ), southern naiad ( $1.37 \pm 0.39$ ,  $n = 14$ ), sago pondweed ( $0.50 \pm 0.22$ ,  $n = 14$ ), wild celery ( $0.05 \pm 0.42$ ,  $n = 11$ ), and Eurasian watermilfoil ( $-0.13 \pm 0.26$ ,  $n = 12$ ). There was evidence from a competing model ( $w_i = 0.11$ ;  $R^2_m = 0.34$ ,  $R^2_c = 0.47$ ; Gross 2018:97) that females acquired 0.52 kcal/g ( $\pm 0.34$  kcal/g) more energy from vegetation than males and that TME declined 0.20 kcal/g ( $\pm 0.16$  kcal/g) for every 100 g increase in initial mass.

We estimated energetic carrying capacity at 318 random points within 20 wetlands across three years (2015–2017) within the Midwest, USA (Simpson et al. 2017, Gross 2018). Across all points, *Ceratophyllum* was the most commonly encountered genera ( $n = 188$ ) of submersed aquatic vegetation, followed by *Myriophyllum* ( $n = 64$ ), *Najas* ( $n = 47$ ), *Elodea* ( $n = 41$ ), and *Stuckenia* ( $n = 36$ ). These five genera comprised 91.5% of the total energy density across all points and years. Extrapolated energy density estimated at sample points ranged from 0 to 5,624 EUD/ha ( $\bar{x} = 426 \pm 52$ ) and biomass estimates ranged from 0 to 2,340 kg/ha (dry) ( $\bar{x} = 204 \pm 22$ ). Evidenced from the best supported model ( $w_i = 0.68$ ;  $R^2_m = 0.19$ ,  $R^2_c = 0.27$ ; Gross 2018:80), energy density was 195 EUD/ha (85% CL = 39 – 964) greater at managed points than unmanaged points, decreased 2 EUD/ha (85% CL = 1 – 3) for every 100 cm increase in water depth, increased 9 EUD/ha (85% CL = 6 – 12) for every 100 cm increase in Secchi depth, and increased 3 EUD/ha (85% CL = 0 – 11) if emergent vegetation was present.

We used newly derived submersed aquatic vegetation energy density estimates and those presented in Soulliere et al. (2017:65) to update estimated forage energy across wetland types used by waterfowl during the non-breeding period in the Joint Venture Region (Table 1). We then applied the updated energy estimates to early (1939–1942) and late (1943–1959) historic

and contemporary (2005–2006) habitat resource availability across 16 wetland sites in the IRV (Stafford et al. 2007a,b). The best supported model ( $w_i = 0.96$ ;  $R^2_m = 0.46$ ,  $R^2_c = 0.63$ ; Table 2) accounting for variability in total energy density included the proportion of non-persistent emergent wetland and time period. Energy density (EUD/ha) increased 21.1% (85% CI = 17.2 – 25.2) for every 10% increase in the proportion of non-persistent emergent (i.e., moist-soil) wetland at a site. Relative to the early historic period (1938–1942), energy density was 7.8% (85% CI = –2.6 – 17.2) and 30.0% (85% CI = 18.6 – 39.8) less in the late historic period (1943–1959) and contemporary (2005–2006) period, respectively. Moreover, energy density was 24.1% (85% CI = 12.2 – 34.3) less in the contemporary period than the late historic period (Table 3,4).

Mallard use days between 1 October and 15 December 1950–1959 averaged 1,807,358 (range: 9,750 – 10,294,900;  $n = 13$  wetlands, 36 wetland-year combinations) at aerially-surveyed wetland sites within the IRV (Stafford et al. 2010). There were two competing models explaining variation in mallard use days; the first ( $w_i = 0.43$ ,  $R^2_m = 0.71$ ,  $R^2_c = 0.87$ ; Table 5) included refuge, total wetland area, interspersed-juxtaposition index, and proportion of the site containing aquatic bed, whereas, the second ( $w_i = 0.22$ ,  $R^2_m = 0.69$ ,  $R^2_c = 0.86$ ; Table 5) included refuge, total wetland area, interspersed-juxtaposition index, and total energetic use days. Model averaged estimates indicated that mallard use days decreased 20,593 (95% CI = 4,774 – 36,412) for every 1% increase in the proportion of aquatic bed and 9,244 (95% CI = 864 – 17,624) for every increase of 10,000 energetic use days. Moreover, for every hectare increase in total wetland area, mallard use days increased 4,596 (95% CI = 2,658 – 6,534). Mallard use days at sites increased 279,397 (95% CI = –294,588 – 853,382) for every increase in the classification of refuge (i.e., 25% range) and 46,781 (95% CI = 19,943 – 73,618) for every point increase in the interspersed-juxtaposition index.

Diving duck use days across 13 wetland sites during 1950–1959 (36 wetland-year combinations) averaged 31,227 (range: 0 – 319,547). The best supported model ( $w_i = 0.32$ ,  $R^2_m = 0.27$ ,  $R^2_c = 0.43$ ; Table 6) explaining variation in diving duck use days included total wetland area. An increased in 1 ha of wetland area resulted in 77 (95% CI = 28 – 127) additional diving duck use days.

Mallard use days across 9 wetland sites in the contemporary period (2005–2006) averaged 559,188 (range: 82,300 – 1,112,600). The best supported model ( $w_i = 0.44$ ,  $R^2 = 0.36$ , Table 7) indicated mallard use was positively related to the proportion of refuge and increased 226,264 UDs (95% CI = 36,266 – 416,262) for every increase in the classification of refuge (i.e., 25% range).

## **Discussion**

On average, the metabolizable energy of submersed aquatic vegetation was considerably less than TME of other plant-based (e.g., seeds and winter buds) waterfowl foods but comparable to the range of invertebrate values (McClain 2017:25). Several vegetation species provided mallards and gadwall with a positive source of digestible energy. Unexpectedly, mallards assimilated greater energy from most vegetation species than gadwall, which regularly consume an herbivorous diet. In general, submersed aquatic vegetation species that were low in fiber and high in protein had greatest TME content irrespective of gross energy. Additionally, we found anecdotal evidence that vegetation collected across a temporal gradient in fall exhibited disparate crude protein, fiber, and gross energy content, which may impact energy availability to non-breeding waterfowl. Estimates of TME for submersed aquatic vegetation will allow conservation planners to more accurately evaluate wetland management practices and refine energetic carrying capacity estimates for wetlands containing aquatic macrophytes.

Despite relatively low TME of many SAV species, significant biomass in select wetland classes (i.e., freshwater pond) contributed extensive energy to non-breeding waterfowl in the Upper Midwest. Our submersed aquatic vegetation biomass estimates were greater than Brasher et al. (2007) and DiBona (2007) who found submersed aquatic vegetation on average contributed minimal biomass (10 – 100 kg/ha, Brasher et al. 2007; 1 – 110 kg/ha, DiBona 2007) during fall in Ohio and New Jersey, respectively. Instead, our SAV biomass estimates ( $\bar{x} = 206$  kg/ha; range 0 – 2,340,  $n = 315$ ) were comparable to estimates from coastal impoundments in Louisiana (200 – 274 kg/ha; Winslow 2003). Many submersed aquatic vegetation species produce seeds and winter buds, and harbor abundant invertebrates consumed by waterfowl, which contribute an additional energy source in aquatic bed habitats not accounted for in our estimates. For example, McClain et al. (2018) estimated up to 167 ( $\bar{x} = 51$  EUDs) additional energetic use days attributed to invertebrates in aquatic bed wetland class at the Emiquon Preserve in the IRV.

Our results suggest that contemporary energy density (EUD/ha) has declined since Bellrose and the INHS (Bellrose 1941, Bellrose et al. 1979) surveyed wetlands in the IRV in the mid-20<sup>th</sup> Century. This decline in energy availability is surprising despite a near 3-fold increase (12.4% early to 32.5% contemporary; Stafford et al. 2010) in the coverage of non-persistent wetland class which contained the greatest energy density among classes (i.e., 2.14 Million kcal/ha). However, the loss of alternate wetland classes such as aquatic bed (i.e., persistent emergent, aquatic bed, and floating-leaved aquatic classes) and an overall increase in forested wetland classes (i.e., bottomland and scrub-shrub) seem to counteract the non-persistent increase (Table 4). Specifically, the proportion of total EUDs available from the aquatic bed wetland class declined from 44–54% historically to ~5% contemporarily. Reasons for habitat change are discussed extensively in Stafford et al. (2010) but alteration of the Illinois River system leading



to disconnected backwaters, sedimentation, and introduction of non-native species are prevailing foundations. Substantial gains in energy density following restoration of former floodplain wetlands in the IRV (i.e., Emiquon Preserve and Hennepin and Hopper Lakes) are not reflected in our contemporary estimates (McClain et al. 2018), but demonstrate how disconnection from dynamic uncontrolled hydrological conditions can allow restoration of aquatic bed and non-persistent emergent vegetation communities. For example, McClain et al. (2018) found significant and consistent forage production contributing approximately 5,500 EUD/ha annually across aquatic bed, persistent emergent, and non-persistent vegetation communities during 3-yr study at Emiquon Preserve.

An important yet untested assumption of energetic carrying capacity models is that waterfowl distribute in an ideal and free manner relative to food density. Our analysis of historic and contemporary aerial survey numbers and habitat classification suggest that energy density was not an important factor influencing diurnal distribution of mallard and diving ducks during fall in the IRV. In fact, there was a negative relationship between total energetic use days and cumulative mallard abundance during the historic period. Yetter et al. (2018) found that radiomarked mallards used open water wetlands nearly 50% of the time diurnally in the IRV. They posited that food accessibility in agricultural fields within a short distance of wetlands allowed mallards to select wetland habitats based on disturbance avoidance or alternative motivations beyond food availability (Yetter et al. 2018). Further investigation suggest that mallard use days exceeded estimated energetic carrying capacity at 1 of 9 wetland sites in the contemporary period, while mallard use days exceeded carrying capacity at 66% (20 of 36) of wetland-year combinations during 1950–1959. Potential changes in hunting intensity, availability of alternative habitats, or shifts in temporal feeding behavior may result in patterns of

wetland use by mallards. Mallard use historically and contemporarily was significantly tied to the proportion of sanctuary habitat provided at surveyed wetland locations suggesting that areas free of anthropogenic disturbance are important for mallards during the hunting season (Beatty et al. 2014, Lancaster et al. 2015, Lancaster 2018, Yetter et al. 2018).

We recommend conservation planners update energetic carrying capacity estimates of semi-permanent, aquatic bed habitats using our estimates of TME, species composition, and biomass of submersed aquatic vegetation. We have provided an updated fall energy density table (i.e., Table 1) that we suggest be adopted by state (i.e., Illinois Department of Natural Resources Wetlands Campaign) and regional (i.e., Upper Mississippi River and Great Lakes Joint Venture) conservation planners to allocate conservation efforts in their respective regions. Our results suggest that energetic carrying capacity alone does not regulate the quality of wetlands to waterfowl in the IRV during fall. Both historically and contemporarily, large wetland area, a complex of wetland classes, and some degree of waterfowl sanctuary were important attributes of wetlands used by large concentrations of non-breeding waterfowl in the IRV. Conservation planners should consider the contribution of these attributes to the management of waterfowl and other waterbirds when evaluating competing wetland management practices and projects (Hine et al. 2017, Blake-Bradshaw 2018, Bradshaw 2018, McClain et al. 2018). Moreover, conservation planners may consider seeking opportunities to conserve wetlands in areas with managed hydrology that allows the establishment and maintenance of dynamic wetland classes (Hine et al. 2017).

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Table 1. Estimates of fall forage energy (kJ/ha)<sup>a</sup> in wetland types (NWI classes) used by waterfowl during the non-breeding period in the Upper Mississippi River and Great Lakes region. Studies were weighted by sampling framework<sup>b</sup> and mean fall energy estimates were calculated by weighted mean within wetland type. “Total energy available” (bold)<sup>c</sup> was determined by multiplying weighted means by 0.7 to account for food depletion, and these values were used for planning. Updated<sup>d</sup> from Soulliere et al. (2017:65).

Source	Emergent	Aquatic Bed	Forested	Unconsolidated (Open Water)	Mudflat	Weight
Bowyer et al. (2005)	9,916,080					2
Brasher et al. (2007)	4,210,075					3
	2,500,877					3
Donnermeyer (1982)		8,400,000				1
Greer (2007)	17,170,090					2
	12,818,730					2
Hine et al. (2015)	22,786,669	32,920,867		2,175,783		3
K.P. Kenow (unpub.)	2,895,360	4,203,000		81,600		3
	45,384,000	1,424,400				3
		4,788,000				3
Korschgen et al. (1988)		4,793,190				1
McClain et al. (2018)	7,417,462	5,754,407		16,779		3
Osborn et al. 2017	6,965,783	1,898,076	1,232,552	0	1,741,318	2
Gross (2018)		603,483				5
Smith et al. (2012)					486,281	3
Stafford et al. (2011)	7,230,998					3
Weighted fall average	12,793,713	6,969,949	1,232,552	620,226	988,296	
Total energy available (kJ/ha)	<b>8,955,599</b>	<b>4,878,964</b>	<b>862,786</b>	<b>434,158</b>	<b>691,807</b>	

<sup>a</sup> A mean 12 kJ/g of food was used to represent true metabolizable energy of all available forage (Miller 1987, Kaminski et al. 2003) unless studies used diet specific metabolizable energy estimates (i.e., McClain et al. 2018). 1 ha = 2.47acres, 1 kJ = 0.239 kcal.

<sup>b</sup> Studies weighted for regional information value based on sampling framework: 1 = <2 states and < 2 years and non-random samples; 2 = <2 states and <2years, >1 year replication; 3 = >1 year replication; 4 = >1 state replication; and 5 = replicated >1 year and > 1 state.

<sup>c</sup> Estimated energy density in croplands is calculated as 75% availability/accessibility of waste corn (1,691,172 kJ/ha) and soybeans (753,120 KJ/ha; Reinecke and Kaminski 2005).

<sup>d</sup> Updates included: updating McClain (2017) to McClain et al. (2018); updating McClanahan (2015) to Osborne et al. (2017) and including a value of 0 and 1,741,318 kJ/ha for unconsolidated wetlands and mudflat reported therein; updating Simpson and Hagy (unpublished) to Gross (2018) and including aquatic bed estimates using true metabolizable energy estimates in Gross (2018); adding estimates of mudflat from Smith et al. (2012); calculating the weighted average for the unconsolidated wetland class across fall periods only; Updating the formula for calculation of weighted fall average in the emergent wetland class.



Table 2. Model selection results for general linear mixed models that examined variation in energy density (EUD/ha) with respect to time period and the proportion of non-persistent and aquatic bed wetland at 16 surveyed wetlands sites in the Illinois River Valley 1939–1959 and 2005–2006. Number of parameters ( $K$ ), model weights ( $w_i$ ), and model deviance (Dev.) are displayed with differences in second order Akaike’s information criterion ( $\Delta AIC_c$ ) from the best supported model.

Model <sup>a</sup>	$K$	$\Delta AIC_c^b$	$w_i$	Dev.
NonPE + Period	6	-	0.96	-77.1
NonPE	4	6.4	0.04	-87.98
Aqbed	4	26.7	0.00	-108.26
Null	3	46.2	0.00	-129.88
Period	5	50.3	0.00	-129.66

<sup>a</sup> Period = year class (early historic [1939–1942], late historic [1943–1959], and contemporary [2005–2006]), NonPE = proportion of non-persistent class wetland, Aqbed = proportion of aquatic bed class wetland.

<sup>b</sup> AICc of the top model was 89.97

Table 3. Summary of energy density (energetic use days [EUD/ha]), and the proportion of non-persistent emergent (NPE), aquatic bed (AQ-B), forested (FO), unconsolidated – open water (OP-W), mudflat (MUD), and cropland (AG) wetland classes at 16 wetland sites across three time periods in the Illinois River Valley.

Wetland Site	$\bar{x}$ EUD	$\bar{x}$ NPE	$\bar{x}$ AQ-B	$\bar{x}$ FO	$\bar{x}$ OP-W	$\bar{x}$ MUD	$\bar{x}$ AG
<b>Anderson Lake</b>	<b>1,962</b>	<b>8.9</b>	<b>35.2</b>	<b>2.8</b>	<b>52.8</b>	<b>0.0</b>	<b>0.4</b>
1939–1942	1,729	14.2	17.5	4.3	64.1	0.0	0.0
1943–1959	2,378	6.6	52.8	2.4	38.2	0.0	0.0
2005–2006	766	7.3	0.0	1.5	88.5	0.0	2.7
<b>Bath Lake</b>	<b>3,064</b>	<b>44.8</b>	<b>0.0</b>	<b>11.3</b>	<b>39.3</b>	<b>0.5</b>	<b>4.1</b>
1939–1942	3,422	50.1	0.0	28.7	21.2	0.0	0.0
1943–1959	2,881	42.2	0.0	7.8	49.4	0.6	0.0
2005–2006	3,619	52.6	0.0	11.7	6.7	0.6	28.4
<b>Big Lake</b>	<b>2,703</b>	<b>4.3</b>	<b>67.5</b>	<b>3.4</b>	<b>24.8</b>	<b>0.0</b>	<b>0.0</b>
1939–1942	2,785	0.9	76.7	1.8	20.7	0.0	0.0
1943–1959	3,470	5.1	90.6	0.0	4.3	0.0	0.0
2005–2006	1,610	16.8	7.8	13.3	62.0	0.1	0.0
<b>Chautauqua NWR</b>	<b>1,400</b>	<b>5.7</b>	<b>23.0</b>	<b>8.1</b>	<b>63.0</b>	<b>0.2</b>	<b>0.0</b>
1939–1942	1,511	3.4	31.0	7.6	58.0	0.0	0.0
1943–1959	1,131	2.9	20.0	6.1	71.0	0.0	0.0
2005–2006	2,460	33.8	1.1	22.2	40.0	2.9	0.0
<b>Clear Lake</b>	<b>2,780</b>	<b>37.1</b>	<b>4.9</b>	<b>23.3</b>	<b>33.4</b>	<b>0.6</b>	<b>0.7</b>
1939–1942	3,396	47.8	4.3	19.5	26.9	1.4	0.0
1943–1959	2,494	32.4	5.0	22.3	40.2	0.0	0.0
2005–2006	1,786	19.2	5.9	37.7	32.2	0.0	5.0
<b>Crane Lake</b>	<b>2,153</b>	<b>14.3</b>	<b>30.4</b>	<b>7.3</b>	<b>46.6</b>	<b>1.5</b>	<b>0.0</b>
1939–1942	1,844	14.7	20.2	3.9	61.2	0.0	0.0
1943–1959	3,199	15.5	60.8	11.4	12.0	0.2	0.0
2005–2006	990	10.6	0.0	9.0	71.7	8.7	0.0
<b>Cuba Island</b>	<b>3,272</b>	<b>40.0</b>	<b>14.8</b>	<b>25.2</b>	<b>19.8</b>	<b>0.1</b>	<b>0.0</b>
1939–1942	2,792	25.6	26.8	29.4	18.1	0.0	0.0
1943–1959	3,707	48.7	12.5	19.8	19.0	0.0	0.0
2005–2006	2,492	34.2	0.0	38.4	26.6	0.8	0.0
<b>Douglas Lake</b>	<b>2,447</b>	<b>6.9</b>	<b>53.6</b>	<b>9.7</b>	<b>28.9</b>	<b>0.0</b>	<b>0.9</b>
1939–1942	3,062	7.2	72.7	8.9	11.2	0.0	0.0
1943–1959	1,780	2.3	41.7	5.6	50.3	0.0	0.0
2005–2006	1,988	19.2	13.3	25.0	35.3	0.0	7.1

Table 3 (Continued)

<b>Goose Fulton Co.</b>	<b>2,871</b>	<b>22.4</b>	<b>37.5</b>	<b>6.8</b>	<b>32.0</b>	<b>0.0</b>	<b>1.2</b>
1939–1942	3,452	25.8	50.2	1.2	22.8	0.0	0.0
1943–1959	1,874	4.7	40.3	4.2	50.8	0.0	0.0
2005–2006	2,705	33.5	9.3	20.4	31.7	0.2	5.0
<b>Ingram Lake</b>	<b>3,105</b>	<b>36.0</b>	<b>18.6</b>	<b>12.4</b>	<b>32.9</b>	<b>0.1</b>	<b>0.0</b>
1939–1942	2,265	2.0	57.1	10.7	30.0	0.1	0.0
1943–1959	3,385	47.3	5.7	13.0	33.9	0.1	0.0
<b>Jack Lake</b>	<b>3,244</b>	<b>33.6</b>	<b>27.8</b>	<b>9.4</b>	<b>28.7</b>	<b>0.3</b>	<b>0.1</b>
1939–1942	2,952	11.7	61.0	5.1	22.3	0.0	0.0
1943–1959	2,650	33.9	8.4	8.6	49.1	0.0	0.0
2005–2006	5,014	76.8	0.0	19.9	1.1	1.7	0.6
<b>Moscow Bay</b>	<b>2,568</b>	<b>37.2</b>	<b>0.2</b>	<b>2.4</b>	<b>59.4</b>	<b>0.9</b>	<b>0.0</b>
1943–1959	1,933	26.8	0.2	0.7	72.3	0.0	0.0
2005–2006	5,107	78.8	0.0	9.0	7.8	4.4	0.0
<b>Quiver Lake</b>	<b>1,745</b>	<b>21.2</b>	<b>3.3</b>	<b>15.0</b>	<b>57.9</b>	<b>2.3</b>	<b>0.2</b>
1939–1942	1,418	15.6	4.1	10.4	67.6	2.2	0.0
2005–2006	3,053	43.6	0.1	33.5	18.7	3.0	1.2
<b>Rice Lake</b>	<b>2,436</b>	<b>5.9</b>	<b>54.4</b>	<b>19.9</b>	<b>19.5</b>	<b>0.4</b>	<b>0.0</b>
1939–1942	2,552	4.3	61.2	18.7	15.9	0.0	0.0
1943–1959	2,538	5.0	59.1	22.0	14.0	0.0	0.0
2005–2006	1,477	15.8	5.4	11.0	63.9	3.8	0.0
<b>Sawmill Lake</b>	<b>1,198</b>	<b>1.9</b>	<b>22.7</b>	<b>19.0</b>	<b>56.2</b>	<b>0.0</b>	<b>0.2</b>
1939–1942	1,329	0.4	30.2	14.0	55.4	0.0	0.0
2005–2006	805	6.4	0.1	34.2	58.5	0.0	0.8
<b>Swan Lake</b>	<b>2,505</b>	<b>17.2</b>	<b>35.9</b>	<b>7.9</b>	<b>37.8</b>	<b>0.4</b>	<b>0.8</b>
1939–1942	1,843	3.1	42.1	6.3	47.9	0.7	0.0
1943–1959	4,432	52.5	30.1	1.2	16.2	0.0	0.0
2005–2006	3,230	38.2	17.0	20.8	19.2	0.0	4.9
<b>Period Subtotal</b>							
<b>1939–1942</b>	2,300	12.4	38.4	10.1	38.7	0.4	0.0
<b>1943–1959</b>	2,510	22.1	26.5	10.4	40.9	0.1	0.0
<b>2005–2006</b>	2,473	32.5	4.0	20.5	37.6	1.7	3.7
<b>Total</b>	<b>2,417</b>	<b>19.5</b>	<b>28.2</b>	<b>11.8</b>	<b>39.5</b>	<b>0.4</b>	<b>0.5</b>

Table 4. Proportion of energetic use days associated with wetland classes at wetland sites within the Illinois River Valley across periods.

Period	Non-persistent Emergent	Aquatic Bed	Mudflat	Cropland	Open Water	Forested
1939–1942	39%	54%	0%	0%	4%	3%
1943–1959	47%	44%	0%	0%	7%	3%
2005–2006	82%	5%	0%	1%	6%	6%

Table 5. Model selection results for general linear mixed models that examined variation in cumulative mallard use days between 1 October and 15 December with respect to explanatory variables measured at 16 surveyed wetlands sites in the Illinois River Valley 1950–1959. Number of parameters ( $K$ ), model weights ( $w_i$ ), and model deviance (Dev.) are displayed with differences in second order Akaike’s information criterion ( $\Delta AIC_c$ ) from the best supported model.

Model <sup>a</sup>	$K$	$\Delta AIC_c^b$	$w_i$	Dev.
Refuge + Area + IJI + Aqbed	8	0.0	0.43	-1105.3
Refuge + Area + IJI + EUD	8	1.4	0.22	-1106.7
Refuge + Area + IJI	7	2.3	0.14	-1111.0
Refuge + Area + IJI + NonPE	8	2.9	0.10	-1108.2
Refuge + Area + IJI + NonPE + PEM	9	4.1	0.06	-1105.8
Refuge + Area + Aqbed	7	6.8	0.01	-1115.4
Area	5	7.1	0.01	-1121.8
Refuge + Area + EUD	7	7.7	0.01	-1116.4
Refuge + Area + NonPE	7	7.7	0.01	-1116.4
Refuge + Area	6	9.2	0.00	-1120.9
Refuge + Area + Opnwtr	7	10.4	0.00	-1119.1
Refuge + Area + Mudflt	7	12.1	0.00	-1120.7
Refuge + Area + Frst	7	12.3	0.00	-1120.9
Refuge	5	22.0	0.00	-1136.6
Null	4	22.0	0.00	-1139.3

<sup>a</sup> Area = total wetland area, EUD = energetic use days, Refuge = classification of the proportion of refuge at the site, IJI = interspersed-juxtaposition index, NonPE = proportion of non-persistent class wetland, Aqbed = proportion of aquatic bed class wetland, Mudflt = proportion of mudflat, Opnwtr = proportion of open water class wetland, Frst = proportion of forested class wetland, PEM = proportion of persistent emergent class wetland.

<sup>b</sup> AICc of the top model was 1126.65

Table 6. Model selection results for general linear mixed models that examined variation in cumulative diving duck use days between 1 October and 15 December with respect to explanatory variables measured at 16 surveyed wetlands sites in the Illinois River Valley 1950–1959. Number of parameters ( $K$ ), model weights ( $w_i$ ), and model deviance (Dev.) are displayed with differences in second order Akaike’s information criterion ( $\Delta AIC_c$ ) from the best supported model.

Model <sup>a</sup>	$K$	$\Delta AIC_c^b$	$w_i$	Dev.
Area	5	0.0	0.32	-883.1
EUD	5	2.0	0.12	-885.2
Refuge + Area	6	2.1	0.11	-882.4
Refuge + Area + NonPE	7	2.4	0.10	-879.5
Null	4	3.8	0.05	-889.7
Refuge + Area + IJI	7	3.8	0.05	-881.0
Refuge	5	4.0	0.04	-887.1
Refuge + Area + Aqbed	7	4.3	0.04	-881.4
Refuge + Area + EUD	7	4.5	0.03	-881.7
Refuge + Area + IJI + NonPE	8	4.8	0.03	-878.6
Refuge + Area + Mudflt	7	5.0	0.03	-882.2
Refuge + Area + Opnwtr	7	5.2	0.02	-882.3
Refuge + Area + Frst	7	5.2	0.02	-882.3
Refuge + Area + IJI + Aqbed	8	6.4	0.01	-880.2
Refuge + Area + IJI + EUD	8	6.5	0.01	-880.3

<sup>a</sup> Area = total wetland area, EUD = energetic use days, Refuge = classification of the proportion of refuge at the site, IJI = interspersed-juxtaposition index, NonPE = proportion of non-persistent class wetland, Aqbed = proportion of aquatic bed class wetland, Mudflt = proportion of mudflat, Opnwtr = proportion of open water class wetland, Frst = proportion of forested class wetland.

Table 7. Model selection results for linear models that examined variation in cumulative mallard use days between 1 October and 15 December with respect to explanatory variables measured at 9 surveyed wetlands sites in the Illinois River Valley 2005–2006. Number of parameters ( $K$ ), model weights ( $w_i$ ), and model deviance (Dev.) are displayed with differences in second order Akaike’s information criterion ( $\Delta AIC_c$ ) from the best supported model.

Model <sup>a</sup>	$K$	$\Delta AIC_c^b$	$w_i$	Dev.
Refuge	3	-	0.44	-252.0
Null	2	0.38	0.37	-257.2
EUD	3	2.99	0.10	-255.0
Area	3	4.61	0.04	-256.6
Refuge + EUD	4	6.03	0.02	-250.8
Refuge + Area	4	6.45	0.02	-251.2
Area + EUD	4	9.15	0.00	-253.9
Refuge + Area + Mudflt	5	12.93	0.00	-245.7
Refuge + Area + Aqbed	5	16.66	0.00	-249.4
Refuge + Area + IJI	5	17.24	0.00	-250.0
Refuge + Area + EUD	5	17.99	0.00	-250.8
Refuge + Area + Frst	5	18.17	0.00	-250.9
Refuge + Area + NonPE	5	18.27	0.00	-251.0
Refuge + Area + Crop	5	18.39	0.00	-251.2
Refuge + Area + Opnwtr	5	18.43	0.00	-251.2

<sup>a</sup> Area = total wetland area, EUD = energetic use days, Refuge = classified proportion of refuge at the site, IJI = interspersed-juxtaposition index, NonPE = proportion of non-persistent class wetland, Aqbed = proportion of aquatic bed class wetland, Mudflt = proportion of mudflat, Opnwtr = proportion of open water class wetland, Frst = proportion of forested class wetland.

<sup>b</sup>  $AIC_c$  of the top model was 262.8.

Submitted by:

A handwritten signature in blue ink that reads "Aaron Yetter". The signature is written in a cursive style with a large initial 'A' and a distinct 'Y'.

Aaron P. Yetter

Date: 12/21/2018