



Habitat Relations

Wetland Food Resources for Spring-Migrating Ducks in the Upper Mississippi River and Great Lakes Region

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ABSTRACT Wetlands in the Upper Mississippi River and Great Lakes Region (UMRGLR) must annually sustain populations of migrating waterfowl from the mid-continent of North America. We used multi-stage sampling to estimate plant and invertebrate food biomasses (kg/ha) for ducks in 3 wetland habitat types at 6 stop-over locations in the UMRGLR during 2006 and 2007. Total biomass was greatest in palustrine emergent (PEM; \bar{x} = 208 kg/ha, SE = 23, median = 120), followed by palustrine forested (PF; \bar{x} = 87 kg/ha, SE = 7; median = 43), and lacustrine–riverine (LR; \bar{x} = 52 kg/ha, SE = 7; median = 27) wetlands. Ducks that foraged in forested and LR wetlands encountered the least food abundance during spring in the UMRGLR. Our estimates of food abundance were the lowest reported among other landscape scale surveys from mid-continent North America. About 1 in every 5 PEM wetlands and over half of our PF and LR wetlands that we sampled contained <50 kg/ha of food, suggesting many had little or no forage value to ducks during spring. Biomass of plant foods generally exceeded invertebrate biomass in all habitat types, although invertebrate biomass estimates exceeded plant biomass in 8 of 29 sites when considered by wetland type and year. Total food biomass estimates varied widely (\bar{x} = 6–425 kg/ha) between years and among habitats; thus, using global arithmetic means to estimate food abundance for conservation planning obscures fine scale temporal and spatial variation that may be necessary for management on local and sub-regional levels. Distributions of food biomass estimates were right-skewed, causing us to question whether arithmetic means realistically represent levels of food abundance that all ducks encounter during spring migration. Alternative measures of central tendency (e.g., median) may be more biologically realistic, particularly if spring-migrating ducks are not distributed in an ideal-free manner with respect to food abundance. Future research should determine how ducks distribute themselves in relation to variation in food abundance in space and time during spring migration to strengthen the biological approach to conservation planning in non-breeding Joint Venture areas of the North American Waterfowl Management Plan. © 2011 The Wildlife Society.

KEY WORDS conservation planning, estimation, habitat management, invertebrate abundance, mid-continent North America, multi-stage sampling, seed abundance.

Despite ongoing loss and degradation, wetlands in the Upper Mississippi River and Great Lakes Region (UMRGLR) support large proportions of mid-continent populations of

migrant waterfowl. Dabbling and diving ducks (subfamilies *Anatinae* and *Aythiinae*) rely on plant and invertebrate food resources in these wetlands during spring migration to acquire energy and protein needed to complete migration and breed (LaGrange and Dinsmore 1989, Devries et al. 2008). The UMRGLR is critically positioned between wintering and breeding areas for ducks in North America; thus, food resources in UMRGLR wetlands must support the needs of millions of ducks annually (Soulliere et al. 2007).

Late winter and early spring represent a critical time period, as the physical condition of ducks during this time can influence breeding effort (Anteau and Afton 2004, Arzel et al. 2006). Although the relationship among spring food

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resource, body condition, and breeding success has been somewhat equivocal for ducks and varies among species (i.e., capital vs. income breeders; see Bonnet et al. 1998), recent studies have demonstrated associations between reproductive performance and habitat conditions during spring migration (Newton 2006, Devries et al. 2008, Martin et al. 2009). Devries et al. (2008) showed that female mallards (*Anas platyrhynchos*) arriving on breeding grounds with more nutrient reserves had greater nesting propensity, clutch sizes, and earlier nest initiation and hatch dates compared to females on breeding grounds with fewer nutrient reserves.

The UMRGLR Joint Venture (JV) is responsible for planning and delivery of wetland habitat conservation for ducks in the region. Conservation is guided by daily ration (i.e., bioenergetics) models that use estimates of food abundance (kg/ha) to calculate energetic carrying capacities (duck-energy days; DEDs) of wetlands types in the region (Reinecke et al. 1989, Reinecke and Loesch 1996). Other JVs in North America also have undertaken large-scale assessments of food abundance to develop and refine biologically based habitat objectives to meet waterfowl population goals put forth by the North American Waterfowl Management Plan. Stafford et al. (2006a), Kross et al. (2008), and Foster et al. (2010) estimated moist soil seed, rice, corn, and soybean abundance across the southeastern United States; however, estimates of plant and invertebrate biomass from a wide range of wetland habitats were not available for the UMRGLR. Recent evidence suggests that ducks encounter the least abundance of food resources during late winter and spring compared to other seasons (Brasher et al. 2007, Anteau and Afton 2009, Greer et al. 2009). Consequently, the UMRGLR JV shifted its habitat conservation strategy from meeting energy needs during fall to providing adequate foraging habitat during late winter and spring (Soulliere et al. 2007). Current estimates used by the UMRGLR JV for planning purposes focus exclusively on plant food biomass and were primarily derived from estimates obtained outside the spring migration period (Korschgen et al. 1988, Heitmeyer 1989, Steckel 2003, Bowyer et al. 2005, Stafford et al. 2006a). A strong biological foundation for the UMRGLR JV waterfowl habitat conservation strategy requires reliable estimates of food biomass. Improved understanding of temporal and spatial variation in food abundance among stopover locations and habitat types will allow conservation planners to estimate habitat area requirements and target priority areas for future protection, restoration, and enhancement of wetlands in the region.

We conducted a large-scale sample survey to quantify biomass of plant and invertebrate food resources for ducks from 3 wetland types at 6 stop-over locations in the UMRGLR during springs 2006 and 2007. Our objectives were to: 1) precisely ($CV \leq 15\%$) estimate plant (i.e., seeds and tubers) and invertebrate biomass (kg/ha) in palustrine emergent (PEM), palustrine forested (PF), and lacustrine-riverine (LR) wetland types (Cowardin et al. 1979), and 2) compare our estimates with those currently used by the UMRGLR JV.

STUDY AREA

We chose study sites with stopover locations known to support large numbers of migrating waterfowl in Illinois, Michigan, Ohio, and Wisconsin (Bellrose 1977, Bookhout et al. 1989). These sites represented 2 latitudinal and 3 longitudinal cross-sections of the UMRGLR (Fig. 1). The UMRGLR JV implementation plan (1998) designated each site as a focus area in recognition of their regional significance to waterfowl. Each study site encompassed approximately 520 km² and site boundaries were oriented to encompass the major hydrologic features (e.g., major rivers, lake shorelines, and/or wetland complexes) and the widest possible range of wetland types at each site. Western study sites included the Cache River (89° 3' W, 37° 18' N) region of southern Illinois, the Illinois River (90° 12' W, 40° 12' N) region of central Illinois, and the southeastern glaciated region of east-central Wisconsin (88° 50' W, 43° 48' N). Eastern study sites included the Scioto River (82° 59' W, 39° 40' N) in south-central Ohio, the western Lake Erie (82° 59' W, 41° 27' N) marshes of northern Ohio, and the eastern shore of Saginaw Bay (83° 25' W, 43° 45' N) in Michigan. A complete review of long-term average (LTA) climatic conditions for each study area can be found in Straub (2008) and Hitchcock (2008). Departure from LTA for precipitation and mean daily temperature before and during the times we sampled varied by study area (Tables S1 and S2, available online at <http://onlinelibrary.wiley.com>). Total precipitation during the growing season before (May–Aug 2005) our first year of sampling was 7.6 cm below LTA, averaged across all study areas, whereas it was only 1.5 cm below LTA before the second year of sampling. Mean daily temperatures during the growing season prior to both years we sampled were near (<0.3° C) LTAs; however, temperatures during spring 2006 were above LTA for all study areas and averaged 2.1° C above LTA across all study areas.

METHODS

Sampling Design

We used ArcGIS 9.0 (Environmental Systems Research Institute, Inc., Redlands, CA) to define a 520-km² rectangular grid at each study site. Grids were identical each year except in Wisconsin, where we shifted the grid approximately 30 km south in 2007 because few ducks used the area in 2006 and we had difficulties gaining access from landowners to randomly-selected wetlands. We divided each grid into 16-ha cells. We used National Wetlands Inventory (NWI) or Wisconsin Wetlands Inventory (WWI) digital datasets to classify all wetlands within grid cells (Cowardin et al. 1979, Johnston 1984, Johnston and Meysembourg 2002). We followed Cowardin et al. (1979) to classify study-site wetlands. We confined our sampling frame to only those cells with ≥ 0.8 ha of total wetland area. We randomly selected 35–45 cells without replacement at each study site in 2006 and 2007.

We visited all wetlands in randomly selected 16-ha cells to ground-truth the NWI and WWI digital wetland coverages.

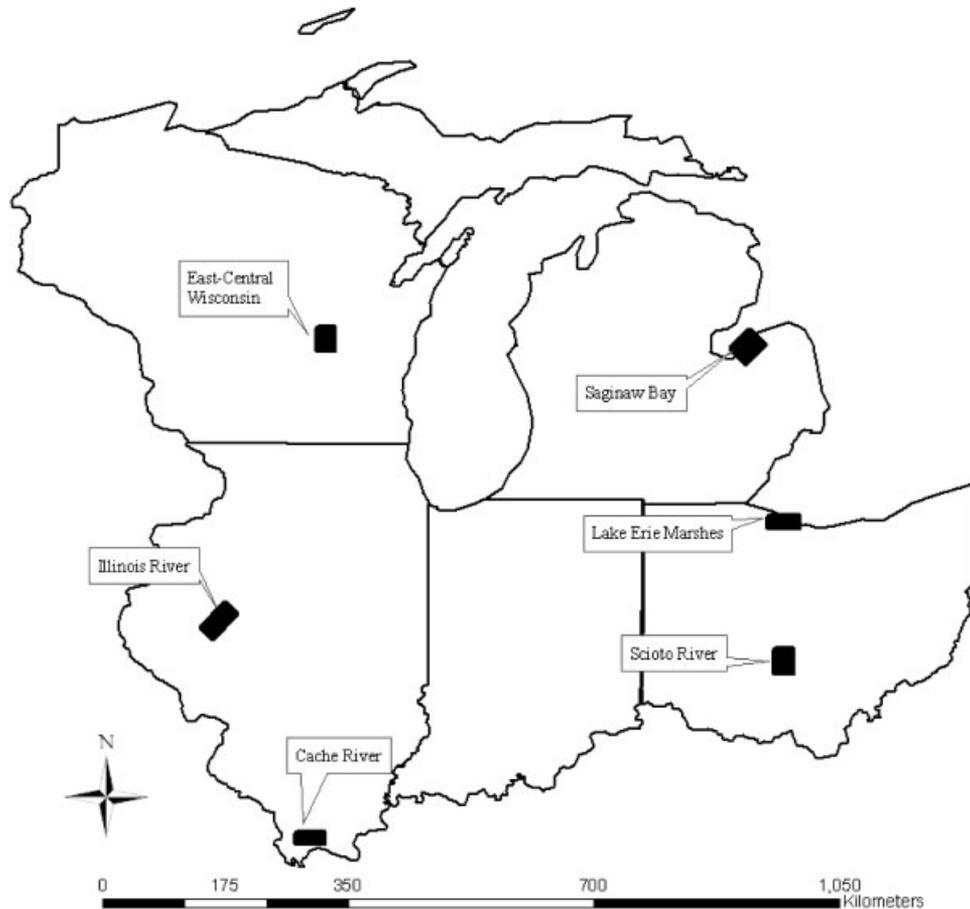


Figure 1. Locations (■) of study sites within the Upper Mississippi River and Great Lakes Region, USA where duck food biomass was estimated during February–May 2006–2007.

We re-classified wetlands as PEM, PF, or LR based on observed hydrological and vegetation characteristics when field observations differed from digital coverages (Cowardin et al. 1979). Palustrine emergent wetlands were primarily shallow and deep marshes with persistent or seasonal emergent vegetation, PF wetlands were primarily forested or scrub-shrub habitats, and LR wetlands were large or deep lakes and rivers. We then chose a random subset of wetlands and sampled from the population of wetlands within cells. We allocated our sampling effort among the 3 wetland habitat types in proportion to their relative abundance within each study area. This allowed us to more intensively sample the most common wetland types within each study area.

Sample Collection

We sampled wetlands to estimate biomass of duck foods during 2 time periods in 2006 and 2007: 1) immediately following ice-thaw or before migrating ducks arrived, and 2) after most ducks departed from each study site as determined from concurrent observations of duck abundance and migration chronology (Table S3, available online at <http://onlinelibrary.wiley.com>). We sampled plant and invertebrate biomass with 2 nektonic net-sweep and 2 benthic core samples from each wetland during both sample periods. We sampled nektonic biomass by sweeping a D-shaped net (500-mm mesh, 0.072-m² opening, Ward's Natural

Science, Rochester, NY) in the water column within a 100 cm × 50 cm, 500-μm mesh side-panel drop box. We sampled benthic biomass by extracting a 7-cm diameter substrate core (10-cm depth) from within the drop box. We washed all samples in the field through a 500-μm sieve bucket and placed them in polyethylene bags containing 10% formalin solution. We separated non-food material from plant and invertebrate food items in the laboratory. We dried all samples at 60° C for 48 hr to reach constant mass and weighed them to the nearest 0.1 mg. We report all biomass density estimates as kg/ha (dry mass). We defined duck foods as any invertebrate or plant taxon that was found in esophagi from a concurrent diet study of mallards, blue-winged teal (*Anas discors*), gadwall (*Anas strepera*), ring-necked duck (*Aythya collaris*), and lesser scaup (*Aythya affinis*; Hitchcock 2008) or food items known to be consumed by at least 1 species of duck in the UMRGLR (Havera 1999).

Statistical Analyses

We used a multi-stage sampling design to estimate plant and invertebrate biomass in randomly selected wetlands at each study site. Multi-stage sampling can yield estimates of means and variances that are less biased than those derived from simple random sampling. Multi-stage sampling is particularly appropriate for large-scale natural resource surveys where accounting for varying sample selection probabilities

is necessary (Conroy and Smith 1994, Stafford et al. 2006b). We used the SPSURVEY package (Kincaid et al. 2008) in R 2.8.1 (R Development Team 2006) to estimate plant and invertebrate biomass, which uses Taylor series linearization to estimate variances of means. We designated cells as primary sampling units, wetlands within cells as secondary units, and point samples (i.e., sweep and core samples) within wetlands as tertiary units. We calculated the probability of selecting each cell by dividing the number of sampled cells by the total number of cells at each study site. The probability of sampling a wetland was the reciprocal of the number of wetlands of each type sampled within each cell. We calculated the probability of collecting a nektonic sweep sample by dividing the area sampled (0.50 m²) by the wetland area. We did not calculate sampling probabilities for core samples because they were always taken within the mesh drop box; thus, probabilities were always equal and would not have influenced the mean or variance. The reciprocal of the product of the 3 selection probabilities (i.e., cell, wetland, and sweep) was the sample weight used for estimation (Stafford et al. 2006b). We also specified a finite population correction for each study site as the population of cells that contained ≥ 0.8 ha of wetlands. Finite population corrections are used to adjust variance estimates when a substantial fraction of the total population of interest has been sampled (Kincaid et al. 2008).

We calculated overall within-year estimates for each habitat type by averaging study area-specific means. Overall, we calculated between-year estimates for each habitat type by averaging them as un-weighted annual means. We estimated variances and 95% confidence limits of means across sites by summing year-specific variances and dividing by the square of the number of years (i.e., 2²; Stafford et al. 2006a, Kross et al. 2008). We used the BOXPLOT.STATS function in R 2.8.1 to calculate 95% confidence limits for medians. Median 95% confidence limits were calculated as ± 1.58 the interquartile range/ \sqrt{n} and were based on asymptotic normality of the median (McGill et al. 1978).

RESULTS

Within years and sites, all 95% confidence intervals of mean plant and invertebrate biomass estimates, overlapped between sampling periods for each habitat type. Therefore, we present estimates of duck food biomass across time periods for each study site, wetland type, and year. Although estimates within habitat types varied among sites and between years, we met our a priori objective to precisely (CV $\leq 15\%$) estimate food biomass in each habitat across years. We collected 934, 666, and 453 samples from 229, 149, and 104 wetlands in PEM, PF, and LR habitats, respectively, during springs 2006 and 2007. We did not sample PF wetlands at Saginaw Bay and east central Wisconsin, or LR wetlands at Cache River, because these wetland types were rare or absent in these study areas. Plant biomass was primarily concentrated in the substrate (core samples) at each study area and habitat type with mean proportions ranging from 97.6% in PF wetlands at Lake Erie to 99.6% in LR wetlands at Saginaw Bay. Likewise, we

found most invertebrate biomass in the substrate, with mean proportions ranging from 87.1% in PF wetlands at Lake Erie to 99.4% in LR wetlands at Illinois River.

Invertebrate foods were generally less abundant than plant foods (on a dry weight basis), but exceeded plant biomass estimates in 8 of 29 sites when considered by wetland type and year (Fig. 2). Invertebrates contributed the greatest

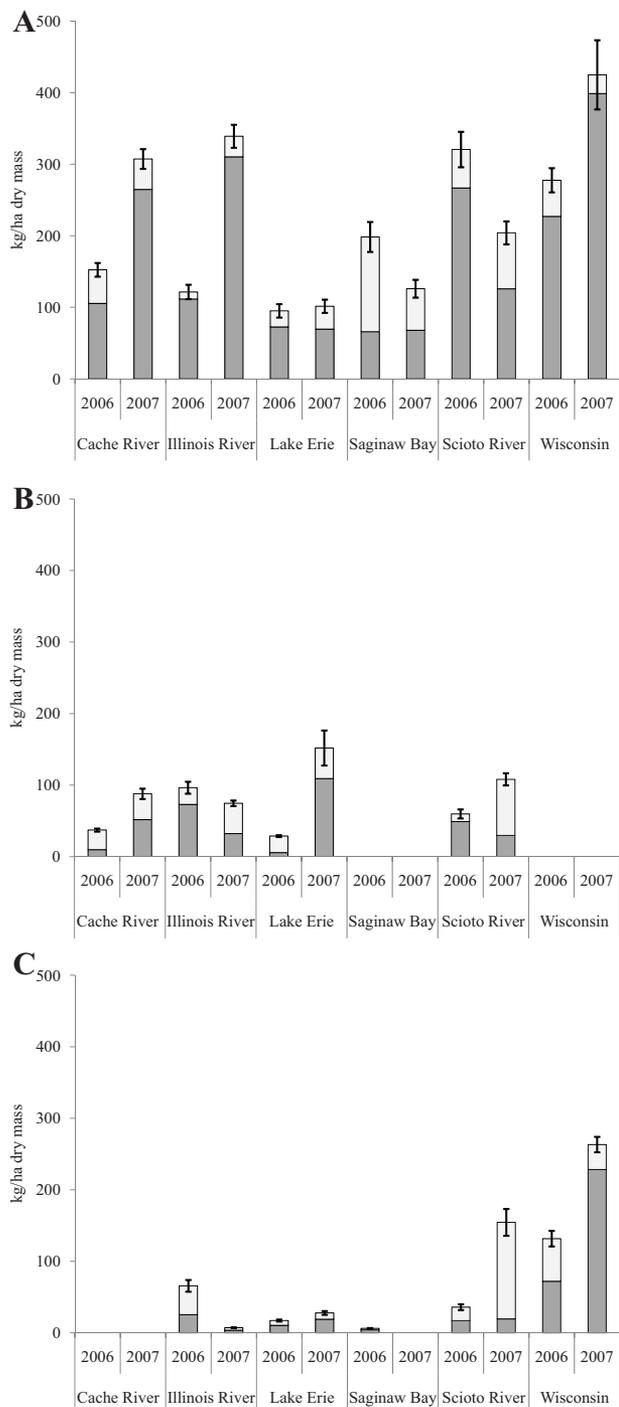


Figure 2. Mean plant (dark gray) and invertebrate (light gray) biomass (kg/ha; dry mass), relative to total estimated biomass, for palustrine emergent (A), palustrine forested (B), and lacustrine-riverine (C) wetlands at sites in the Upper Mississippi River and Great Lakes Region during February–May 2006 and 2007. Standard error bars represent ± 1 SE around the total biomass estimate.

proportion of total food biomass in LR wetlands (39.7%), followed by PF wetlands (37.9%) and PEM wetlands (26.4%) across years and study areas. The greatest contribution of invertebrates to total food biomass was 81% from LR wetlands at Scioto River, whereas the least was 8% from PEM wetlands at Illinois River across years and study areas (Fig. 2).

Estimates of seed and invertebrate biomass varied widely between years and among sites and wetland habitat types (Tables S4 and S5 available online at <http://onlinelibrary.wiley.com>). Wetland specific-estimates within sites varied substantially (up to >3 orders of magnitude) for each wetland habitat type. The distributions of biomass estimates within each habitat type were right-skewed for all 3 wetland types (Fig. 3). Mean total food abundance exceeded the value assumed by the UMRGLR JV waterfowl conservation strategy for the PEM wetland type. Median total food biomass was below the mean and the values assumed by the UMRGLR JV in all 3 wetland types.

Palustrine emergent wetlands had the greatest total food biomass with a global mean of 208 kg/ha (95% CI: 190–226 kg/ha; Table 1) and median of 120 kg/ha (95% CI: 101–138 kg/ha). Pooled across years, total food biomass in PEM wetlands ranged from 98 kg/ha at Lake Erie to 351 kg/ha at Wisconsin, whereas year-specific biomass ranged from 95 kg/ha at Lake Erie in 2006 to 425 kg/ha at Wisconsin in 2007. Four of 6 study areas had greater total biomass in 2007 than in 2006. The greatest relative difference in total biomass between years at any site occurred at Illinois River where biomass increased 73.6% from 121 kg/ha in 2006 to

339 kg/ha in 2007. Of all PEM wetlands sampled, 18.3% contained ≤ 50 kg/ha of total food biomass; a biomass threshold below which ducks are thought to cease foraging (Reinecke et al. 1989). Wetland-specific estimates within sites and across both years for total food biomass ranged from 24 kg/ha to 854 kg/ha (Cache River), 44 kg/ha to 733 kg/ha (Illinois River), 5 kg/ha to 1,697 kg/ha (Wisconsin), 11 kg/ha to 738 kg/ha (Scioto River), 2 kg/ha to 431 kg/ha (Lake Erie), and 1 kg/ha to 1,491 kg/ha (Saginaw Bay).

Palustrine forested wetlands had a global mean biomass of 87 kg/ha (95% CI: 80–94 kg/ha; Table 1) and median of 43 kg/ha (95% CI: 35–51 kg/ha). Pooled across years, total food biomass in PF wetlands ranged from 6 kg/ha at Saginaw Bay to 90 kg/ha at Lake Erie, whereas year-specific biomass ranged from 6 kg/ha at Lake Erie in 2006 to 152 kg/ha at Lake Erie in 2007. Three of the 4 sites had greater total biomass in 2007 than 2006. The greatest relative difference in total biomass between years at any site occurred at Lake Erie, where biomass increased 84.1% from 29 kg/ha in 2006 to 152 kg/ha in 2007. Of all PF wetlands sampled, 51.7% had ≤ 50 kg/ha of total food biomass. Wetland-specific estimates within sites and across years for total food biomass ranged from 0 kg/ha to 851 kg/ha (Cache River), 9 kg/ha to 628 kg/ha (Illinois River), 0 kg/ha to 1,140 kg/ha (Scioto River), and 5 kg/ha to 1,018 kg/ha (Lake Erie).

Lacustrine–riverine wetlands had a global mean of 52 kg/ha (95% CI: 34–69 kg/ha; Table 1) and median of 27 kg/ha (95% CI: 12–42 kg/ha). Across years, total food biomass in LR wetlands ranged from 62 kg/ha at Cache River to

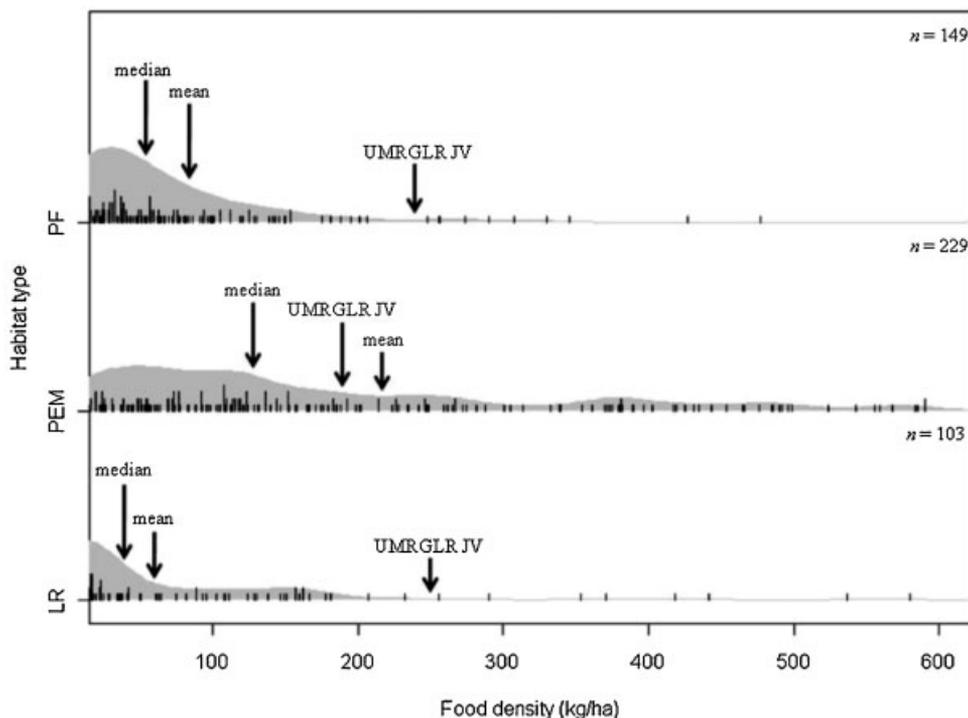


Figure 3. Dot plot depicting distribution of total duck food biomass in palustrine emergent (PEM), palustrine forested (PF), and lacustrine–riverine (LR) wetlands (●) relative to median and mean from this study and the estimate used by the Upper Mississippi River and Great Lakes Region Joint Venture (UMRGLRJV; Soulliere et al. 2007). Shaded region represents distribution and was generated with BEANPLOT function (Kampstra 2008) in R 2.8.1. Mean and median values for each habitat type are across site and years. Wetlands (n) were sampled during February–May 2006 and 2007.

Table 1. Estimated means (\bar{x}), standard errors (SE), coefficients of variation (CV), and median of total food biomass (kg/ha dry mass) collected in palustrine emergent, palustrine forested, and lacustrine–riverine wetlands at 6 study sites in the Upper Mississippi River and Great Lakes Region, USA, during February–May 2006 and 2007. Mean food density for all sites (All) was calculated as an un-weighted mean of annual means.

| Site ^a | Palustrine emergent | | | | | | | Palustrine forested | | | | | | | Lacustrine–riverine | | | | | | |
|-------------------|---------------------|-----------|---------------|-----------|----|----|-------------|---------------------|---------------|-----------|----|----|-------------|-----------|---------------------|-----------|----|----|--|--|--|
| | n PSU ^b | n samples | Total biomass | | | | n PSU | n samples | Total biomass | | | | n PSU | n samples | Total biomass | | | | | | |
| | | | Median | \bar{x} | SE | CV | | | Median | \bar{x} | SE | CV | | | Median | \bar{x} | SE | CV | | | |
| CR | 28 | 154 | 131 | 230 | 19 | 8 | 61 | 280 | 47 | 62 | 7 | 11 | Not sampled | | | | | | | | |
| IR | 19 | 84 | 167 | 230 | 24 | 10 | 41 | 228 | 62 | 85 | 10 | 11 | 22 | 95 | 12 | 36 | 7 | 18 | | | |
| LE | 39 | 160 | 69 | 98 | 13 | 13 | 24 | 72 | 25 | 90 | 22 | 24 | 18 | 66 | 18 | 22 | 3 | 14 | | | |
| SB | 57 | 188 | 139 | 162 | 24 | 15 | Not sampled | | | | | | 10 | 32 | 11 | 6 | 2 | 27 | | | |
| SR | 21 | 102 | 141 | 262 | 32 | 12 | 23 | 86 | 39 | 84 | 11 | 14 | 25 | 110 | 16 | 95 | 19 | 20 | | | |
| WI | 65 | 246 | 151 | 351 | 59 | 17 | Not sampled | | | | | | 28 | 150 | 104 | 197 | 16 | 8 | | | |
| All | 229 | 934 | 120 | 208 | 23 | 11 | 149 | 666 | 43 | 87 | 7 | 9 | 103 | 453 | 27 | 52 | 7 | 14 | | | |

^a CR = Cache River, IR = Illinois River, LE = Lake Erie Marshes, SB = Saginaw Bay, SR = Scioto River, WI = East-central Wisconsin.

^b PSU = Primary sampling units or number of wetlands sampled.

197 kg/ha at Wisconsin, whereas year-specific total biomass ranged from 6 kg/ha at Saginaw Bay in 2006 to 263 kg/ha at Wisconsin in 2007. Three of the 4 sites had greater total biomass in 2007 than 2006. The greatest relative difference in total biomass between years at any site occurred at Illinois River, where total food biomass was 90.4% less in 2007 (7 kg/ha) than in 2006 (66 kg/ha). Of all LR wetlands sampled, 63.5% had ≤ 50 kg/ha of total biomass. Wetland-specific estimates within sites and across both years for total food biomass ranged from 2 kg/ha to 256 kg/ha (Illinois River), 2 kg/ha to 580 kg/ha (Wisconsin), 0 kg/ha to 711 kg/ha (Scioto River), 0 kg/ha to 157 kg/ha (Lake Erie), and 1 kg/ha to 162 kg/ha (Saginaw Bay).

DISCUSSION

Our estimates of food abundance were based on a large sample ($n = 481$) of diverse wetlands that included a variety of ownership and management categories throughout the geographic extent of the UMRGLR. The multi-stage sampling design permitted us to account for varying sampling probabilities among study areas, years, and habitat types. Our estimates specifically focused on plant and invertebrate foods that were known to be consumed by spring-migrating ducks based on concurrent diet analyses (Hitchcock 2008).

Ninety-five percent confidence intervals about mean food abundance estimates for ducks in all 3 wetland types we sampled did not include any of the estimates used to establish habitat objectives in the UMRGLR JV (Soulliere et al. 2007). Our global estimate for PEM wetlands (208 kg/ha) modestly exceeded the level of food abundance assumed by the JV for shallow semi-permanent and deep marsh (188 kg/ha). Habitat objectives for this habitat type are likely sufficient given current waterfowl population goals of the JV. Current habitat objectives established by the UMRGLR JV for forested and LR wetlands are inaccurate and very liberal, given that our estimates of food abundance for PF (87 kg/ha) and LR (52 kg/ha) wetlands were 2.6 (226 kg/ha) and 4.9 (256 kg/ha) times lower than assumed by the UMRGLR JV for those habitat types, respectively. Thus, the amount of habitat required to support populations of spring-migrating ducks that forage in forested and LR wetlands has been, to this point, substantially underestimated. Our results suggest

duck species that forage in forested wetlands, such as wood ducks (*Aix sponsa*), and LR wetlands, such as lesser scaup and other diving ducks, likely encounter the least amount of food, relative to other species, during spring in the UMRGLR. Research has shown that ducks abandon food patches when food abundance drops below a foraging threshold (e.g., 50 kg/ha for rice fields; Reinecke et al. 1989, Greer et al. 2009) during fall and winter. No studies have measured foraging thresholds in wetland habitats during spring. We cannot, therefore, assume that foraging thresholds measured elsewhere can be applied to our results obtained from naturally vegetated wetland habitats during spring. Nevertheless, about 1 in every 5 PEM wetlands and over half of our PF and LR wetlands we sampled contained < 50 kg/ha of duck food biomass. If a 50-kg/ha foraging threshold applies to the wetlands we sampled, our results indicate many wetlands, especially PF and LR, may have limited or no forage value to ducks during spring.

Few studies have estimated biomass of food resources for ducks during spring migration. Brasher et al. (2007) sampled passively- and active-managed wetlands in central and northern Ohio during springs 2000–2002. Brasher et al. (2007) presented results in DEDs/ha, so we converted their results to biomass to facilitate comparisons with our estimates. Averaged across years and management regimes (i.e., passive and active), spring DEDs/ha values from Brasher et al. (2007) were equivalent to 14 kg/ha of plant biomass (M. G. Brasher, Gulf Coast Joint Venture, personal communication). Our global estimate of plant biomass in PEM wetlands was 11 times greater than estimates from Brasher et al. (2007), whereas our site-specific estimate of plant biomass from Lake Erie marshes was 6.5 times greater than Brasher et al. (2007). We acknowledge that these differences could have been caused in part by different sampling methodologies. Brasher et al. (2007) used a stove-pipe sampler that collected biomass from the substrate surface and water column, whereas we sampled from the water column and the top 10 cm of the substrate, where we found nearly all (range across sites: 97.6–99.6%) plant food biomass. Bartonek and Hickey (1969) also reported few seeds ($< 1\%$ total biomass) in the water column, and Baldassare (1980) found $> 85\%$ of seeds in substrate samples. Because

food biomass is almost entirely within or on the substrate of wetlands during spring, the depths at which ducks can obtain food from within substrates must be determined when considering the actual availability of foods consumed by different species or foraging guilds. Research in this area is limited. Canvasbacks (*Aythya valisineria*) consume sago pondweed (*Potamogeton pectinatus*) tubers up to 20 cm below the substrate surface (Anderson and Low 1976). Some dabbling ducks (e.g., teal) likely do not forage deep into the substrate (if at all), and northern shovelers (*Anas clypeata*) forage almost entirely near the water surface (Euliss et al. 1991). Thus, our estimates of food abundance apply to dabbling and diving ducks in the aggregate, presuming that the duck community at large, rather than any particular species, can fully exploit the food sources we sampled.

Our estimates did not include subterranean plant parts or submerged aquatic vegetation (SAV), which are primary foods for ducks in deep-water habitats (Korschgen et al. 1988, Hartke et al. 2009). Korschgen et al. (1988) estimated that winter buds from wild celery (*Valisineria americana*) produced 358 kg/ha in autumn in deepwater habitats in Wisconsin. Winslow (2003) estimated SAV biomass was 199–274 kg/ha in coastal impoundments in Louisiana during winter. However, winter weather conditions in the UMRGLR typically cause SAV to disassociate by spring (Schloesser and Manny 1990, Wersal et al. 2006). Therefore, SAV contributed negligibly to total food biomass in our study, a finding supported by Brasher et al. (2007) and DiBona (2007).

Despite including invertebrate biomass, our estimates of total food abundance during spring were 3–10 times less than estimates from studies that measured food abundance in autumn. Kross et al. (2008) estimated 496 kg/ha of seed in moist soil wetlands during late autumn 2002–2004 in the Mississippi Alluvial Valley. Bowyer et al. (2005) found that seed abundance in a large moist-soil wetland at Chautauqua National Wildlife Refuge in central Illinois ranged from 329 kg/ha to 1,231 kg/ha in October. Fredrickson and Taylor (1982) estimated that intensively managed moist soil units in Missouri produced about 1,630 kg/ha of seed. Diminished levels of food are to be expected in spring because of depletion by foraging wildlife (Barney 2008, Foster et al. 2010) and deterioration of seeds (Nelms and Twedt 1996) throughout autumn and winter. Regardless, our estimates support earlier work (Brasher et al. 2007) and the assumption of the UMRGLR JV waterfowl implementation plan that spring is the most food-limited season for non-breeding ducks. Additional research will reveal if our findings are unique to the UMRGLR.

Our study is the first design-based sample survey to simultaneously estimate abundances of aquatic invertebrates and plant seeds from wetlands used by ducks during spring. Invertebrate foods were generally less abundant than plant foods, based on dry mass. Plant biomass, mostly seeds, are an annually renewed resource which exists as a standing crop that can be measured at discrete points in time. Conversely, invertebrate populations turnover inter-annually, so abundance can fluctuate widely within seasons (Murkin and

Kadlec 1986, Anteau and Afton 2008). Consequently, our estimates of invertebrate biomass reflect only standing crop at specific points in time and, therefore, do not account for renewal of invertebrate foods. As a result, we conservatively estimated the potential contributions of invertebrates to meeting nutritional requirements of spring-migrating ducks. Because many ducks switch from a diet of primarily plant material to an invertebrate diet near the end of winter or during spring migration (Miller 1987, Gammonley and Heitmeyer 1990, Miller et al. 2009), we must recognize and manage for sufficient invertebrate abundance during spring.

Within study area variation, measured as the range of estimates from individual wetlands, for each habitat type varied by up to >3 orders of magnitude. At least 2 reasons explain why we encountered large within wetland variation in total biomass. The first is related to our sampling design. We took few samples (4 cores and sweeps each) within many ($n = 481$) wetlands over a large-geographic area as opposed to taking many samples from a few wetlands covering a smaller area. We based this decision on our priority to capture maximal regional variability given how many samples we could process. We knowingly sacrificed our precision of estimates within wetlands but as a result, our inferential scope extends well beyond what would have been appropriate had we sampled intensively within wetlands. Another reason for large within-wetland variation is the inherent diversity of wetland types within each wetland class sampled (i.e., PEM, PF, LR). Many sub-categories of wetlands (e.g., temporary, moist-soil, cattail, etc.) that influence food abundance for ducks occur within each of the 3 habitat types that we used. Further, some wetlands within a category differ with respect to their management regime (e.g., active vs. passive). The hierarchical classification of Cowardin et al. (1979) uses numerous combinations of wetland subsystems, classes, and modifiers to uniquely classify wetlands, although we generalized to only 3. Because of the internal heterogeneity and diversity of wetland types within and especially across our 6 study areas, we were unable to derive precise estimates of food abundance for very specific habitat types, even with a large (>2,000) number of samples. We acknowledge that local wetland-specific characteristics and the intensity of sampling within wetlands influence estimates of duck food abundance. However, we present estimates for 3 wetland habitat types that correspond to a landscape-scale resolution that is useful for conservation planning purposes. As such, our estimates include variation from the many sub-categories within each habitat type.

Waste grain from agriculture is readily consumed by some duck species (Manly et al. 2004, Greer et al. 2009) and could potentially compensate for low levels of food abundance in wetlands during spring. However, Straub (2008) found that waste grain biomass estimates from spring in corn (33 kg/ha) and soybean (14 kg/ha) fields of the Upper Midwest were less than total biomass estimates from all wetlands sampled in this study. Similarly, Foster et al. (2010) estimated abundance of corn, soybean, and grain sorghum at 39 kg/ha, 26 kg/ha, and 19 kg/ha, respectively, during January in

Tennessee. Further, evidence suggests waste grain declines to levels after harvest that are likely unprofitable for ducks to exploit during winter and spring (Barney 2008, Foster et al. 2010, Pearse et al. 2010). Although croplands may be a primary source of energy in some areas after winter, our data indicates that greater densities of duck foods are found in wetland habitats.

Non-breeding JVs derive habitat objectives from energetic carrying capacity (i.e., duck energy days) as estimated from arithmetic means of food biomass studies. Combined with estimates of use-rates (i.e., duck use-days), this approach provides information to evaluate when and where habitat surpluses or deficits might occur for wintering and migrating ducks (Loesch et al. 1994, Wilson and Esslinger 2002, Soulliere et al. 2007). This assumption that mean food biomass expresses food availability as encountered by the typical duck or the target population as a whole goes largely unquestioned. However, duck food distributions are often skewed (Brasher 2010) and the median is considered to be a more suitable measure of central tendency of skewed distributions. Thus, arithmetic means possibly misrepresent levels of food abundance typically encountered by spring-migrating ducks when calculated from a skewed sample distribution of biomass, as in our study. We suggest that the best measure of central tendency of biomass estimates depends on how ducks are distributed in relation to food abundance.

Right-skewed distributions with many low or nil values are a common characteristic of duck food biomass data, even more so in spring compared to other seasons (Stafford et al. 2006a, Kross et al. 2008). We observed right-skewed distributions of food biomass in all 3 wetland types we sampled, with many wetlands containing ≤ 50 kg/ha and few containing >500 kg/ha of food (Fig. 3). Thus, arithmetic mean biomass estimates calculated from right-skewed distributions may overestimate levels of food abundance experienced by individual ducks and by the population as a whole. We contend that the arithmetic mean is a useful estimate of food abundance for conservation planning if spring-migrating ducks distribute themselves in an ideal-free manner (sensu Fretwell 1972) with respect to distribution and abundance of food in space and time. However, a number of intrinsic and extrinsic forces, independent of food, contribute to spatial and temporal patterns of duck migration. Examples include fidelity to migration routes that connect breeding and wintering ranges (Ashley et al. 2010), chronology of weather events that favor or inhibit migration (Schummer et al. 2010), availability of secure resting areas, or other non-food factors (Webb et al. 2010). The more that duck distributions diverge from ideal-free with respect to food, the greater the arithmetic mean should over-estimate the level of food abundance that ducks encounter during spring migration. We suggest that the median represents a more biologically meaningful estimate of central tendency in such situations. Medians are readily interpreted for conservation planning as the 50% quantile where spring-migrating ducks encounter low versus high levels of food abundance, if ducks are distributed independently of food abundance. Conversely, the median becomes an increasingly conservative

estimate of food abundance as duck distribution in relation to food resources approaches the ideal-free condition.

MANAGEMENT IMPLICATIONS

Spring-migrating ducks likely experience less food biomass relative to other non-breeding seasons. Therefore, priorities for continental-scale conservation planning should continue to recognize the importance of protecting, restoring, enhancing, and managing wetland habitats used by spring-migrating ducks in large regional landscapes such as the UMRGLR. At more local scales we encourage wetland managers to consider waiting to flood some wetlands until late winter or early spring because this has been shown to increase seed biomass availability (Heitmeyer 2006, Greer et al. 2007). Our estimates of plant, invertebrate, and total duck food biomass during spring migration should be used to refine wetland habitat objectives of the UMRGLR JV. Forested and LR wetlands had substantially less food than currently assumed by the UMRGLR JV so habitat needs for these wetland types have been underestimated.

We caution, however, that applying global values in daily ration models for conservation planning across broad spatial and temporal scales may be too coarse for habitat conservation at local scales. Instead, models that account for spatial and temporal variation might better represent the dynamic nature of food resources and habitat needs of spring-migrating ducks in the UMRGLR. We encourage conservation planners and wetlands managers to understand the underlying distributions from which energetic carrying capacity estimates are derived and the consequences of applying different measures of central tendency. Because biomass estimates are used to estimate carrying capacity and derive habitat objectives, large differences between mean and median food biomass could directly affect habitat conservation objectives. Clearly, research is needed to better understand how spring-migrating ducks distribute themselves in relation to variation in food abundance in space and time. Future studies should seek to identify thresholds of use and subsequent abandonment of foraging habitats and incorporate these values into conservation plans as giving-up densities. Such efforts will better illuminate which estimates of central tendency of food biomass best represent the relationship of duck use rates to energetic carrying capacity of wetland habitats.

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LITERATURE CITED

- Anderson, M. G., and J. B. Low. 1976. Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. *Journal of Wildlife Management* 40:233–242.
- Anteau, M. J., and A. D. Afton. 2004. Nutrient reserves of lesser scaup during spring migration in the Mississippi flyway: a test of the spring condition hypothesis. *Auk* 121:917–929.
- Anteau, M. J., and A. D. Afton. 2008. Amphipod densities and indices of wetland quality across the upper-Midwest, USA. *Wetlands* 28:184–196.
- Anteau, M. J., and A. D. Afton. 2009. Wetland use and feeding by lesser scaup during spring migration across the upper Midwest, USA. *Wetlands* 29:704–712.
- Arzel, C., J. Elmberg, and M. Guillemain. 2006. Ecology of spring-migrating Anatidae: a review. *Journal of Ornithology* 147:167–184.
- Ashley, P., K. A. Hobson, S. L. Van Wilgenburg, N. North, and S. A. Petrie. 2010. Linking Canadian harvested juvenile American black ducks to their natal areas using stable isotope methods. *Avian Conservation and Ecology* 5(2).
- Baldassare, G. A. 1980. Residual seeds as potential spring waterfowl foods in small, man-made impoundments. *Prairie Naturalist* 12:1–8.
- Barney, E. S. 2008. Change in availability and nutritional quality of post-harvest waste corn on waterfowl staging areas near Long Point, Ontario. Thesis, University of Western Ontario, London, Canada.
- Bartonek, J. C., and J. J. Hickey. 1969. Selective feeding by juvenile diving ducks in summer. *Auk* 86:443–457.
- Bellrose, F. C. 1977. Species distribution, habitats, and characteristics of breeding dabbling ducks in North America. Pages 1–17 in T. A. Bookhout, editor. *Waterfowl and wetlands—an integrated review*. Proceedings of the 39th Midwest Fish and Wildlife Conference, Madison, Wisconsin, USA.
- Bookhout, T. A., K. D. Bednarik, and R. W. Kroll. 1989. The Great Lakes marshes. Pages 131–156 in L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, USA.
- Bonnet, X., D. Bradshaw, and R. Shine. 1998. Capital versus income breeding: an ectothermic perspective. *Oikos* 83:333–342.
- Bowyer, M. W., J. D. Stafford, A. P. Yetter, C. S. Hine, M. M. Horath, and S. P. Havera. 2005. Moist-soil plant seed production for waterfowl at Chautauqua National Wildlife Refuge, Illinois. *The American Midland Naturalist* 154:331–341.
- Brasher, M. E., J. D. Steckel, and R. J. Gates. 2007. Energetic carrying capacity of actively and passively managed wetlands for migrating ducks in Ohio. *Journal of Wildlife Management* 71:2532–2541.
- Brasher, M. E. 2010. Duck use and energetic carrying capacity of actively and passively managed wetlands in Ohio during autumn and spring migration. Dissertation, The Ohio State University, Columbus, USA.
- Conroy, M. J., and D. R. Smith. 1994. Designing large-scale surveys of wildlife abundance and diversity using statistical sampling principles. *Transactions of the North American Wildlife and Natural Resources Conference* 59:159–169.
- Cowardin, L. M., V. Carter, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS—79/31. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.
- Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). *Auk* 125:618–628.
- DiBona, M. T. 2007. Seasonal food availability for wintering and migrating dabbling ducks and its implications for management at the Hackensack Meadowlands of New Jersey. Thesis, University of Delaware, Newark, USA.
- Euliss, N. H., R. L. Jarvis, and D. S. Gilmer. 1991. Feeding ecology of waterfowl wintering on evaporation ponds in California. *Condor* 93:582–590.
- Foster, M. A., M. J. Gray, and R. M. Kaminski. 2010. Agricultural seed biomass for migrating and wintering waterfowl in the southeastern United States. *Journal of Wildlife Management* 74:489–495.
- Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Fish and Wildlife Service Resource Publication 148, Washington, D.C., USA.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, New Jersey, USA.
- Gammonley, J. H., and M. E. Heitmeyer. 1990. Behavior, body condition, and foods of buffleheads and lesser scaups during spring migration through the Klamath Basin, California. *Wilson Bulletin* 102:672–683.
- Greer, A. K., B. D. Dugger, D. A. Graber, and M. J. Petrie. 2007. The effects of seasonal flooding on seed availability for spring migrating waterfowl. *Journal of Wildlife Management* 73:1125–1133.
- Greer, D. M., B. D. Dugger, K. J. Reinecke, and M. J. Petrie. 2009. Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 73:1125–1133.
- Hartke, K. M., K. H. Kriegel, G. M. Nelson, and M. T. Merendino. 2009. Abundance of wigeongrass during winter and use by herbivorous waterbirds in a Texas coastal marsh. *Wetlands* 29:288–293.
- Havera, S. P. 1999. *Waterfowl of Illinois: status and management*. Illinois Natural Survey Special Publication 21, Urbana, USA.
- Heitmeyer, M. E. 1989. Agricultural/wildlife enhancement in California: The Central Valley Habitat Joint Venture. *Transactions of the North American Wildlife and Natural Resources Conference* 54:391–402.
- Heitmeyer, M. E. 2006. The importance of winter floods to mallards in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:101–110.
- Hitchcock, A. N. 2008. Diets of spring-migrating waterfowl in the Upper Mississippi River and Great Lakes Region. Thesis, Southern Illinois University-Carbondale, Carbondale, USA.
- Johnston, C. A. 1984. Mapping Wisconsin's wetlands. *Wisconsin Natural Resources* 8:4–6.
- Johnston, C. A., and P. Meysembourg. 2002. Comparison of the Wisconsin and National Wetlands Inventories. *Wetlands* 22:386–405.
- Kampstra, P. 2008. Beanplot: a boxplot alternative for visual comparison of distributions. *Journal of Statistical Software* 28:1–9.
- Kincaid, T., T. Olsen, D. Stevens, C. Platt, D. White, and R. Remington. 2008. *Spsurvey: spatial survey design and analysis*. R package version 2.0. <<http://www.epa.gov/nheerl/arm/>>. Accessed 10 Feb 2011.
- Korschgen, C. E., L. S. George, and W. L. Green. 1988. Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River. Pages 237–249 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, USA.
- Kross, J., R. M. Kaminski, K. J. Reinecke, E. J. Penny, and A. T. Pearse. 2008. Moist-soil seed abundance in managed wetlands in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:707–714.
- LaGrange, T. G., and J. J. Dinsmore. 1989. Habitat use by mallards during spring migration through central Iowa. *Journal of Wildlife Management* 53:1076–1081.
- Loesch, C. R., K. J. Reinecke, and C. K. Baxter. 1994. Lower Mississippi Valley joint venture evaluation plan. North American Waterfowl Management Plan, Vicksburg, Mississippi, USA.
- Manly, S. W., R. M. Kaminski, K. J. Reinecke, and P. D. Gerard. 2004. Waterbird foods in winter-managed ricefields in Mississippi. *Journal of Wildlife Management* 68:74–83.
- Martin, K. H., M. S. Linberg, J. A. Schmutz, and M. R. Bertram. 2009. Lesser scaup breeding probability and female survival on Yukon Flats, Alaska. *Journal of Wildlife Management* 73:914–923.
- McGill, R., J. W. Tukey, and W. A. Larsen. 1978. Variations of box plots. *American Statistician* 32:12–16.

- Miller, M. R. 1987. Fall and winter foods of northern pintails in the Sacramento Valley, California. *Journal of Wildlife Management* 51: 405–414.
- Miller, M. R., E. G. Burns, B. E. Wickland, and J. M. Eadie. 2009. Diet and body mass of wintering ducks in adjacent brackish and freshwater habitats. *Waterbirds* 32:374–387.
- Murkin, H. R., and J. A. Kadlec. 1986. Relationships between waterfowl and macroinvertebrate densities in a northern prairie marsh. *Journal of Wildlife Management* 50:212–217.
- Nelms, C. O., and D. J. Twedt. 1996. Seed deterioration in flooded agricultural fields during winter. *Wildlife Society Bulletin* 24:85–88.
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* 147:146–166.
- Pearse, A. T., G. L. Krapu, D. A. Brandt, and P. J. Kinzel. 2010. Changes in agriculture and abundance of snow geese affect carrying capacity of sandhill cranes in Nebraska. *Journal of Wildlife Management* 74:479–488.
- R Development Team Core (version 2.8.1). 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reinecke, K. J., R. M. Kaminski, D. J. Moorhead, J. D. Hodges, and J. R. Nassar. 1989. Mississippi Alluvial Valley. Pages 203–247 in L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, USA.
- Reinecke, K. J., and C. R. Loesch. 1996. Integrating research and management to conserve wildfowl (*Anatidae*) in the Mississippi Alluvial Valley, U.S.A. *Gibier Faune Sauvage, Game and Wildlife* 13:927–940.
- Schloesser, D. W., and B. A. Manny. 1990. Decline of wild celery buds in the lower Detroit River, 1950–1985. *Journal of Wildlife Management* 54:72–76.
- Schummer, M., R. M. Kaminski, A. H. Raedeke, and D. A. Graber. 2010. Weather-related indices of autumn-winter dabbling duck abundance in middle North America. *Journal of Wildlife Management* 74:94–101.
- Soulliere, G. J., B. A. Potter, J. M. Coluccy, R. C. Gatti, C. L. Roy, D. R. Luukkonen, P. W. Brown, and M. W. Eichholz. 2007. Upper Mississippi River and Great Lakes Region joint venture waterfowl habitat conservation strategy. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.
- Stafford, J. D., R. M. Kaminski, K. J. Reinecke, and S. W. Manley. 2006a. Waste rice for waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:61–69.
- Stafford, J. D., K. J. Reinecke, R. M. Kaminski, and P. D. Gerard. 2006b. Multi-stage sampling for large scale natural resource surveys: a case study of rice and waterfowl. *Journal of Environmental Management* 78:353–361.
- Steckel, J. D. 2003. Food availability and waterfowl use on mid-migration habitats in central and northern Ohio. Thesis, The Ohio State University, Columbus, USA.
- Straub, J. N. 2008. Energetic carrying capacity of habitats used by spring-migrating waterfowl in the upper Mississippi River and Great Lakes region. Thesis, The Ohio State University, Columbus, USA.
- Upper Mississippi River, Great Lakes Region Joint Venture Management Board. 1998. Upper Mississippi River and Great Lakes Region joint venture implementation plan update. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.
- Webb, E. B., L. M. Smith, M. P. Vrtiska, and T. G. Lagrange. 2010. Effects of local and landscape variables on wetland bird habitat use during migration through the rainwater basin. *Journal of Wildlife Management* 74:109–119.
- Wersal, R. M., J. D. Madsen, B. R. McMillan, and P. D. Gerard. 2006. Environmental factors affecting biomass and distribution of *Stuckenia Pectinata* in the Heron Lake System, Minnesota, USA. *Wetlands* 26:313–321.
- Wilson, B. C., and C. G. Esslinger. 2002. North American Waterfowl Management Plan, Gulf Coast Joint Venture: Texas Mid-Coast Initiative. North American Waterfowl Management Plan, Albuquerque, New Mexico, USA.
- Winslow, C. J. 2003. Estimation of waterfowl food abundance in coastal freshwater marshes of Louisiana and Texas. Thesis, Louisiana State University, Baton Rouge, USA.

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