ENERGETIC CARRYING CAPACITY OF HABITATS USED BY SPRING-

MIGRATING WATERFOWL IN THE UPPER MISSISSIPPI RIVER AND GREAT

LAKES REGION

A Thesis

Presented in Partial Fulfillment of the Requirements for

the Degree Master of Science in the

Graduate School of The Ohio State University

By

Jacob N. Straub, B.S.

*****

The Ohio State University
2008

Masters Examination Committee:

Dr. Robert J. Gates, Adviser

Dr. Tina Yerkes

Dr. Craig Davis

Dr. Stan Gehrt

Approved by

_____
Adviser
Graduate Program in Natural Resources

ABSTRACT

The Upper Mississippi River and Great Lakes region (UMRGLR), including Wisconsin, Illinois, Indiana, Ohio, and Michigan, are part of an important migration corridor for >12 million waterfowl annually. Waterfowl rely on wetland and cropland habitats in the region to secure nutrients needed to complete life-history events. Wetland loss in some of these states exceeds 95% of historic levels, raising concern that food resources may be insufficient to support spring-migrating waterfowl. The goal of this project was to improve understanding of food resource density and energy availability in wetlands and adjacent cropland habitats used by spring-migrating waterfowl in the UMRGLR. I collected plant and invertebrate food samples during two periods in spring 2006 in three wetland habitat classes (palustrine emergent, palustrine forested, lacustrine/riverine) and croplands (corn and soybean) at six study areas in the UMRGLR. I used two methods to convert food abundance to energetic carrying capacity (ECC) estimates (duck use days/ha [dud/ha]). The first method assumes constant food, habitat, and daily energy requirements (ECC_u), while the second uses foraging guild- (i.e., small dabbling, grazing dabbling, omnivorous dabbling, and diving duck) specific food habits and energy requirements (ECC_w). Total estimated food biomass in wetlands consisted almost entirely (>98%) of seeds, tubers, and invertebrates from benthic (substrate) samples. I failed to detect a statistically significant difference between ECC_u and ECC_w in 15 of 21 paired-t-test comparisons. The largest difference occurred in

lacustrine/riverine wetlands in east-central Wisconsin where ECC_u (59 dud/ha) was 88% below ECC_w (482 dud/ha). ECC_w varied among study sites ($F_{5,504}$ = 14.46, $P<0.001$), and habitat types ($F_{2,504}$ = 47.67, $P<0.001$) but did not differ by sampling period ($F_{1,504}$ = 0.46, $P = 0.500$). ECC_w was consistently greatest in palustrine emergent habitats (range across sites = 613 – 1,287 dud/ha), and least in lacustrine habitats (range across sites = 22 – 342 dud/ha). Cropland ECC was more variable than in wetland habitats (ranges across sites = 146- 3,303 dud/ha). Croplands had sufficient food energy to support large numbers of waterfowl but few species are capable of foraging in this habitat. Invertebrates did not contribute substantially to total food biomass or ECC for most sites and habitat types. My estimates of ECC were below what the UMRGLR Joint Venture assumes habitats provide. The greatest difference was in lacustrine habits where site-specific habitat estimates were 82-99% lower than the Joint Venture estimate. Thus, waterfowl that use lacustrine / deep water habitats may be energy-limited during spring migration in the UMRGLR. My study examined the extent to which habitats used by spring-migrating waterfowl in the UMRGLR can provide food energy abundance. Conservation planners need reliable food abundance estimates for croplands, marshes, natural lakes, rivers, impoundments, and riparian forests that individually and collectively contribute to the total habitat resource that supports spring-migrating in the UMRGLR. My results provide a basis for understanding variation in food resource abundance along latitudinal and longitudinal gradients in the region and can strengthen the biological foundation of strategic planning of habitat conservation to achieve population goals of the North American Waterfowl Management Plan.

ACKNOWLEDGMENTS

I wish to thank Tina Yerkes, Craig Davis and Stan Gehrt for serving on my committee. Tina has been instrumental in many aspects of my project and encouraged me to pursue a master's degree while I was working with DU in Michigan. I wish to thank John Coluccy for review of my thesis draft as well as advice and assistance with project planning. I also would like to express my gratefulness to Bob Gates for serving as my graduate adviser. Bob provided motivation and support when I most needed it and his confidence in my abilities allowed me to truly demonstrate my potential as a student and researcher. I look forward to working with Bob in the future. In addition, I have enjoyed having Bob as a friend, as it was always nice having another "cheesehead" around.

I am indebted to Bill and Vivian Young as well as Elmer and Eleanor Naffein for allowing myself and my field crew to use their accommodations at Marbill Island in Michigan. I truly enjoyed my time spent with them and Elmer's "home-made" wine. The accommodations were far more than any graduate student could ever ask for. My experiences and memories on one of the last remaining Great Lakes coastal wetlands will always be cherished.

I wish to express my gratitude to all the individuals who helped with the development and execution of this project. I extend a great thanks to all the field technicians who helped on this project, especially Alan Leach, Ron Sting, and Matt Schroeder, although I'm still not sure if they liked working with me or simply liked the fact they could legally shoot ducks in the spring. I must also acknowledge all the hard work of the "seed" technicians including, Casey Wright, Mariah Linkhart, Chriss Grimm, Carly Kestler, Dustin Kasier, and Gretchen Walburn have put forth. They have put in countless hours identifying, sorting, and counting the seemingly endless supply of samples. Jay Hitchcock and Rich Schultheis at Southern Illinois University have been great research partners and I look forward to working with them in the future. Josh Stafford and Steve Matthews provided critical statistical advice when I most needed it. Finally I would like express my thanks to the people, past and present in the Terrestrial Wildlife Ecology Lab at Ohio State whose interaction and friendship I have come to truly appreciate.

I would like to thank my dad who introduced me to the outdoors at a young age and has inspired me to be the man I am today. I have greatly appreciated his full support

in every major decision I have made throughout my life. In addition, Rachel Schultz has

taught me to appreciate wetlands for more than just the fact they can support ducks. Her

calmness and encouragement during times of chaos have been exceptional, and I'm not

sure I could have been as successful without her.

VITA

September 4, 1981……………….................................. ....Born – West Bend, WI

Education

December 2004…………………………..B.S. University of Wisconsin-Stevens Point, Stevens
Point, WI.

Major Field (Natural Resource Management –
Land Use Planning option)

Major Field (Geography – Physical Environment)

Minor Field (Geographical Information Systems)

Professional Experience

March 2005 – September 2005……………GIS Intern, Ducks Unlimited's Great Lakes/Atlantic
Regional Office, Ann Arbor, MI

September 20005 – present……………………..Graduate Research and Teaching Associate,
The Ohio State University, Columbus, OH

FIELDS OF STUDY

Major Field: Natural Resources
Area of emphasis: Wetlands and Waterfowl Ecology and Management

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The Upper Mississippi River and Great Lakes Region (UMRGLR) is an important

migration corridor for nearly 12 million waterfowl and accounts for nearly 500 million

waterfowl use-days annually (Soulliere et al. 2007). The UMRGLR is located between

two important waterfowl wintering areas (Mid-Atlantic Coast and the Mississippi

Alluvial Valley), and the important breeding areas of the Prairie Pothole and Boreal

Forest regions in the northern U.S. and Canada. A variety of wetland systems occur

throughout the UMRGLR including palustrine, lacustrine, and riverine wetlands

(Cowardin et al. 1979). Glaciated lakes, depressions, and beaver (*Castor canadensis*)

ponds comprise most of the habitat in the northern UMRGLR, while habitat in the

southern portion is primarily floodplain wetlands, man-made reservoirs and the major

river systems of the Mississippi and Ohio rivers (Soulliere et al. 2007). Coastal marshes

of Lakes Superior, Michigan, Erie and Huron also contain > 15,000 ha of wetland habitat

(Bookhout et al 1989).

Wetland loss in the UMRGLR has been and continues to be substantial. Less

than 15% of historic wetland habitat remains in Ohio, Iowa, Indiana, and Illinois (Dahl

2006). Most wetland loss in rural areas is caused by agricultural conversion (Frayer et al

1983). However urban development and expansion are the leading causes of wetland loss

in densely populated areas (Ducks Unlimited 2005).   The uncertain consequences of global climate change and spread of exotic or invasive species also place increasing pressures on remaining wetlands in the UMRGLR (Johnson et al. 2005).

Historically, waterfowl research focused on the breeding grounds, as populations were thought to be primarily driven by conditions experienced here. Species distribution, habitat relationships, and diets of waterfowl were all intensively examined (Trauger and Stoudt 1978, Bellrose 1979, Swanson et al. 1979). However, habitat conditions and nutrient resources encountered during the non-breeding period have been linked to subsequent breeding success and other fitness-related measures, such as survival and recruitment (Ankney and MacInnes 1978, Hepp 1984, Hohman et al. 1988, Batt et al. 1992, Zimin et al. 2002, Devries et al. 2008). Thus, much research emphasis shifted to the non-breeding period. Here, most studies were predominately conducted during autumn and winter because of its importance to over-winter survival and managing harvest (for review see Weller 1988).

Recent population modeling of mallards (*Anas platyrynchos*) has demonstrated that population growth (λ) is most sensitive to nest success, duckling survival, and non-breeding survival (Hoekman 2002, Coluccy 2008). Devries et al. (2008) examined individual reproductive investment and nesting success of mallards in the prairie-parklands of Canada. Their results showed that females with better body condition when arriving on the breeding grounds had higher nesting propensity and clutch sizes, as well as earlier nest initiation and hatch dates compared to females in poorer body condition. Thus, the ability of waterfowl to secure nutrients during spring migration should have a direct effect on population growth rates (Afton 1984, Anteau and Afton 2004, Newton

2006). Indeed, the importance of food availability at spring stop-over sites, when birds are preparing for the ensuing nesting period, has been demonstrated (LeGrange and Dinsmore 1988, Jorde et al. 1995, Anteau and Afton 2008). Until recently, autumn and winter were assumed to be the most limiting portion of the non-breeding season to sustaining growth of waterfowl populations, however a great deal of attention has shifted to better understand how habitat factors during spring migration might limit waterfowl population growth rates.

Despite the potential importance of spring migration, relatively little is known regarding spring stopover ecology, which continues to be one of the least studied aspects of avian migration (Lindstrom 1995, Yerkes et al. 2008). In particular, there are few studies of food availability for waterfowl during spring migration (but see LeGrange and Dinsmore 1985, DeRoia and Bookhout 1989) although numerous studies have measured food abundance during autumn migration and winter (Manley et. al. 2004, Boyer et. al. 2005, Stafford et al. 2006a, Brasher et al. 2007, Kross et al. 2008).

Quantity and quality of habitats that waterfowl encounter during spring migration may differ from autumn migration. Heavy rains and melt-water from winter snowfall flood crop fields, wetlands, and forested bottomlands during spring. In addition, most emergent wetlands have considerably different characteristics in spring compared to autumn as non-persistent emergent and submergent vegetation senesces, falls into the water column, and decays overwinter. This changes the structure and density of vegetation in palustrine emergent and aquatic bed wetlands (Galatowitsch and van der Valk 1996). The decaying plant matter also supports blooms of invertebrates that become available to spring-migrating waterfowl as they move northward (Euliss and

3

Grodhaus 1987). Waterfowl utilize these flooded habitats as they migrate northward, accumulating energy and nutrients required for the subsequent breeding season (LeGrange and Dinsmore 1988, Heitmeyer 2006). Availability of plant foods to spring-migrating waterfowl likely varies among wetlands with decomposition rates, substrate firmness, and consumption by non-waterfowl species (Nelms and Twedt 1996, Greer 2006). Although spring flooding may increase habitat availability for spring-migrating waterfowl relative to autumn, abundance and quality of plant food for waterfowl could be greatly reduced near the end of winter when waterfowl need nutrients to begin spring migration. The degree to which invertebrate populations compensate for overwinter loss of plant food is unknown.

Indeed, food resources have been found to be less abundant in spring compared to autumn. Greer et al. (2007) demonstrated that spring-flooded impoundments had low food abundance compared to fall-flooded, likely due to depletion by wintering waterfowl. Brasher et al. (2007) demonstrated a similar pattern in central and northern Ohio as wetlands sampled during spring had far less food energy compared to autumn. In addition, some plant seeds partially decompose, thereby diminishing the energy and nutrient contents of plant food resources (Nelms and Twedt 1996). Rising water levels during spring limit foraging opportunities for dabbling and other shallow water foraging species, though may create foraging opportunities for species that forage in deeper water (Fredrickson and Drobney 1979, Riley and Bookhout 1993).

Food abundance varies among wetland habitats (Bowyer et al. 2005, Greer et al. 2007, Johnson 2007). Factors such as hydrology, vegetation structure, disturbance, management regime, soils, and substrate composition all affect food availability. Seed

resources are usually most abundant in managed moist soil impoundments where water levels are manipulated to promote growth of high-yielding moist soil plant seeds and tubers (Fredrickson and Taylor 1982), although passively-managed wetlands also produce abundant food (Brasher et al. 2007). Invertebrate abundance fluctuates within and among seasons (Murkin and Kadlec 1986, Anteau and Afton 2008). Unlike over-wintering seeds and tubers, invertebrates are continually renewed as populations emerge and grow. Thus, the standing crop of invertebrates at any single point in time underestimates the total quantity of food resources available to supply energy and protein to spring-migrating waterfowl.

Collectively, seeds, tubers, and invertebrates provide the necessary energy and nutrients for spring-migrating waterfowl. Plant seeds and tubers typically provide more true metabolizable energy (TME) in the form of carbohydrates (Baldassarre and Bolen 2006), while invertebrates are an essential source of protein (Krapu and Swanson 1975). While carbohydrates are readily converted into lipids that are mobilized for energy needed during migration and nesting (Ricklefs 1974), protein is especially important in late spring and summer when hens lay nutrient-rich eggs (Krapu 1981).

Most waterfowl begin to switch from a diet of primarily plant material that is high in carbohydrates to an invertebrate diet with high protein near the end of winter, during spring migration, or after arriving on nesting grounds (Taylor 1978, Heitmeyer 1985, Lovvorn 1987, Miller 1987, Gammonley and Heitmeyer 1990, but see Gruenhagen and Fredrickson 1990). The timing of this dietary shift is unknown and likely varies with species. Hitchcock (Southern Illinois University personal communication) found that lesser scaup (*Athya affinis*) consumed higher proportions of invertebrates as they moved

north during spring migration. There is conflicting evidence from food habit studies, whether the transition to a high protein diet occurs during spring migration because nutritional requirements change, or due to declining abundance of high-carbohydrate plant foods (Lovvorn 1987). Smith (2007) found that lesser scaup and mallards collected during spring consumed primarily plant matter, although plant matter was less abundant where ducks foraged than animal matter. In contrast, Pederson and Pederson (1983) found that mallards in March and April consumed foods in proportion to their availability. Although spring-migrating waterfowl utilize both plant and invertebrate food resources extensively to obtain energy and nutrients, the extent and timing with which these resources become available to waterfowl in the UMRGLR is unknown.

The Upper Mississippi River and Great Lakes Region (UMRGLR) Joint Venture has taken a lead role in conservation planning for waterfowl and their habitats in the region. The UMRGLR Joint Venture boundaries encompass the Great Lakes marshes and the Ohio, Illinois, upper Mississippi, and lower Missouri river systems (Figure 1.1). The UMRGLR Joint Venture strives to conserve and enhance critical habitat to meet breeding waterfowl population goals established by the North American Waterfowl Management Plan (NAWMP).

The UMRGLR Joint Venture and other non-breeding habitat Joint Ventures have developed a landscape level bio-energetic approach which seeks to identify the amount of foraging habitat required to meet waterfowl population goals set by the North American Waterfowl Management Plan (NAWMP), and to prioritize areas for habitat protection, restoration, and enhancement. The bioenergetics approach requires understanding of food energy abundance of habitats and daily energetic requirements of ducks. The

UMRGLR Joint Venture has utilized this approach to calculated carrying capacity (i.e., duck use days/ha [dud/ha]) estimates that are used to derive habitat objective required to support breeding population goals of NAWMP. Previous evidence suggests that waterfowl may be limited by available food energy during spring (Brasher et al. 2007). Consequently, the UMRGLR Joint Venture recently shifted its focus from autumn migration to providing adequate habitat for wintering and spring-migrating waterfowl.

The bioenergetics approach assumes that waterfowl can access and consume all food items within all suitable habitats they encounter during spring migration. More realistically, species-specific differences in preference and utilization of individual food items and habitats are well documented (Nudds 1983, DuBowy 1988). Daily energy requirements of waterfowl also vary among and within species with body mass and composition (Miller and Eadie 2006). Furthermore, current recommendations for the UMRGLR Joint Venture waterfowl conservation strategy are derived from small-scale studies that focused strictly on plant food resources (Korschgen et al 1988, Heitmeyer 1989, Steckel 2003, Boyer et al. 2005, Stafford et al. 2006a). Other NAWMP joint venture regions have undertaken large-scale assessments of habitat carrying capacity. Stafford et al. (2006a) and Kross et al. (2008) estimated moist soil seed and rice abundance across the Mississippi Alluvial Valley. However, to my knowledge no study has attempted to estimate energetic carrying capacity from plant and invertebrate food resources over a broad range of wetland and agricultural habitats on a large regional scale such as the Upper Midwest. More precise measures of food energy abundance and patterns of temporal and spatial variation in plant and invertebrate food abundance in different habitat types will strengthen the biological foundation of habitat conservation

Figure 1.1. Locations of study sites within the Upper Mississippi River/Great Lakes Region Joint Venture where energetic carrying capacity was estimated during February-May 2006.

strategies for the UMRGLR Joint Venture, allowing conservation planners to more efficiently anticipate waterfowl habitat needs and target priority areas for future protection, restoration, and enhancement efforts. Undoubtedly, large-scale studies are needed to direct wetland conservation efforts over broad geographic regions to complement what has been learned at local scales (Flather and Sauer 1996, Haig 1998).

Therefore the specific research questions I addressed include; 1) what factors are most important in explaining variation in food density in habitats utilized by spring-migrating waterfowl? 2) What is the relative contribution of invertebrates to total food biomass and do invertebrates increase in abundance over time? 3) Do energetic carrying capacity estimates accounting for guild-specific requirements differ from the more traditional approach to estimating carrying capacity? 4) Do observed waterfowl utilization rates exceed energetic carrying capacity estimates, indicating that food energy may be a limiting factor during spring migration? The following research objectives were pursued to answer these questions:

1) Identify factors (i.e., study site, habitat type, sampling period) explaining variation in seed and invertebrate food density (kg/ha).

2) Precisely (CV <15%) estimate food density (kg/ha) from both plant and invertebrate food sources for spring-migrating waterfowl in four habitat types.

3) Compare changes in relative contributions of plant and invertebrate food sources to total food biomass over time, sites, and habitats.

4) Compare two models of energetic carrying capacity and explore potential differences in these methods in relation to importance of conservation planning in the UMRGLR.

5) Compare energetic carrying capacity (dud/ha) with observed waterfowl utilization rates (bud/ha) of wetlands and croplands habitats.

CHAPTER 2

STUDY AREAS AND METHODS

I selected six study sites in four states based on their importance as mid-migration stopover sites for waterfowl (Figure 1.1). These sites were purposively selected to provide two latitudinal cross-sections of north-south migration paths within the UMRGLR. The western study sites included the Cache River region of southern Illinois, the Illinois River region of central Illinois, and the southeastern glaciated region of east-central Wisconsin. The eastern study sites from south to north included the Scioto River in south-central Ohio, the western Lake Erie marshes of northern Ohio, and the eastern shore of Saginaw Bay in Michigan. Jurisdictionally, all sites were within the Mississippi Flyway.   The majority of waterfowl that use this region are from birds using the Mississippi River corridor (Bellrose 1968) but there is also a large influx of waterfowl from the Atlantic coast (T. Yerkes personal communication). Habitat types and amounts varied by study site (Table1.1). According to National Wetland Inventory (1990) data (NWI), the Illinois River site had the most wetland area (> 14,000 ha) while the Scioto River site had the least (< 1,000 ha). Palustrine forested wetlands were the most abundant wetland type at the Cache and Illinois River sites; palustrine emergent wetlands were most common in the east-central Wisconsin, Lake Erie marshes, and Saginaw Bay sites, while lacustrine habitat was most prevalent at the Scioto River site. Agriculture

11

Study Site	Habitat Type	Source	Area (ha)
Cache River	palustrine-forested	NWI	4,608
	palustrine-emergent	NWI	790
	lacustrine	NWI	141
	cropland	SMI	6,215
Illinois River	palustrine-forested	NWI	7,717
	palustrine-emergent	NWI	2,143
	lacustrine	NWI	4,450
	cropland	SMI	4,959
Wisconsin	palustrine-forested	WWI	1,608
	palustrine-emergent	WWI	6,004
	lacustrine	WWI	180
	cropland	SMI	20,109
Scioto River	palustrine-forested	NWI	259
	palustrine-emergent	NWI	274
	lacustrine	NWI	413
	cropland	SMI	2,075
Lake Erie Marshes	palustrine-forested	NWI	2,010
	palustrine-emergent	NWI	2,130
	lacustrine	NWI	1,854
	cropland	SMI	7,369
Saginaw Bay	palustrine-forested	NWI	1,080
	palustrine-emergent	NWI	13,150
	lacustrine	NWI	6
	cropland	SMI	3,048

Table 1.1. Waterfowl habitat areas (ha) at six study sites in the Upper Mississippi River and Great Lakes Region where energetic carrying capacity was estimated during February-May 2006. Source: National Wetlands Inventory (NWI), Wisconsin Wetlands Inventory (WWI) and Ducks Unlimited, Inc. Soil Moisture Index (SMI).

was the predominant land use at all six sites. The UMRGLR experiences a wide range of annual climatic conditions that influence the length of the growing season, the number of ice-free days, and surface hydrology. As a result waterfowl use of this area is closely tied to seasonal and annual variation in weather conditions (Reid et al 1989, Stafford et al. 2007).   The UMRGLR Joint venture implementation plan (1998) has designated each site as a focus area in recognition of their regional significance as waterfowl habitat. Each study area encompassed approximately 520 km^2. Study site boundaries were oriented to capture the major hydrologic features (i.e., major rivers, lake shorelines and/or wetland complexes) and representative habitat types at each site.

Cache River

The Cache River site, centered near Cairo, IL, included a 44 km reach of the lower Cache River and Cypress Creek. The Cache River watershed encompasses 927 km^2 with elevation 85 – 102m above sea level. Mean annual temperature is 13.7 C, with average winter temperatures ranging from 3.2 – 8.3 C, and spring temperatures ranging from 8.5 – 18.8 C (Illinois State Water Survey 2008). Mean annual rainfall is 122.7 cm; greatest precipitation occurs in late winter and spring (Illinois State Water Survey 2008).

The lower Cache River is highly modified and its hydrology differs from the upper section. Channel modifications have introduced major changes to the Cache River's hydrology over the past 100 years. The Post Creek Cutoff constructed around 1915 diverted water from the Cache River which now flows directly into the Ohio River. The Cache River floodplain is bordered by upland deciduous forests consisting of oaks (*Quercus spp.*) and hickories (*Carya spp.*) with interspersed rocky bluffs. Most (68%) of

the lower cache river floodplain has been cleared for agriculture (Hutchison 1987, Demissie et al. 1990). Forested wetlands characterize the Cache River floodplain, with 70% identified as bottomland hardwood forest and 16% as bald cypress (*Taxodium distichum*) swamp totaling over 5,497 ha collectively (Havera 1999). In fact, the watershed encompasses most of the remaining bald cypress swamps in southern Illinois (Dorge et al. 1984).

The Cache river floodplain is important for waterfowl and other birds as over 250 species occur within the region. The RAMSAR Convention designated the Cache River a wetland of international importance. The wetlands reserve program (WRP) has increased managed wetland areas in recent years. The Frank C. Bellrose federal waterfowl reserve, within the Cypress Creek National Wildlife Refuge, is managed to provide migratory waterfowl and shorebirds with moist soil habitats where water level are manipulated and periodic mechanical disturbance is used to promote growth of desirable wetland food plants.

Illinois River

The Illinois River study site is centered near Chandlersville, IL along a 45 km reach of the Illinois River and includes part of Chautauqua and Emiquon National Wildlife Refuges, and Sanganois and Anderson Lake public wildlife areas. Mean annual temperature is 10.8 C with average winter temperatures ranging from -1.9 – 4.8 C , and spring temperatures ranging from 4.4 –16.9 C (Illinois State Water Survey 2008).

The Illinois River is historically known as one of the most important areas for migrating waterfowl in all of North America (UMRGLR Joint Venture Management

Board 1998). The Illinois River has been greatly altered since it was impounded and dredged for navigation in the early 1900s. Sediments from farmed uplands in the watershed are now deposited in floodplain lakes when river levees are overtopped during flood events. Prior to human alteration, natural flows of clear water allowed growth of emergent and submergent waterfowl food plants in backwater lakes and side-channels of the Illinois River floodplain. Runoff from surrounding uplands, and sediment transported into side-channels and bottomland lakes during Illinois River flood events has created turbid conditions, soft substrates, and sedimented backwater lakes. In addition, exotic fish (e.g. *Cyprinus* spp.) stir up bottom sediments, uproot vegetation, and re-suspend contaminants, leading to secondary loss of wetland vegetation. Floodplain forests have also changed from hard to soft-mast producing species (Havera 1999). The natural flood pulse pattern essential to that system is presently impaired (Sparks et al. 1998; Koel & Sparks 2002). The river now has unnaturally high water levels in the summer, with several minor floods in midsummer that often drown moist-soil plants.

Despite these large scale changes in environmental quality, the Illinois River floodplain still serves as an important migration staging area for waterfowl each year. Chautauqua NWR has been designated a Western Hemisphere Shorebird Network Site and a Globally Significant Bird Area (Havera 1999). The Chautauqua NWR supports roughly 45% of waterfowl use of the Illinois segment of the Mississippi Flyway and nearly 70% of the waterfowl that use the Illinois River Corridor (USFWS 2004). Over 1.5 million mallards have been recorded using the area during one census period (Havera 1999).

East-central Wisconsin

This site was located near Waupun, WI in the Upper Rock River watershed in southeastern Wisconsin, including portions of the Horicon National Wildlife Refuge and extending into Dodge and Fond du Lac counties. Mean annual temperature is 7.6 C, with average winter temperature ranging from -1.9 – -6.3 C and spring temperatures ranging from 0.2 –14.3 C (Midwest Regional Climate Center 2008). Mean annual rainfall is 83.9 cm; greatest precipitation occurs in late summer and early fall (Midwest Regional Climate Center 2008).

Surrounding land use consists largely of highly productive agriculture supported by rich peaty soils and glacial outwash. Most of the agricultural land is used for dairy farming. Wetland habitat in this area of Wisconsin is predominately cattail (*Typha* spp.) marsh, although some wetlands are managed to promote hemi-marsh habitat. The most recent glaciations created numerous pothole wetlands which are attractive sources of breeding habitat for many waterfowl. In fact, this site has the most significant numbers of nesting blue winged teal, mallards and some diving ducks, compared to my other study sites (Van Horn and Gatti 2006). Dodge and Fond du Lac counties, including the Horicon area, are only 7 and 11% forested, respectively (Craven and Hunt 1984).

The Horicon Marsh system is considered the largest cattail (*Typha* spp.) marsh in the United States. The marsh consists of a shallow basin drained by the Rock River. The northern 8,367 ha is managed by the U.S. Fish and Wildlife Service as Horicon NWR and the remainder is managed by the Wisconsin Department of Natural Resources. There are 216 species of birds that commonly use Horicon Marsh. Another 32 species occasionally occur there (USFWS, 1994). Recognizing the diversity of flora and fauna and the large

16

populations of waterfowl that Horicon Marsh supports, the RAMSAR convention designated Horicon Marsh as an Wetland of International Importance in 1990 (Davis 1994). However, severe problems continue to threaten the habitat resources of Horicon marsh. The most severe problem is siltation due to soil erosion from surrounding watersheds. Other major problems include rough fish infestation (mainly *Cyprinus carpio*), purple loosestrife (*Lythrum salicaria*) infestation, high inflow of nutrients (primarily phosphorous) into the marsh from surrounding farms, pastures and barnyards, and overall loss of native vegetation communities.

East-central Wisconsin has been identified as the region of Wisconsin that contains the majority of migratory habitat for waterfowl (UMRGLR Joint Venture 1998). The importance of this region for migration, staging and nesting Canada geese (*Branta canadensis*) has been well documented (Craven and Hunt 1984, Heinrich and Craven 1992), and is also important for many duck species (Stollberg 1950, VanHorn et al. 2006, Wisconsin Department of Natural Resources 2008).

Scioto River

The Scioto River study site was centered on a 45 km segment of the Scioto River approximately 15 km south of Columbus, OH. Mean annual temperature is 10.5 C with average winter temperatures ranging from -3.06 – 5.67 C, and spring temperatures ranging from -1.11 – 15.5 C (Midwest Regional Climate Center 2008). Mean annual snowfall is 36.1 cm, with highest snowfalls in January, and the mean annual rainfall is 99.1 cm (Midwest Regional Climate Center 2008).

The Scioto River area has numerous flat plains, many of which have been cleared and farmed, and numerous small streams that remain open in winter and are tributaries to the larger Scioto River. The lower Scioto River valley is very large compared to the width of the river itself where melt-waters from retreating Ice Age glaciers carved the valley exceptionally wide. Besides being Ohio's longest river, the Scioto River Watershed is home to more species of fish and mussels than any other Ohio watershed. Principal wetland areas within the site include Stage's Pond Nature Preserve, which encompasses two glacially formed kettle lakes and surrounding wetland communities, and Calamus Swamp, a primarily cattail marsh. Forested wetlands are primarily restricted to the banks of the Scioto River and Big Darby Creek. Despite the lack of wetland area, there are hundreds of hectares of private land enrolled in the Conservation Reserve Enhancement Program (CREP). So far, farmers have enrolled more than 22,000 ha in 15-year conservation agreements throughout the 1.6 million-hectare Scioto River Watershed (The Nature Conservancy 2008). Flooded CREP areas provided access to abundant food resources and increased the amount of usable habitat for waterfowl. Since many of these CREP fields are within the Scioto River floodplain , they often become inundated with floodwater during late winter and spring.

The Scioto River study site had the smallest total wetland area (946 ha) among the six study sites, so this area's importance to waterfowl is not well understood. Most of this is the Scioto River itself. However the Scioto river valley likely serves as important American black duck (*Anas rubripes*) and mallard wintering and migration habitat (UMRGLR Joint Venture 1998).

Lake Erie Marshes

The Lake Erie site was located about 2 km South of Port Clinton, Ohio, centered around Sandusky Bay, Ohio. Mean annual temperature is 10.6 C with average winter temperatures ranging from 0.4 – 2.9 C, and spring temperatures ranging from 3.6 – 15.8 C. Mean annual snowfall is 25.9 cm, with highest snowfalls in January, and the mean annual rainfall is 95.6 cm.

The western Lake Erie marshes historically consisted of freshwater tidal marshes bordering the Sandusky and Muddy Creek Bays. High water levels over the past several decades have eradicated these naturally occurring marshes and current wetlands are mostly impounded marshes actively managed by the Ohio Department of Natural Resources Division of Wildlife, U.S. Fish and Wildlife Service or private waterfowl hunting clubs. A landscape matrix of tiled agricultural fields surrounds Sandusky Bay, leaving very little ephemeral flooded agricultural habitat; although many hunt clubs actively flood croplands in the fall (Olson 2003, Baranowski 2007).   The Winous Point Marsh Conservancy (WPMC), located near the center of the Lake Erie site is the first private duck hunting club in North America. WPMC consists of 570 ha of wetland habitats and harbors thousands of waterfowl and shorebirds during fall and spring migration (Farney 1975, Olson 2003, Steckel 2003, Baranowski 2007). The Lake Erie marshes have always been important migration areas for waterfowl (Bookhout 1989). Aerial surveys conducted by the Ohio Division of Wildlife confirm that hundreds of thousands of waterfowl heavily use habitats in this region during both autumn and spring migrations.

Saginaw Bay

The Saginaw Bay study site was centered near Sebewaing, MI on the eastern shore of Saginaw Bay between Fish Point State Game Area and Sand Point. Mean annual temperature is 7.06 C, with average winter temperatures ranging from to -6.11 – 3.11 C, and spring temperatures ranging from -5.33 – 11.5 C. Mean annual snowfall is 85.6 cm and mean annual rainfall is 66 cm with the greatest precipitation occurring in late summer (Midwestern Regional Climate Center 2008).

The study site emcompassed shallow waters within 5 km of the Lake Huron shoreline, including Wildfowl Bay, and adjacent uplands and inland marshes < 5 km from the shoreline. Several barrier islands with wetland and upland habitats were included in the study site, including Middle Grounds, Heisterman, Maisou, Defoe, Pitcher's Reef, and Lone Tree Islands. These islands formed a boundary between the shallower waters east of the islands and deeper water to the west. Water levels fluctuate seasonally and daily, typical of freshwater coastal marshes (Bishop 1990). The highest water levels occur when prevailing winds are from the north to northeast, while low water levels occur during a south to southwest wind. Bottom sediments throughout the bay range in size from large pebbles to clay, while medium to fine grained quartz sand is also common (Wood 1964). Nalepa et al. (1995) estimated that 70% of the bottom consists of sand, cobble, and gravel and 30% consists of silt/mud within the shallow waters of inner bay.

The adjacent upland is largely rural and land use is primarily agriculture. Poorly drained, nutrient rich loamy soils underlie most of the area. Nearly all of the agricultural fields have been tiled to promote rapid run-off of surface water, discharging sediments

into the bay. Major drainage systems include the Sebewaing River, Pigeon River, several wide sand channels formed from glacial melt-water streams, and many man-made channels including the Shebeon drain (Smith 1901).

Wetland habitats are primarily associated with the shallow waters of Saginaw Bay and at Fish Point WA. The National Wetlands Inventory (NWI) identified >13,150 ha of coastal wetland habitat as seasonally emergent wetland. These habitats typically lack submergent vegetation and are dominated by bulrush (*Scirpus spp.*) in spring. Much of the wetland habitat identified by the NWI has been destroyed due to wave action and discharge of sediments into Saginaw Bay from adjacent croplands. In addition, common reed (*Phragmites australis*) a non-native species has colonized and displaced much of the native vegetation in these habitats. Cropland dominates the upland habitats; three main crop types grown in the area including corn (*Zea mays*), soybean (*Glycine max*), and sugar beet (*Beta vulgaris*).

METHODS

Food Sample Collection

Sampling Design and Allocation

I used a Geographical Information System (GIS) to overlay 2,292 16-ha square
grid cells over combined wetlands inventory and soil moisture index (SMI) coverages of
each study site. I used the Wisconsin Wetlands Inventory (WWI; Johnnston 1984) to
identify wetlands at the Wisconsin study site and The National Wetlands Inventory
(NWI; National Wetlands Inventory 1990) for all other sites. The source date of imagery
used for both the NWI and WWI varied from 1978 –1984. Grid cells with > 0.8 ha of
wetland habitat were classified into one of three sampling strata based on wetland habitat
and wet soil composition. I chose this size threshold to increase the chance of
encountering wetlands within a cell in the field since NWI and WWI can potentially
misclassify smaller wetlands (Tiner 1997). I similarly classified the remaining cells as
cropland cells when they contained >8 ha of cropland identified as "prone" to flooding by
the SMI coverage (Ducks Unlimited 2005a). Wetland cells took priority over cropland
cells because cropland was the dominant land-use at all sites thus at some sites there
would not have been enough wetland cells to take an adequate sample from. Cells that
contained < 0.8 ha of NWI data and < 8 ha of SMI were not included in my sampling
design. At the Illinois River study site, adequate samples could not be obtained from

22

selected cells so I drew samples from habitats outside my selected cells. These samples were selected by convenience sampling but were selected in proportion to the amounts of habitat in the area.

I further stratified wetland cells based on the predominant wetland type (Cowardin et al. 1979) within the cell. Wetland cells were classified as palustrine emergent (PEM), palustrine forested (PF), or lacustrine (LC). I used the Animal Movements extension in ArcView 3.3 (Hooge and Eichenlaub 1997) to randomly select wetland and cropland cells from each study site. Wetland cell types (i.e., PF, PEM, LC) were selected in proportion to their availability at each study site. Therefore, my sampling frame represented 16 ha cells, where there was at least 0.8 ha of wetland or cropland habitats potentially usable by waterfowl.

I ground-truthed cells to determine the types of habitats actually present within each randomly selected cell using a Dell PDA 750 with ArcPad (ESRI 2001). I classified and confirmed wetlands within cells as palustrine forested (PF), palustrine emergent (PEM) or lacustrine (LC) based on their hydrological characteristics and dominant vegetation present at the time of each visit following the criteria of Cowardin et al. (1979). I classified cropland (AG) habitats according to the crop type present. I used maps with aerial photographs of the cell to delineate the boundaries of all habitat types during each visit to a cell. Interpreting these maps and aerial photographs, I also estimated the percentage of the wetland that was >30 cm deep. At each site a number quota of food samples was identified based on processing capacity in the laboratory. I sampled only as many cells as necessary to fill the quota. All or nearly all cells were surveyed for waterfowl use, whereas a subset of cells was used to obtain food samples.

Wetland Food Biomass

Sampling dates varied by study site, depending on timing and duration of passage of waterfowl through each site during spring 2006. A pre-migration sample was always taken immediately following ice-thaw, before migrating waterfowl arrived. A post-migration food sample occurred after most waterfowl departed from each study site (Appendix 1). I determined migration chronology from observed waterfowl use on my study cells. I randomly selected wetlands in proportion to their occurrence within a particular study site to estimate biomass (kg/ha) of both plant and invertebrate food items. I obtained two samples from shallow (< 30 cm) and deep (>30 cm) zones of each wetland except where the deep zone was absent. Thus, I obtained four total samples per wetland per sampling round for most wetlands. I sampled nektonic biomass by sweeping a d-frame net (33 cm diameter, 500 μm mesh) in the water column within a 100 cm x 50 cm x 75 cm, 500 μm mesh side panel drop box. I then sampled benthic biomass by inserting a core sampler (7 cm diameter) 10 cm into the substrate at a random location within the drop box. I washed samples in the field using a 500 μm sieve bucket and placed them into a 3.8 l labeled polyethylene bag containing 10% formalin solution. I categorized each sampling location into one of four distinct vegetation cover classes (mostly vegetated, interspersed vegetation, vegetated edges and mostly open water (Stewart and Kantrud 1971). I recorded the UTM coordinates of the sample location using a Global Positioning System (GPS).

Cropland Plant Food Biomass

I used a technique modified from Frederick et al. (1984) to sample plant food biomass in cornfields. I randomly placed a 14-m nylon rope perpendicular to planting rows, and then selected one side of the rope to sample by coin flip. I collected all whole and partial corn ears that retained grains within 1 m of the rope over a distance of 14 m. I defined a partial corn ear as one that had at least 1 corn kernel adhering to it. I also collected individual corn kernels by inserting a core sampler (7 cm diameter) 3 cm into the substrate placed at five systematic locations along the 14 m rope. I sampled soybean fields by randomly placing the drop box (100 cm x 50 cm) and collecting (by hand when not flooded or the d-net when flooded) all soybean seeds that were present within the box. I placed samples in labeled 3.8 l polyethylene bags. Cropland samples were taken back to a lab, where they were allowed to air dry before being placed in a convection oven for 48 hours at 60 C to constant mass.

Laboratory Methods

Wetland food samples collected in the field were sent to Southern Illinois University at Carbondale (SIUC) where they were hand-picked to separate all non-food material from waterfowl plant and invertebrate food items. Invertebrates were identified to family or lower taxonomic level when possible by Richard Schultheis, a PhD candidate at SIUC. Seeds were shipped back to the lab at Ohio State University where seeds and tubers were identified to genus (Martin and Barkley 1961, Delorit 1970, Montgomery

1977, Davis 1993), sorted, and dried to constant mass at 60 C for 48 hours in a convection oven before weighing to the nearest 0.0001g. I defined duck food as plant and invertebrate food items known to be consumed by at least one species of waterfowl in the UMRGLR (Martin and Uhler 1951, Farney 1975, Havera 1999, Smith 2007). I counted but did not weigh seeds from the following genera Amaranthus spp., Bidens spp., Cephalanthus spp., Chenopodium spp, Cyperus spp., Echinocloa spp., Eleocharis spp., Leersia spp., Najas., Panicum spp., Polygonum spp., Potamogeton spp., Rumex spp., Sagittaria spp. and Scirpus spp when samples contained < 25 seeds of these genera to reduce processing time spent on small samples. I used the product of the number of seeds from each genus and mean seed mass from a representative sample of each genus to estimate mass to the nearest 0.0001g when samples contained <25 seeds of these genera. Using average seed mass to predict total sample mass was determined by Arzel et al. (2007). I always dried and weighed all other seed genera identified as waterfowl food, and when there were > 25 seeds from the genera listed above. Actual and predicted seed mass was tightly correlated (Figure 2.1) and there was no difference between actual and predicted seed mass (paired $t_{(1.88)}$ = -1.01, P = 0.314). I represented biomass estimates as kg/ha.

$$y = 0.872359x - 0.000004$$
$$R^2 = 0.901091$$
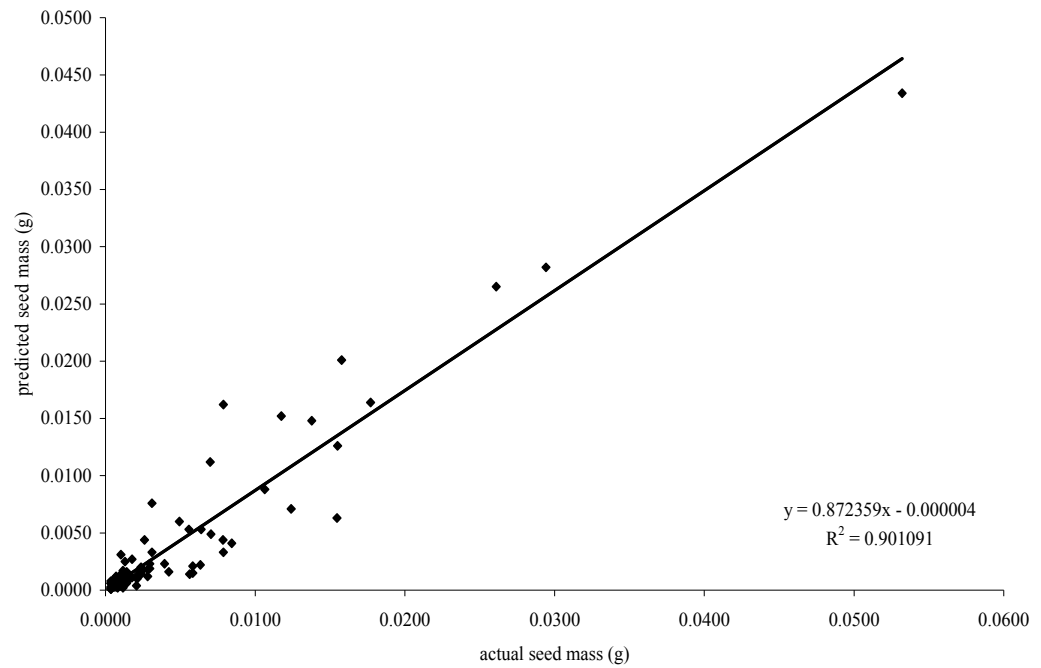
Figure 2.1. Relationship between actual seed mass (g) and predicted seed mass (g) for 15 genera of plant seeds collected form wetland habitats at six study sites in Illinois, Wisconsin, Ohio and Michigan during spring 2006.

Energetic Carrying Capacity

I converted food biomass estimates to energetic carrying capacity (ECC) by using

published values of true metabolizable energy (TME) for seeds, tubers, and invertebrates

(Appendix 2) as described by Reinecke et al. (1989). I substituted TME values for some

taxa when published estimates were not available with those from the closest taxonomic

group. When crude fiber estimates were available, I regressed % fiber content (Havera

1999) on published TME values (Appendix 3) to estimate TME for taxa without

published estimates (Figure 2.2) after Petrie et al. (1998).

I used two methods to calculate ECC, as one of my objectives was to illuminate

differences in duck species-weighted vs. un-weighted ECC estimates. The un-weighted

ECC estimate, hereafter ECC_u, assumes each duck use-day represents a constant daily

energy requirement (DER) of 292 kcal/day (i.e., typical female mallard), and that all

potential food items can be consumed (i.e., no food preferences), from any available

habitat. The formula used to calculate ECC_u per habitat type was;

$$ECC_u \ = \ \sum_{i=1}^{n} \ (mass_i \ \times 1000 \times TME_{i)} \ )/ \ 292 \ kcal/day)$$

where ECC_u = carrying capacity of (dud/ha), n = total number of food items, $mass_i$ =

biomass of particular food item (kg/ha), TME_i = true metabolizable energy (kcal/g) of

food item. I derived the weighted estimate of ECC (hereafter ECC_w) to account for duck

species-specific DER, food habits, and habitat utilization rates of four separate foraging

guilds. The guilds included dabblers (mallard, American black duck, northern pintail

[*Anas acuta]*, wood duck [*Aix sponsa*]), divers (lesser scaup, canvasback [*Aythya

vallisineria*], redhead [*Aythya americana*], ring-necked duck [*Aythya collaris*], and ruddy
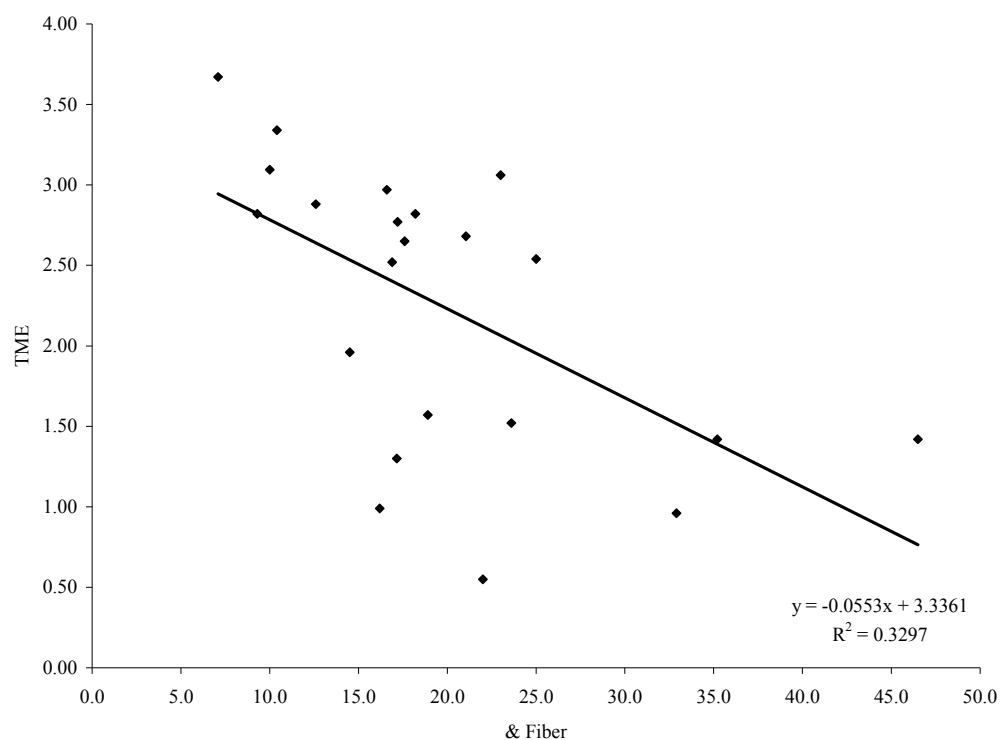
Figure 2.2. Relationship between percent fiber content and true metabolizeable energy (TME) for 22 genera of seeds. Percent fiber content values are from (Havera 1999) and TME (kcal/g) values are from various published sources.

duck [*Oxyura jamaicensis*]), grazers (American wigeon [*Anas americana]* and gadwall [*Anas strepera*]), and teal (blue-winged teal [*Anas discors*], green winged teal [*Anas crecca*], and northern shoveler [*Anas clypeata*]). I estimated a weighted guild-specific DER by averaging DER of all species in a guild following Miller and Eadie (2006; Appendix 4) and multiplying by the proportion of each guild observed in a habitat at a site (Appendix 5). I obtained species-specific food habit data from a concurrent diet study that focused on mallard, gadwall, blue-winged teal, ring-necked duck, and lesser scaup (Jay Hitchcock Southern Illinois University–Carbondale; Appendix 6). I assumed all species of dabblers consumed the same foods as mallards, and similarly substituted ring-necked duck and lesser scaup diets for all divers, gadwall for grazers and blue-winged teal for the teal guild. I also assumed diving ducks foraged only in palustrine emergent and lacustrine wetlands and all food >30 cm depth found in the benthic samples was available only to divers (Appendix 7). Therefore, the weighted ECC_w estimate should be more representative of energetic carrying capacity because it accounts for guild-specific food habits, habitat use, and daily energy requirements.

I also computed a guild-specific ECC estimate (hereafter ECC_{guild}) which uses the same parameters as ECC_w but I did not weight the DER by the proportion of guilds using a habitat at a site. Instead I used a foraging guilds mean DER and assumed all the biomass in a wetland regardless of the presence of other guilds could only be consumed by one guild. Thus, this estimate represents the carrying capacity for each specific guild.

Therefore, ECC_w and ECC_{guild} were estimated with a deterministic equation based on estimated guild specific energetic carrying capacities. The model included inputs: (1) biomass (kg/ha); (2) TME values; (3) daily energy requirements; and (4) proportion of

each guild observed using a particular habitat at each site. The model formula for ECC_w per habitat type was:

$$ECC_w = \sum_{i=1}^{n} \left(\frac{(mass_i \times 1000 \times TME_i)}{\sum_{g=1}^{4} (DER_g \times pH_g)} \right)$$

where ECC_w = carrying capacity (dud/ha), n = total number of food items, $mass_i$ = biomass of particular food item (kg/ha) , TME_i = true metabolizable energy of food item i (kcal/g), DER_g = daily energy requirement of a particular guild (kcal/day), and pH_g = proportion guild observed using a particular habitat. The model formula for ECC_{guild} per habitat type was:

$$ECC_{guild} = \sum_{i=1}^{n} \left(\frac{(mass_i \times 1000 \times TME_i)}{DER_g} \right)$$

where ECC_{guild} = carrying capacity (dud/ha), n = total number of food items, $mass_i$ = biomass of particular food item (kg/ha), TME_i = true metabolizable energy of food item i (kcal/g), DER_g = daily energy requirement of a particular guild (kcal/day).

Waterfowl have been shown to abandon food patches when food biomass drops below a certain threshold where it is no longer energetically profitable to search for food (Reinecke et al. 1989). Several foraging thresholds have been proposed. Reinecke et al. (1989) suggested that waterfowl were unable to forage profitably on waste rice densities <50 kg/ha. Naylor (2002) examined post-winter food densities in wetlands, and concluded that 130 kg/ha was the average foraging threshold, although variability was high among years. Finally, Hagy (Mississippi State University, personal communication) found that food levels were greater than 280 kg/ha after waterfowl abandoned moist-soil wetland sites in Mississippi in late winter. I converted these biomass thresholds to

31

energetic thresholds following Brasher et al. (2007), with corresponding thresholds of 324, 865, and 1,996 dud/ha, respectively.

Waterfowl Use-Days

I censused all waterfowl present in wetland and cropland habitats within the boundaries of 16 ha study cells at each study site. A minimum of 38 cells were surveyed per study site and were visited 1-8 times between the first and last food sampling periods. I did not record ducks that were outside of any study cell even if they occurred on the same wetland that was partially included in a cell. I used maps with aerial photographs to determine the boundaries of each cell in the field. I first counted all species via visual observation using a spotting scope and binoculars and subsequently walked through dense vegetation to flush ducks that were not visible. Care was taken to avoid double-counting ducks that flushed from, and landed on, different parts of the survey plots. I derived estimates of total ducks use-days by averaging the number of ducks (by species) per survey on each wetland or crop unit present within each wetland or crop unit within each cell, separately by study site. The mean number of ducks observed/day was multiplied by the number of days between first and last dates that food samples were collected at each study site to convert mean counts (a mean of one duck observed on each wetland within a cell represented one duck use-day) to duck use-days (DUD) over the entire survey period (35 – 53 days across sites; Appendix 1). Individual estimates of DUD by all unique combinations of site, cell, and wetland were divided by the estimated area of each wetland (within sites and cells) to convert DUD estimates to the same units (DUD/ha) as food energy carrying capacity estimates. These estimates were then

averaged within wetland system or crop categories at each site to obtain waterfowl

utilization rates (DUD/ha) for the same habitat systems used to summarize ECC (AG,

PEM, PF, and LC).

Statistical Analyses

Biomass Density Estimates

I used multi-stage sampling (MSS) to estimate abundance of food energy in

wetland and cropland habitats at each site. Multi-stage sampling provides an un-biased

estimate that is particularly appropriate for large-scale natural resource surveys,

especially those with hierarchical nested designs similar to mine (Conroy and Smith

1994, Stafford et al. 2006b.) My sampling design treated cells as primary sampling units,

wetlands and croplands as secondary units, and plots within wetlands and croplands as

tertiary units. I used PROC SURVEYMEANS in SAS version 8.02 to estimate food

density in wetland and cropland habitats. I performed separate analyses for each study

site. I estimated mean food density per wetland system for all sites with sampling

weights derived for each individual study site. I also estimated biomass density pooled

across sites by using site specific sampling weights. I calculated the probability of

selecting a cell by dividing the number of sampled cells by the total number of cells

available at a site. I calculated the probability of selecting a wetland or cropland unit by

dividing the number of sampled wetlands by the number of wetlands or croplands present

within a cell. I calculated the probability of taking a benthic sample by dividing the area

of the core sampler ($38.23 cm^2$) by the number of possible cores given the area of wetland

or cropland. I calculated the probability of obtaining a nektonic sample by dividing the

33

area of the drop box ($0.5m^2$) by the number possible given the area of the wetland or cropland. The inverse of the product of the 3 selection probabilities (i.e., cell, wetland/cropland, and benthic/nektonic) was the sample weight used in analyses. SURVEYMEANS uses Taylor series linearization to estimate variances of means (SAS Institute 1999:3200). In the case of the Illinois River where I took samples outside of my study cells, I used the mean weight from samples where I did sample within cells at that site.

Individual datum points in a MSS can have a strong influence on the overall mean (Gershunskaya and Huff 2004). I examined marginal plots to examine the influence of individual datum points on the overall means. Marginal plots display box plots of sample values (i.e., kg/ha) versus sample weights. For each analysis, I adjusted the weight of a datum point by assigning it the mean weight of the remaining datum points if a marginal plot identified a datum point as an outlier (i.e., it had both a large sample value and high weight; California Health Interview Survey 2002).

I calculated percent occurrence of plant food items within wetlands by determining the frequency of occurrence for seed or tuber taxa within benthic or nektonic samples, divided by the total number of benthic and nektonic samples. I used PROC SURVEYMEANS to calculate seed and tuber density estimates in wetlands habitats summed across all sites. I summed estimates and variances of benthic and nektonic samples (Stafford 2006a), to provide a single density estimate per habitat type.

Variation in plant and invertebrate food abundance

I used the GLM package (Dobson 1990) in R version 2.4.0 (R Development Core Team 2006) to model the relationships of food abundance as a function of site, sampling period, habitat type, wetland depth zone, and cover class. I only explored relationships in benthic samples since density of food items from benthic samples was vastly greater than nektonic samples and represented the majority of total food biomass (>98%). I performed two analyses; one each with plant food abundance (kg/ha) and invertebrate food abundance (kg/ha) as response variables. I designated site, sampling period, habitat type, wetland depth zone and cover class as fixed explanatory variables. After assessing the normality of the data and inspecting the residuals vs. the fitted values I log-transformed my response variable then applied a generalized linear model using a Gaussian distribution with the identity link.

I used Akaike's Information Criterion (AIC) to identify candidate models that best fit the data (Burnham & Anderson 1998). The AIC identifies the most parsimonious model from a set of candidate models; that is, the model supported most strongly by the data, given the bias corrected, maximized log-likelihood of the fitted model, and a penalty for the number of parameters used. This method of model selection counters the problem of over-fitting and the subsequent loss of precision of parameter estimates. The AIC values of parameter estimates were adjusted for over-dispersion by calculating a variance inflation factor. The AIC value adjusted for over-dispersion is termed the corrected quasi-likelihood AIC (denoted as QAIC). Therefore, I constructed candidate models based on a priori expectations regarding which variables, combinations of variables, and interactions might be biologically meaningful. I considered the best model

to be the one with the lowest QAIC. I used the results from the QAIC to inform

decisions on which factors were most important in explaining variation of my response

variables and summarized the results accordingly.

Invertebrate contribution

I divided the biomass of invertebrates (kg/ha) by the total biomass (kg/ha) for

individual samples to calculate percent contribution of invertebrates to total food biomass

for each nektonic and benthic sample. I used analysis of variance (ANOVA) in R version

2.4.0 to test for differences in percent invertebrate contribution by study site, wetland

system, and sampling period. I ran separate tests for nektonic and benthic samples. I

used a logistic transformation (log(1/1-x)) to normalize percent invertebrate contribution

and meet distributional assumptions of the test. Logistic transformations are applied to

analyze responses such as mine that are restricted to a finite interval (i.e., $0 - 100\%$;

Lesaffre et al. 2006).

Energetic Carrying Capacity

I used ANOVA in R version 2.4.0 to test if ECC_u and ECC_w varied by study site,

habitat type and sampling period. I log transformed (base 10) food energy abundance

estimates to normalize distributions and account for homogeneity of variance prior to

statistical analysis (Quinn and Keough 2002). I used a paired t-test in R version 2.4.0 to

test differences between ECC_u and ECC_w in each of the 21 habitat by site specific

comparisons.

I used PROC SURVEYMEANS in SAS version 8.02 to estimate ECC_u and ECC_w

in wetland and cropland habitats. I computed separate estimates at each study site for

each habitat type. I examined marginal plots to examine individual datum points and their influence on the overall means and adjusted weights if a datum point simultaneously had both a sample value and weight as an outlier (California Health Interview Survey 2002). I multiplied ECC_w and ECC_{guild} by the amount of habitat at a particular site (Table 1.1) to compute species-specific use days a site could potentially support.

CHAPTER 3

RESULTS

Percent Occurrence of plant food items

I summarized % occurrence and biomass (kg/ha) density for 37 genera of seeds.

Seeds from the family Cyperaceae (i.e., sedges and rushes) and Poacae (i.e., grasses)

contributed nearly 60% to total seed biomass in PEM wetlands (Table 3.1) *Polygonum*

spp*., Cornus* spp. *Quercus* spp*.,* and *Cephalanthus occidentalis,* contributed 71% of total

plant biomass in PF wetlands (Table 3.1). *Ipomoea* spp*., Cyperacea*, and tubers from

Sagitaria spp. and *Cyperus* Spp. contributed nearly 50% of total plant biomass in LC

wetlands (Table 3.1). *Polygonum* spp. was the most frequently occurring seed taxon in

all three wetland habitats I sampled. Collectively they accounted for 7.4%, 24.6%, and

6.3% of total plant biomass in PEM, PF, and LC wetlands respectively.

Nektonic food biomass

I sampled 110 PEM wetlands, 84 PF wetlands and 76 LC wetlands across all sites

(Table 3.2). Total food density was greatest in PF wetlands (4.84 kg/ha), followed by

PEM wetlands (2.49 kg/ha), and LC wetlands (0.58 kg/ha; Table 3.2) across all sites.

Within study sites, CVs were mostly greater than my desired level of precision (CV ≤

15%); however, for the total food density combined sites the CVs for PF samples were

the only ones to exceed CV = 15% (Table 3.2). Seed and invertebrate densities were

38

Food item	Palustrine Emergent		Palustrine Forested		Lacustrine	
	% occurrence	kg/ha	% occurrence	kg/ha	% occurrence	kg/ha
Abutilon theophrasti	2%	0.6	< 1%	0.0	1%	0.4
Alisima spp.	8%	0.3	3%	0.1	8%	0.0
Amaranthus spp.	11%	0.8	15%	1.1	16%	0.5
Ambrosia spp.	2%	0.1	1%	0.0	< 1%	0.0
Bidens spp.	31%	4.7	22%	3.3	27%	1.3
Carex spp.	21%	2.0	22%	4.2	14%	0.8
Cephalanthus occidentalis	7%	0.3	21%	7.5	7%	0.9
Ceratophyllum demersum	3%	1.6	< 1%	0.0	< 1%	0.0
Chenopodium spp.	5%	0.6	5%	0.6	5%	0.4
Cladium jamaicense	1%	6.1	< 1%	0.0	< 1%	0.0
Cornus spp.	6%	10.6	15%	16.4	3%	0.5
Cyperus spp.	8%	6.0	8%	0.8	9%	1.2
Digitaria spp.	8%	1.3	4%	0.0	6%	0.1
Echinochloa spp.	37%	9.8	14%	0.7	14%	0.2
Eleocharis spp.	11%	1.1	3%	0.0	4%	0.1
Fagopyrum esculentum	< 1%	0.0	< 1%	1.7	< 1%	0.0
Ipomoea lacunosa	1%	0.7	2%	5.1	2%	4.1
Juncus spp.	2%	0.0	< 1%	0.0	< 1%	0.0
Leersia spp.	43%	8.4	19%	0.5	29%	1.0
Myriophyllum spp.	1%	0.1	< 1%	0.0	< 1%	0.0
Najas spp.	7%	1.1	1%	0.0	3%	0.7
Panicum spp.	13%	1.4	7%	0.2	14%	0.7
Polygonum pennsylvanicum	1%	0.0	1%	5.4	< 1%	0.2
Polygonum spp.	45%	8.9	27%	21.0	29%	1.7
Potamogeton spp.	19%	4.3	4%	0.0	14%	1.5
Quercus spp.	< 1%	0.0	5%	13.6	< 1%	0.3
Rhynchospora corniculata	< 1%	0.0	< 1%	0.0	< 1%	0.0
Rumex crispus	10%	1.0	11%	0.6	5%	0.1
Sagittaria spp.	14%	4.3	3%	0.1	12%	0.1
Scirpus spp.	37%	20.5	12%	0.9	27%	1.6
Setaria spp.	3%	0.1	1%	0.0	1%	0.0
Sida spinosa	1%	0.2	< 1%	0.0	1%	0.0
Sorghum	1%	0.0	< 1%	0.0	< 1%	0.0
Sparganium spp.	5%	2.4	1%	0.2	2%	0.3
Vallisneria americana	1%	0.9	< 1%	0.0	1%	0.0
Vitis spp.	3%	1.1	8%	1.8	1%	0.0
Zannichellia palustris	3%	0.0	1%	0.0	1%	0.0
Unknown grasses	3%	14.2	2%	0.0	2%	0.0
Tuber	6%	7.7	1%	3.7	3%	2.5

Table 3.1. Percent occurrence and mean biomass (kg/ha) of seeds and tubers in benthic and nektonic samples from wetland habitats at six study sites in the Upper Mississippi River and Great Lakes Region, USA during February-May 2006.

Site	Habitat	n		Food Density (kg/ha)											
		wetlands	samples	Seeds			Inverts			Tubers			**Total**		
				$\bar{x}$	SE	CV	$\bar{x}$	SE	CV	$\bar{x}$	SE	CV	$\bar{x}$	**SE**	**CV**
SR	PEM	8	19	4.52	1.50	33%	0.41	0.13	31%	0	0	n/a	**4.93**	**1.56**	**32%**
	PF	13	22	0.64	0.30	48%	0.85	0.27	32%	0	0	n/a	**1.49**	**0.43**	**29%**
	LC	22	42	0.24	0.07	29%	0.17	0.06	37%	0	0	n/a	**0.41**	**0.11**	**27%**
LE	PEM	15	32	0.80	0.19	24%	1.20	0.28	23%	0	0	n/a	**2.00**	**0.33**	**16%**
	PF	13	20	7.08	2.13	30%	3.03	0.74	24%	0	0	n/a	**10.11**	**2.44**	**24%**
	LC	11	18	0.40	0.20	49%	0.37	0.20	54%	0	0	n/a	**0.77**	**0.29**	**33%**
SB	PEM	27	45	0.76	0.46	61%	1.63	0.49	30%	0	0	n/a	**2.39**	**0.69**	**29%**
	PF	0	0	--NOT SAMPLED--											
	LC	9	16	0.03	0.03	40%	0.32	0.08	24%	0	0	n/a	**0.36**	**0.08**	**22%**
CA	PEM	15	32	0.72	0.20	27%	0.94	0.16	17%	0	0	n/a	**1.66**	**0.24**	**15%**
	PF	34	53	5.00	3.18	64%	2.14	0.47	22%	0	0	n/a	**7.14**	**3.39**	**47%**
	LC	0	0	--NOT SAMPLED--											
IR	PEM	11	20	1.83	0.58	32%	0.52	0.18	35%	0	0	n/a	**2.42**	**0.70**	**29%**
	PF	20	40	1.85	1.02	55%	1.85	0.31	17%	0	0	n/a	**3.70**	**1.23**	**33%**
	LC	10	26	0.24	0.09	37%	0.29	0.04	13%	0	0	n/a	**0.53**	**0.09**	**17%**
WI	PEM	34	53	4.02	1.30	32%	1.13	0.30	27%	0	0	n/a	**5.15**	**1.20**	**23%**
	PF	4	6	1.75	1.25	71%	0.89	0.54	60%	0	0	n/a	**2.64**	**1.57**	**59%**
	LC	24	50	0.24	0.14	56%	0.83	0.37	45%	0	0	n/a	**1.07**	**0.38**	**36%**
All Sites	PEM	110	201	1.15	0.24	21%	1.33	0.26	19%	0	0	n/a	**2.49**	**0.36**	**15%**
	PF	84	142	2.86	1.04	36%	1.97	0.25	13%	0	0	n/a	**4.84**	**1.18**	**24%**
	LC	76	152	0.23	0.06	28%	0.35	0.06	18%	0	0	n/a	**0.58**	**0.09**	**15%**

Table 3.2. Estimated means ($\bar{x}$), standard errors (SE), and coefficients of variation (CV) of seed, invertebrate, tuber and total food density (kg/ha) of nektonic samples collected in palustrine emergent (PEM), palustrine forested (PF), and lacustrine (LC) wetlands at six study sites in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006. Mean food density for all sites was calculated using adjusted sampling weights from each individual study site. Wetlands are the total number of wetlands sampled within cells and samples refers to the number of nektonic samples taken within wetlands.

greatest at the Lake Erie marshes study site in PF wetlands, representing 7.08 kg/ha and 3.03 kg/ha respectively.

Benthic Food Biomass

I sampled 111 PEM wetlands, 87 PF wetlands and 76 LC wetlands across all sites (Table 3.3). Marginal plots identified four datum points as having influential weights on the final mean of within-site estimates; five datum points were influential on among-site estimates. Therefore, I performed analyses with adjusted weights. Total food density was greatest in PEM wetlands and ranged from 255 kg/ha at the Scioto River site to 170 kg/ha at the Illinois River site (Table 3.3). Within study sites, CVs were mostly greater than my desired level of precision (CV ≤ 15%); however, for the total food density combined sites the CVs for LC estimates were the only ones to exceed CV of 15% (Table 3.3). Seed density was greatest at the Wisconsin study site in PEM wetlands (212 kg/ha), while invertebrate density was greatest at the Saginaw Bay study site in PEM wetlands (159 kg/ha). Tubers did not contribute substantially to total food biomass but was greatest at the Illinois River site in PEM wetlands (84 kg/ha; Table 3.3).

Invertebrate foods

Error variances of invertebrate food density were constant and were linearly related to explanatory variables as revealed in residual plots. The dispersion parameter of the full model was 2.65, indicating a high amount of autocorrelation, so I used QAIC that corrected for over-dispersion and penalized models with more parameters (Burnham and Anderson 1998). The model containing wetland system was the top approximating model explaining variation in invertebrate food density ($\omega_1 = 0.310$; Table 3.4).

41

Palustrine emergent wetlands averaged 24.5% more invertebrate food density than

lacustrine wetlands (Figure 3.1). I considered the additive model containing wetland

| Site | Habitat | N | | Food Density (kg/ha) | | | | | | | | | | | |
| | | | | Seeds | | | Inverts | | | Tubers | | | **Total** | | |
		wetlands	samples	$\bar{x}$	SE	CV	$\bar{x}$	SE	CV	$\bar{x}$	SE	CV	$\bar{x}$	**SE**	**CV**
SR	PEM	10	23	210	88	42%	43	12	28%	2	1	74%	**255**	**89**	**35%**
	PF	14	24	65	32	49%	11	2	14%	0	0	n/a	**76**	**32**	**42%**
	LC	20	42	28	17	62%	26	17	64%	0	0	n/a	**54**	**23**	**43%**
LE	PEM	14	30	211	65	31%	22	6	28%	0	0	n/a	**233**	**68**	**29%**
	PF	15	24	194	68	35%	23	4	17%	0	0	n/a	**217**	**68**	**31%**
	LC	9	16	25	12	49%	7	2	23%	0	0	n/a	**32**	**12**	**38%**
SB	PEM	27	43	67	20	30%	159	67	42%	0	0	61%	**227**	**70**	**31%**
	PF	0	0	--NOT SAMPLED--											
	LC	10	17	3	1	45%	3	1	25%	0	0	n/a	**6**	**1**	**23%**
CA	PEM	15	39	83	22	26%	60	22	37%	46	28	60%	**190**	**48**	**25%**
	PF	33	51	78	33	43%	27	6	22%	0	0	n/a	**105**	**34**	**32%**
	LC	0	0	--NOT SAMPLED--											
IR	PEM	11	19	78	21	27%	8	3	33%	84	78	93%	**170**	**98**	**58%**
	PF	20	41	72	17	24%	26	6	24%	5	5	98%	**103**	**19**	**18%**
	LC	10	27	30	13	44%	39	16	40%	6	6	94%	**75**	**26**	**35%**
WI	PEM	34	55	212	42	20%	40	21	54%	2	2	89%	**254**	**54**	**21%**
	PF	5	8	186	95	51%	12	8	70%	0	0	n/a	**198**	**100**	**50%**
	LC	24	54	123	20	16%	123	36	29%	0	0	87%	**247**	**43**	**18%**
All	PEM	111	209	118	21	17%	68	15	22%	8	4	56%	**194**	**25**	**13%**
	PF	87	149	82	15	18%	26	4	17%	4	4	97%	**112**	**16**	**14%**
	LC	73	156	19	5	25%	18	5	28%	3	2	96%	**40**	**8**	**20%**

Table 3.3. Estimated means($\bar{x}$), standard errors (SE), and coefficients of variation (CV) of seed, invertebrate, tuber and total food density (kg/ha) of benthic samples collected in palustrine emergent (PEM), palustrine forested (PF), and lacustrine (LC) wetlands at six study sites in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006. Mean food density for all sites was calculated using adjusted sampling weights from each individual study site. Wetlands are the total number of wetlands sampled within cells and samples refers to the number of benthic samples taken within wetlands.

Model	K	QAIC	ΔQAIC	ω_i	R^2
System	3	770.7	0.0	0.310	0.02
System + Period	4	772.0	1.3	0.163	0.02
System + Zone	4	772.7	2.0	0.116	0.02
Period	2	773.1	2.4	0.094	0.00
Zone	2	773.8	3.0	0.068	0.00
System * Period	6	773.9	3.2	0.064	0.03
System + Cover	7	774.0	3.2	0.061	0.04
Site	6	775.3	4.6	0.031	0.02
System* Zone	6	776.2	5.5	0.020	0.02
Site + Period	7	776.3	5.6	0.019	0.03
System + Site	8	776.4	5.7	0.018	0.03
Cover	5	776.7	5.9	0.016	0.01
Site +System +Period	9	777.5	6.8	0.010	0.04
Site* System	18	778.4	7.7	0.007	0.10
Site * Period	11	781.8	11.1	0.001	0.03
System* Cover	15	786.0	15.3	0.000	0.04
Site * System * Period	37	800.8	30.1	0.000	0.13
null	1	982.5	211.8	0.000	n/a

[a] SITE = study site; SYSTEM = wetland system (i.e., palustrine emergent, palustrine forested, lacustrine); PERIOD = sampling period; COVER = vegetation cover type; ZONE = sampling zone (i.e., shallow vs. deep).

Table 3.4. Candidate models explaining variation in benthic invertebrate food density (kg/ha) sampled in wetlands at six sites in the Upper Mississippi River and Great Lakes Region, USA during February-May 2006. Models are ranked by Quasi-Akaike's Information Criterion (QAIC). Also included are the number of estimable parameters (K), model weight (ω_i), and proportion of variance accounted for (R^2).

system and sampling period ($\omega_1 = 0.163$) competitive since it was within 2 ΔQAIC units of the top model. Invertebrate density increased from early to late sampling period (Figure 3.2).

Plant Foods

Error variances of plant food density were constant and were linearly related to explanatory variables as revealed in residual plots. The dispersion parameter of the full model was 4.01, indicating a high amount of autocorrelation, so I used QAIC that corrected for over-dispersion and penalized models with more parameters (Burnham and Anderson 1998).

The top approximating model explaining variation in plant food density was the additive model containing wetland system and study site ($\omega_1 = 0.506$; Table 3.5). Palustrine emergent wetlands averaged 41.5% more plant food density than lacustrine wetlands (Figure 3.1). The east-central Wisconsin site had the greatest food density (Figure 3.3). The next closest model, which I considered competitive since it was within 2 ΔQAIC units, was the additive model of wetland system, study site, and sampling period ($\omega_1 = 0.224$). Similar to invertebrate density, plant food density also increased between early and late sampling periods (Figure 3.2).

Cropland Food Biomass

I adjusted weights of four samples from the east-central Wisconsin study site for the within-site estimates. I adjusted weights for one sample from the east-central Wisconsin site and one sample from the Lake Erie Marshes site for the among-site estimates.
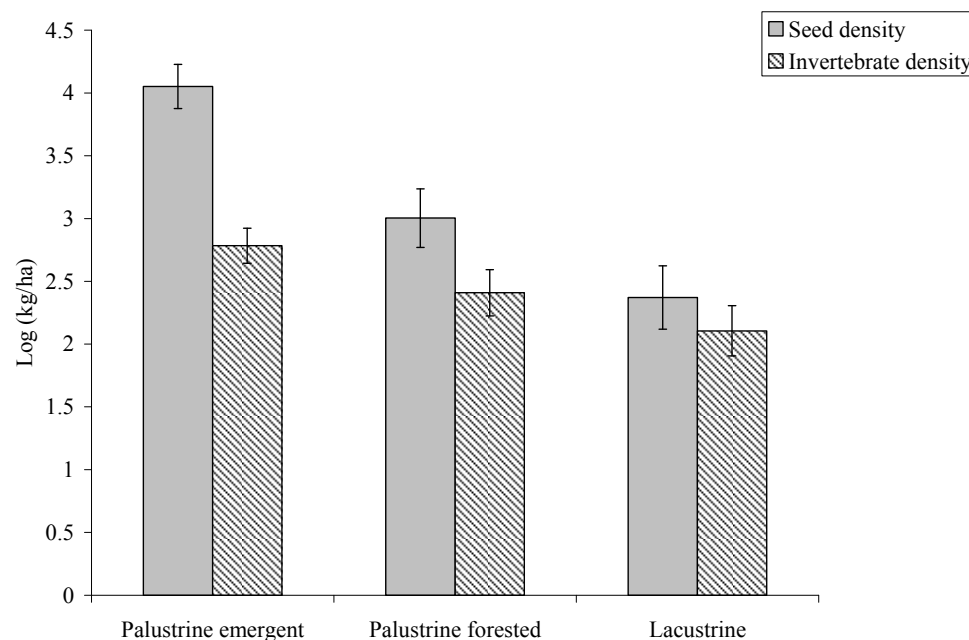
Figure 3.1 Seed and invertebrate densities with standard errors in wetland habitat types, pooled across study sites and sampling periods. Samples were obtained in wetland habitats in Upper Mississippi River and Great Lakes Region during February-May 2006.
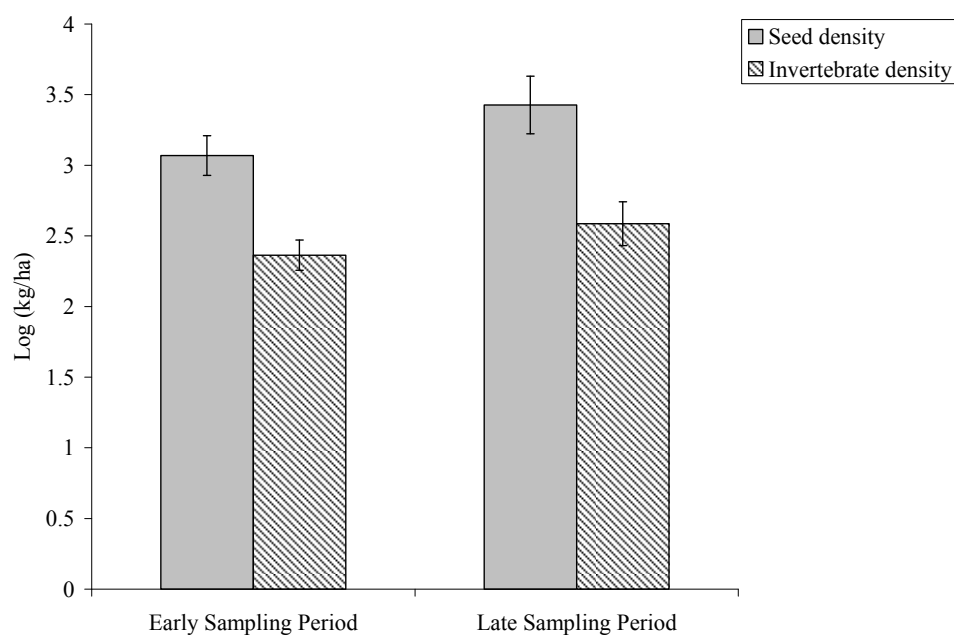
Figure 3.2. Seed and invertebrate densities during early (before arrival of migrating waterfowl) and late(after departure of migrating waterfowl) sampling periods, pooled across study sites and habitat types. Samples were obtained in wetland habitats in Upper Mississippi River and Great Lakes Region during February-May 2006.

Model	K	QAIC	ΔQAIC	ω_i	R^2
System + Site	8	566.6	0.0	0.506	0.17
Site +System +Period	9	568.2	1.6	0.224	0.17
System	3	569.6	3.0	0.111	0.09
System + Zone	4	571.6	5.0	0.041	0.09
System + Cover	7	571.9	5.3	0.036	0.13
System + Period	4	570.9	4.3	0.059	0.10
System * Period	6	574.7	8.1	0.009	0.09
System* Zone	6	574.6	8.1	0.009	0.09
Site	6	578.4	11.8	0.001	0.07
Cover	5	579.2	12.6	0.001	0.05
Period	2	579.8	13.3	0.001	0.00
Zone	2	580.4	13.8	0.001	0.00
Site * System	18	581.6	15.0	0.000	0.19
Site + Period	7	579.8	13.2	0.001	0.07
Site * Period	11	586.2	19.6	0.000	0.08
System* Cover	15	584.7	18.1	0.000	0.13
Site * System * Period	37	611.2	44.6	0.000	0.20
Null	1	717.3	150.7	0.000	n/a

[a] SITE = study site; SYSTEM = wetland system(i.e., palustrine emergent, palustrine forested, lacustrine); PERIOD = sampling period; COVER = vegetation cover type; ZONE = sampling zone (i.e., shallow vs. deep).

Table 3.5. Candidate models explaining variation in benthic plant food density (kg/ha) sampled in wetlands at six sites in the Upper Midwest, USA, during February-May 2006. Models are ranked by Quasi-Akaike's Information Criterion (QAIC). Also included are the number of estimable parameters (K), model weight (ω_i), and proportion of variance accounted for (R^2).
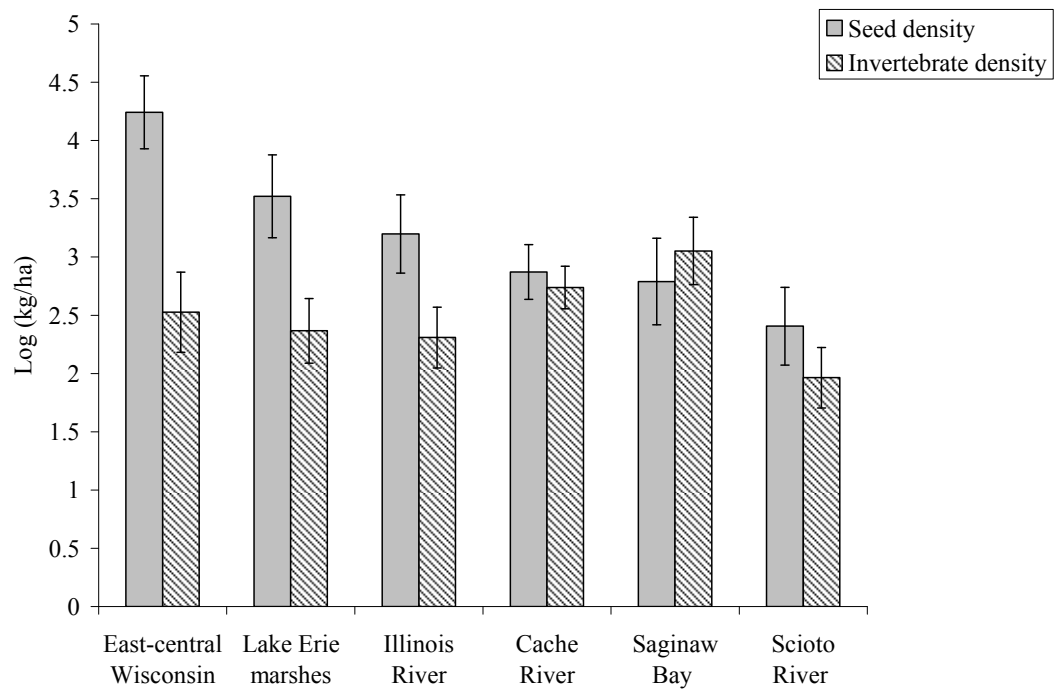
Figure 3.3. Seed and invertebrate density at study sites, pooled across sampling periods and habitat types. Samples were obtained in wetland habitats in Upper Mississippi River and Great Lakes Region during February-May 2006.

I obtained 83 samples from corn fields and 31 from soybean fields across all sites (Table 3.6). Total food density in croplands varied from 223 kg/ha at the Illinois River site to 17 kg/ha at the Lake Erie site (Table 3.6) for the within site estimates. Biomass density from cornfields always exceeded soybean fields (Table 3.6). All estimates from all sites exceeded the desired CV of 15%.

Relative biomass, Plant versus. Invertebrate Foods

Percent invertebrate contribution from benthic samples differed by study site ($F_{(5,505)} = 5.06$, $P < 0.001$) and wetland system ($F_{(2,505)} = 6.79$, $P = 0.001$). I did not detect a difference between sampling periods ($F_{(1,505)} = 0.65$, $P = 0.419$). Benthic invertebrates comprised the highest mean percentage (79%) of total biomass in lacustrine habitats at the Saginaw Bay study site during the late sampling period, while palustrine emergent wetlands at the Illinois River site during the late sampling period comprised the least (15%; Figure 3.4).

Percent invertebrate contribution from nektonic samples differed by study site ($F_{(5,487)} = 9.04$, $P < 0.001$), wetland system ($F_{(2,487)} = 8.52$, $P < 0.001$) and sampling period ($F_{(1,487)} = 5.79$, $P = 0.016$). Lacustrine wetlands at Saginaw Bay during the late sampling period comprised the highest mean percentage (80%) of total biomass, while palustrine forested wetlands in Wisconsin during the early sampling period made up the least (11%, Figure 3.5).

Site[1]	Crop Type	N	Food Density (kg/ha) $\bar{x}$	SE	CV
Scioto River	Corn	18	28	14	51%
	Soybean	13	13	4	34%
	Both crops	31	13	4	31%
Lake Erie	Corn	12	66	33	51%
	Soybean	18	15	8	51%
	Both crops	30	17	7	45%
Saginaw Bay	Corn	24	120	99	82%
	Soybean	0	n/a	n/a	n/a
	Both crops	24	120	99	82%
Illinois River	Corn	18	223	130	58%
	Soybean	0	n/a	n/a	n/a
	Both crops	18	223	130	58%
Wisconsin	Corn	11	108	52	48%
	Soybean	0	n/a	n/a	n/a
	Both crops	11	108	52	48%
All sites	Corn	83	33	14	43%
	Soybean	31	14	6	41%
	Both crops	114	32	13	40%

[1] No cropland samples were obtained from the Cache River site.

Table 3.6. Estimated means($\bar{x}$), standard errors (SE), and coefficients of variation (CV) of corn and soybean food density (kg/ha) found in croplands at six study sites in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006.
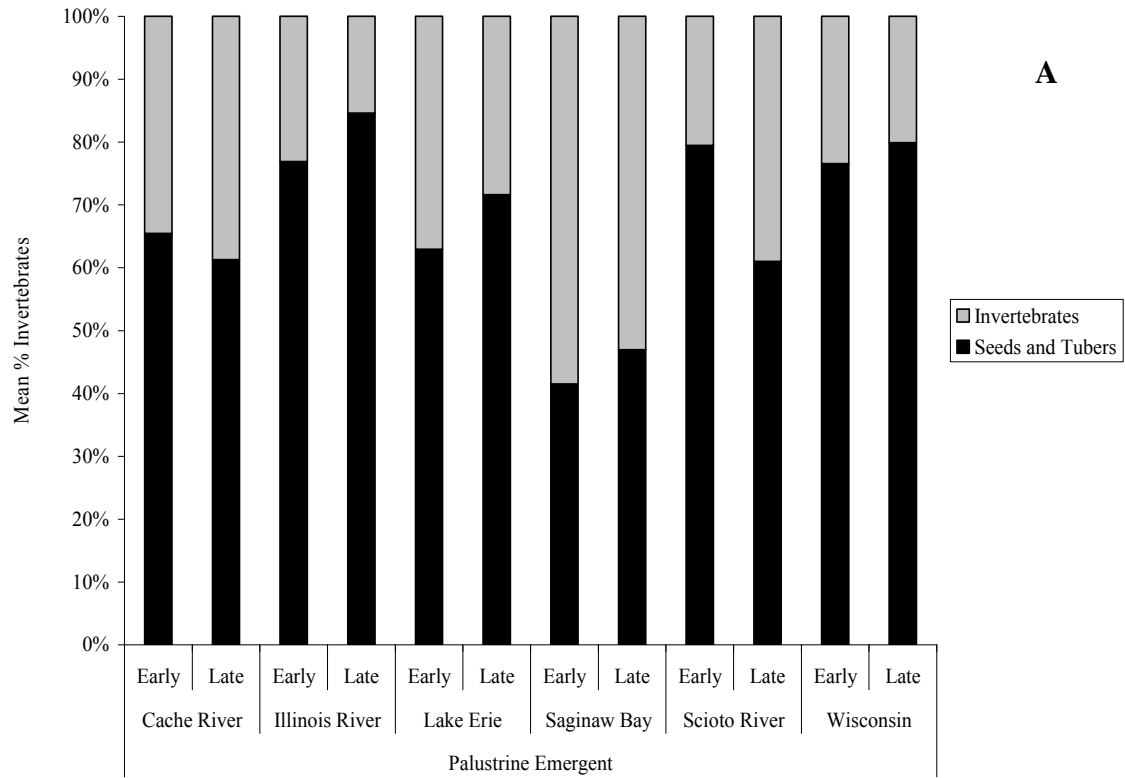
Figure 3.4. Mean % invertebrates of total benthic biomass (kg/ha) in palustrine emergent (A), palustrine forested (B) and lacustrine (C) wetlands sampled in the Upper Mississippi River and Great Lakes Region during February-May 2006. Palustrine forested wetlands were not sampled at Saginaw Bay. Lacustrine wetlands were not sampled at the Cache River.

Figure 3.4 continued
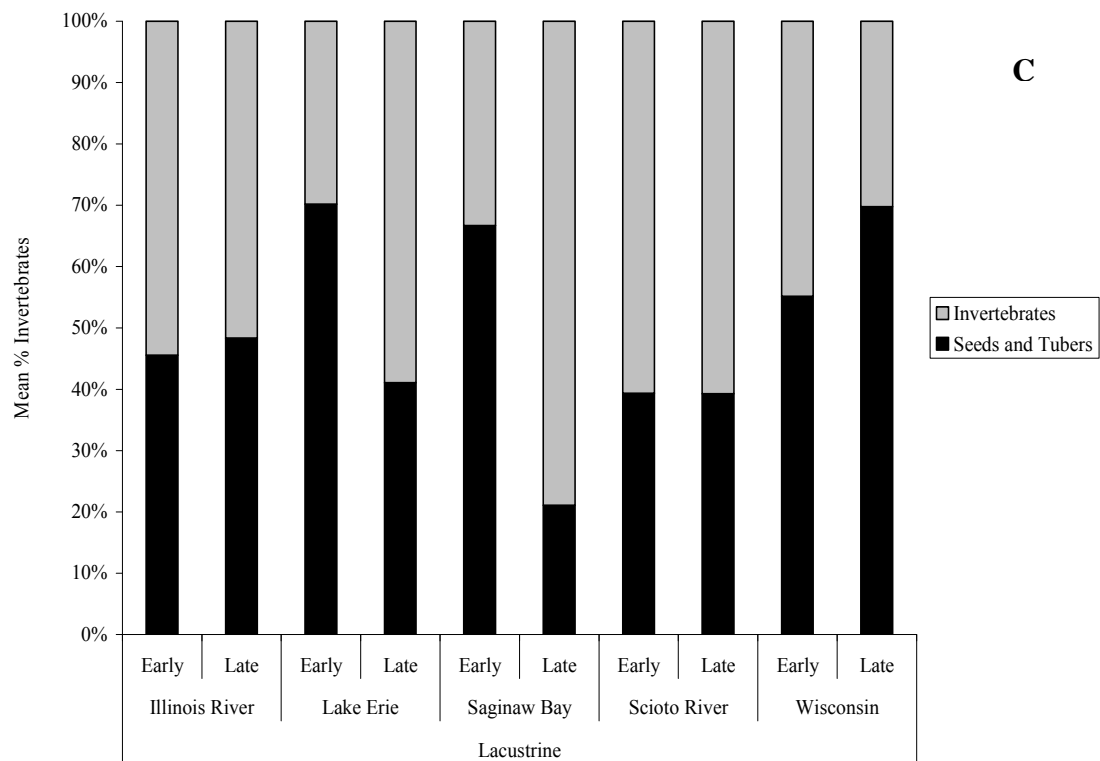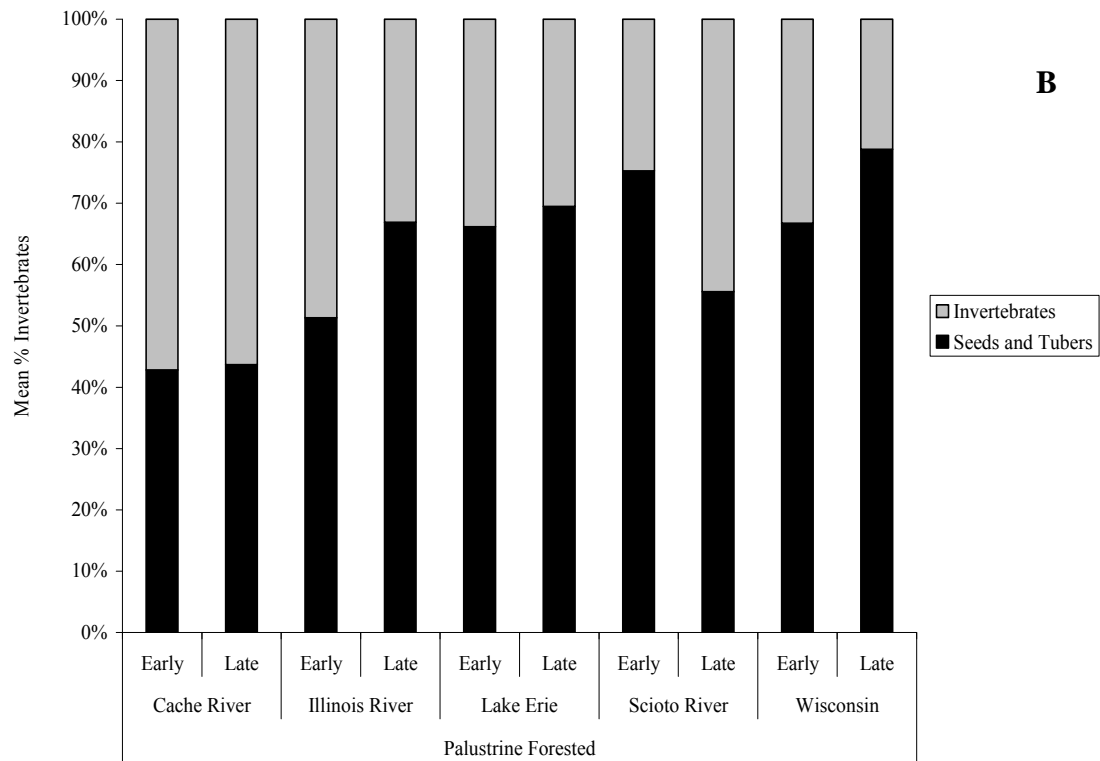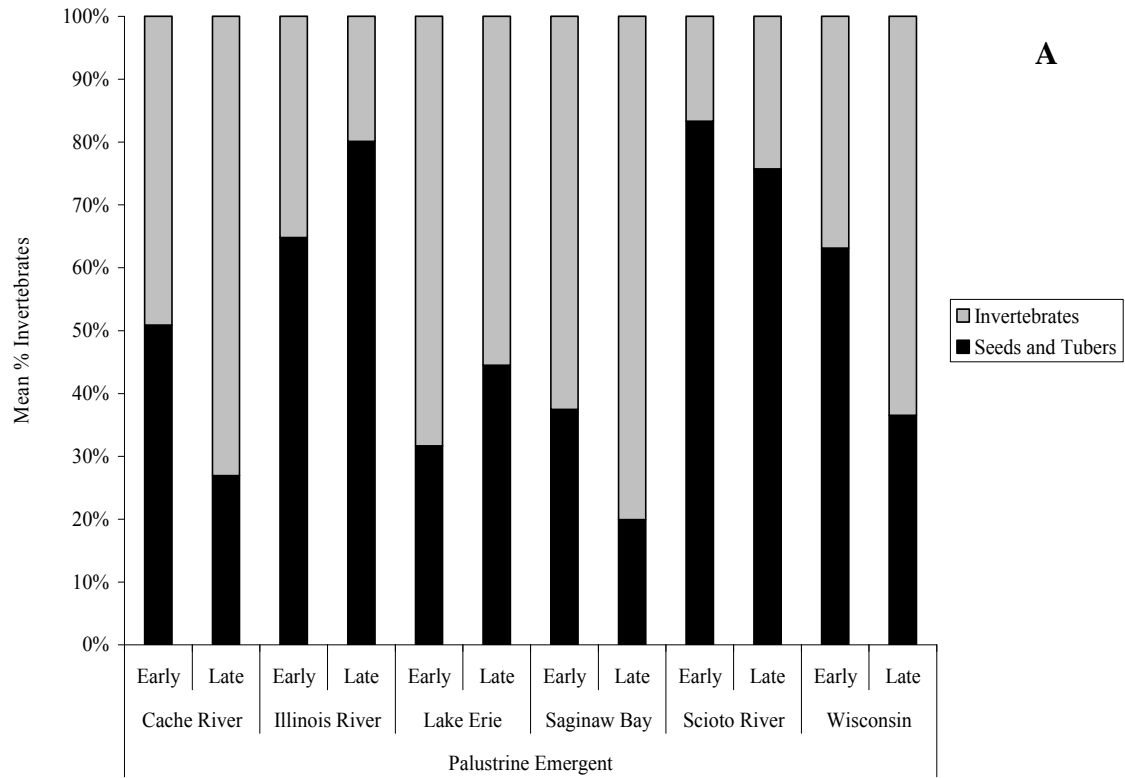
Figure 3.5. Mean % invertebrates of total nektonic biomass (kg/ha) in palustrine emergent (A), palustrine forested (B) and lacustrine (C) wetlands sampled in the Upper Mississippi River and Great Lakes Region during February-May 2006. Palustrine forested wetlands were not sampled at Saginaw Bay. Lacustrine wetlands were not sampled at the Cache River.

Figure 3.5 continued
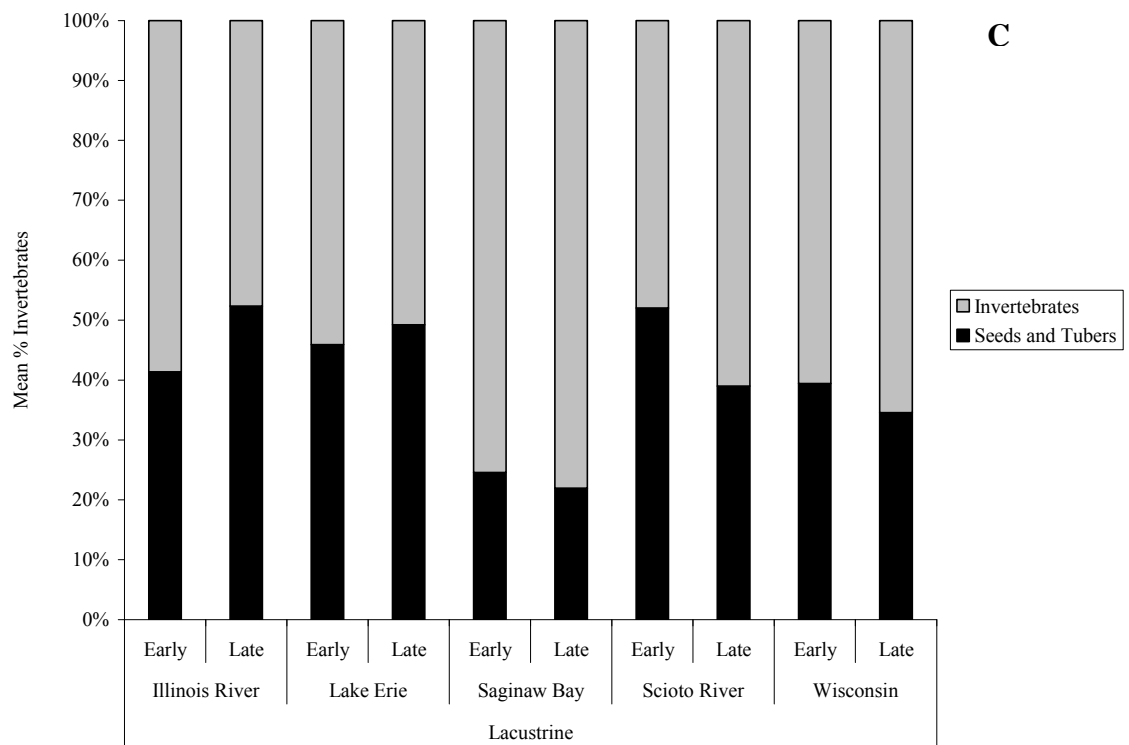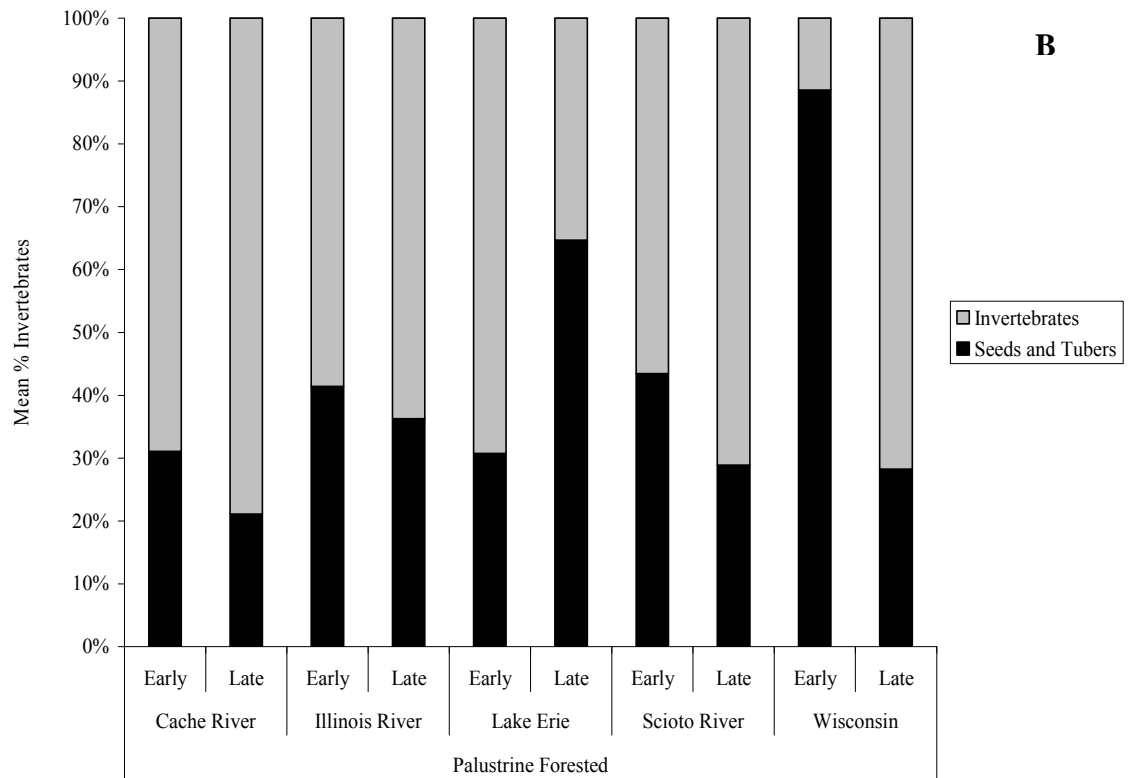
Energetic Carrying Capacity

Weighted vs. un-weighted estimates

I used benthic samples to estimate energetic carrying capacity since nektonic

samples contributed < 2% to overall biomass estimates, and none of the nektonic samples

exceeded foraging thresholds. I adjusted the weight of one datum point each from the

Scioto River, Lake Erie marshes, and the east-central Wisconsin sites.

ECC_u varied ($F_{5,504} = 8.76$, $P<0.001$) among study sites, and habitat types ($F_{2,504} =$

35.33, $P<0.001$) but did not differ ($F_{1,504} = 0.65$, $P = 0.420$) between sampling periods

(Table 3.5). Palustrine emergent wetlands at the Scioto River site had the highest

energetic carrying capacity (1,525 dud/ha) among wetlands, while the Illinois River site

had the highest carrying capacity among croplands (2,798 dud/ha).

ECC_w varied ($F_{5,504} = 14.46$, $P<0.001$) among study sites, and habitat types ($F_{2,504}$

$= 47.67$, $P<0.001$) but did not differ ($F_{1,504} = 0.46$, $P = 0.500$) between sampling periods

(Table 3.6). Palustrine emergent wetlands at the Illinois River site had the highest

energetic carrying capacity (1,287 dud/ha) among wetlands, while the Illinois River site

had the highest carrying capacity among croplands (3,303 dud/ha).

I detected differences between ECC_u and ECC_w in only 6 of 21 habitat by site

paired *t*-test comparisons. Lacustrine wetlands habitats at Scioto River (*t-value* = 5.84,

			Energetic Carrying Capacity (DUD_u/ha) with foraging threshold						
			0 kg/ha				50 kg/ha	130 kg/ha	280 kg/ha
Site[1]	Habitat	N	$\bar{x}$ invertebrate	$\bar{x}$ total	SE	CV	$\bar{x}$	$\bar{x}$	$\bar{x}$
SR	Palustrine Emergent	23	86	1525	632	41%	1276	994	708
	Palustrine Forested	24	22	431	208	48%	287	246	185
	Lacustrine	42	52	272	150	55%	190	126	31
	Cropland	31	n/a	124	38	31%	21	6	1
LE	Palustrine Emergent	30	37	1155	300	26%	920	596	320
	Palustrine Forested	24	46	749	236	32%	520	355	140
	Lacustrine	16	13	177	84	48%	81	17	8
	Cropland	30	n/a	159	69	43%	68	20	11
SB	Palustrine Emergent	43	317	633	166	26%	417	277	140
	Palustrine Forested	---NOT SAMPLED--------------------------------------							
	Lacustrine	17	5	21	7	34%	2	0	0
	Cropland	24	n/a	1512	1244	82%	1450	1376	1252
CA	Palustrine Emergent	39	120	1126	302	27%	880	645	373
	Palustrine Forested	51	53	645	313	49%	478	389	257
	Lacustrine	---NOT SAMPLED--------------------------------------							
	Cropland	---NOT SAMPLED--------------------------------------							
IR	Palustrine Emergent	19	17	1177	736	63%	921	727	596
	Palustrine Forested	41	51	456	100	22%	260	158	60
	Lacustrine	27	78	312	119	38%	185	93	12
	Cropland	18	n/a	2798	1628	58%	2588	2295	1773
WI	Palustrine Emergent	55	79	1167	230	20%	899	585	228
	Palustrine Forested	8	24	697	363	52%	442	346	164
	Lacustrine	54	135	482	267	55%	327	122	10
	Cropland	11	n/a	1354	648	48%	1217	1039	668

[1] SR = Scioto River, LE = Lake Erie, SB = Saginaw Bay, CA = Cache River, IR = Illinois River, WI = Wisconsin

Table 3.7. Estimated means ($\bar{x}$), standard errors (SE), and coefficients of variation (CV) of energetic carrying capacity (ECC_u) with presumed foraging threshold in palustrine emergent, palustrine forested, lacustrine, and cropland habitats at six study sites in the Upper Midwest, USA during February-May 2006. ECC estimates assume all potential food items are available for consumption and all ducks require 292 kcal of energy per day.

Site[1]	Habitat	N	$\bar{x}$ invertebrate	$\bar{x}$ total	SE	CV	50 kg/ha $\bar{x}$	130 kg/ha $\bar{x}$	280 kg/ha $\bar{x}$
							Energetic Carrying Capacity (DUD$_w$/ha) with foraging threshold		
SR	Palustrine Emergent	23	51	1040	598	57%	891	714	491
	Palustrine Forested	24	19	429	242	56%	330	286	218
	Lacustrine	42	4	56	48	84%	39	24	0
	Cropland	31	n/a	146	45	31%	33	8	3
LE	Palustrine Emergent	30	39	1168	317	27%	935	625	354
	Palustrine Forested	24	43	615	221	36%	424	276	86
	Lacustrine	16	14	169	87	52%	73	11	0
	Cropland	30	n/a	164	71	43%	71	21	11
SB	Palustrine Emergent	43	345	613	171	28%	396	251	134
	Palustrine Forested	--------------------------------------NOT SAMPLED-----------------------------							
	Lacustrine	17	5	22			2	0	0
	Cropland	24	n/a	1519	1249	82%	1457	1383	1259
CA	Palustrine Emergent	39	131	1184	328	28%	937	718	435
	Palustrine Forested	51	107	655	305	47%	468	369	250
	Lacustrine	--------------------------------------NOT SAMPLED-----------------------------							
	Cropland	--------------------------------------NOT SAMPLED-----------------------------							
IR	Palustrine Emergent	19	19	1287	743	58%	1030	757	611
	Palustrine Forested	41	50	280	57	20%	103	47	14
	Lacustrine	27	86	342	132	39%	209	115	18
	Cropland	18	n/a	3303	1922	58%	3088	2790	2243
WI	Palustrine Emergent	55	85	1165	211	18%	896	573	198
	Palustrine Forested	8	23	604	307	51%	360	273	91
	Lacustrine	54	9	59	38	64%	36	10	4
	Cropland	11	n/a	1707	817	48%	1565	1384	1012

[1] SR = Scioto River, LE = Lake Erie, SB = Saginaw Bay, CA = Cache River, IR = Illinois River, WI = Wisconsin

Table 3.8 Estimated means ($\bar{x}$), standard errors (SE), and coefficients of variation (CV) of energetic carrying capacity (ECC$_w$) with presumed foraging thresholds in palustrine emergent, palustrine forested, lacustrine, and cropland habitats at six study sites in the Upper Midwest, USA during February-May 2006. ECC$_w$ accounts for guild specific daily energy, food, and habitat requirements (See Tables A.4 - A.6) to estimate dud/ha.

P<0.001; Figure 3.6) and east-central Wisconsin (*T-value* = 6.03, *P*<0.001; Figure 3.7) exhibited the largest differences.

Potential ducks use days decreased up to 39% after subtracting the lowest foraging threshold (50 kg/ha) at the Scioto River site, compared to only 14% at the east-central Wisconsin site where ECC was higher (Figure 3.8). Assuming the greatest foraging threshold (280 kg/ha), potential ducks use days at the Illinois River study site declined 50%, compared to 81% at the Lake Erie marshes site. The contribution of individual habitats types to potential ducks use days varied across study sites (Figure 3.8). After subtracting the lowest forging threshold, potential ducks use days were highest at the east-central Wisconsin study site (> 35,000,000) and lowest at the Scioto River study site (< 1,000,000; Figure 3.8). I found large differences among foraging guilds in potential ducks use days that wetlands at each site could support (Figure 3.9). Total diving duck days were vastly lower at all sites except the Scioto River.

Energetic Carrying Capacity Versus Observed Use

Waterfowl use varied by site and habitat type (Appendix 8). Observed waterfowl use was below energetic carrying capacity in all habitats types in the eastern (OH and MI) sites (Figure 3.10). However, palustrine forested wetlands at the Illinois River site, and lacustrine wetlands at the East-central Wisconsin study site, showed levels of waterfowl use that exceeded carrying capacity (Figure 3.11). Palustrine emergent wetlands consistently received the highest waterfowl use while croplands were used the least among all sites.
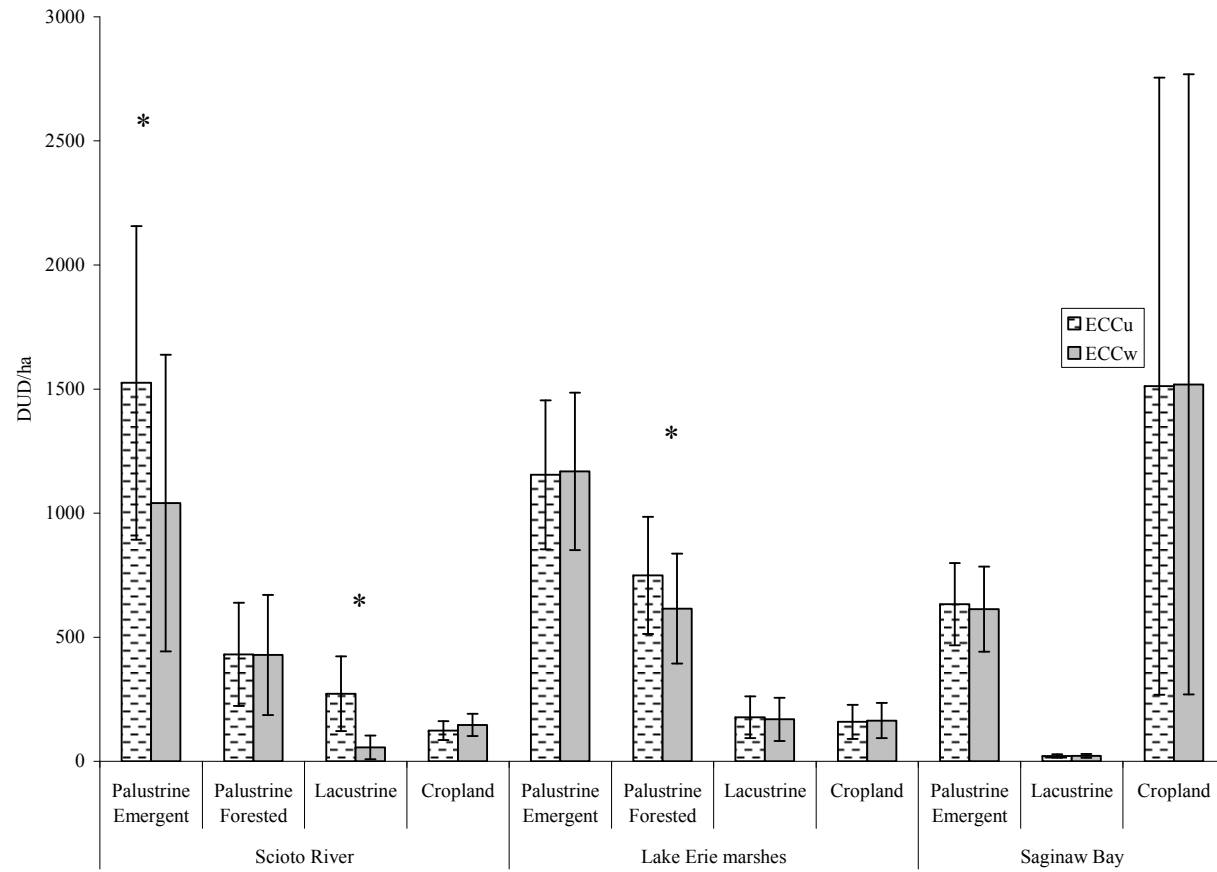
Figure 3.6. Energetic carrying capacity estimates (DUD/ha) +/- standard errors for ECC_u and ECC_w at the Scioto River, Lake Erie Marshes and Saginaw Bay Study sites in wetland and cropland habitats during February-May 2006.
* = significant difference with paired t-test ($P < 0.05$)
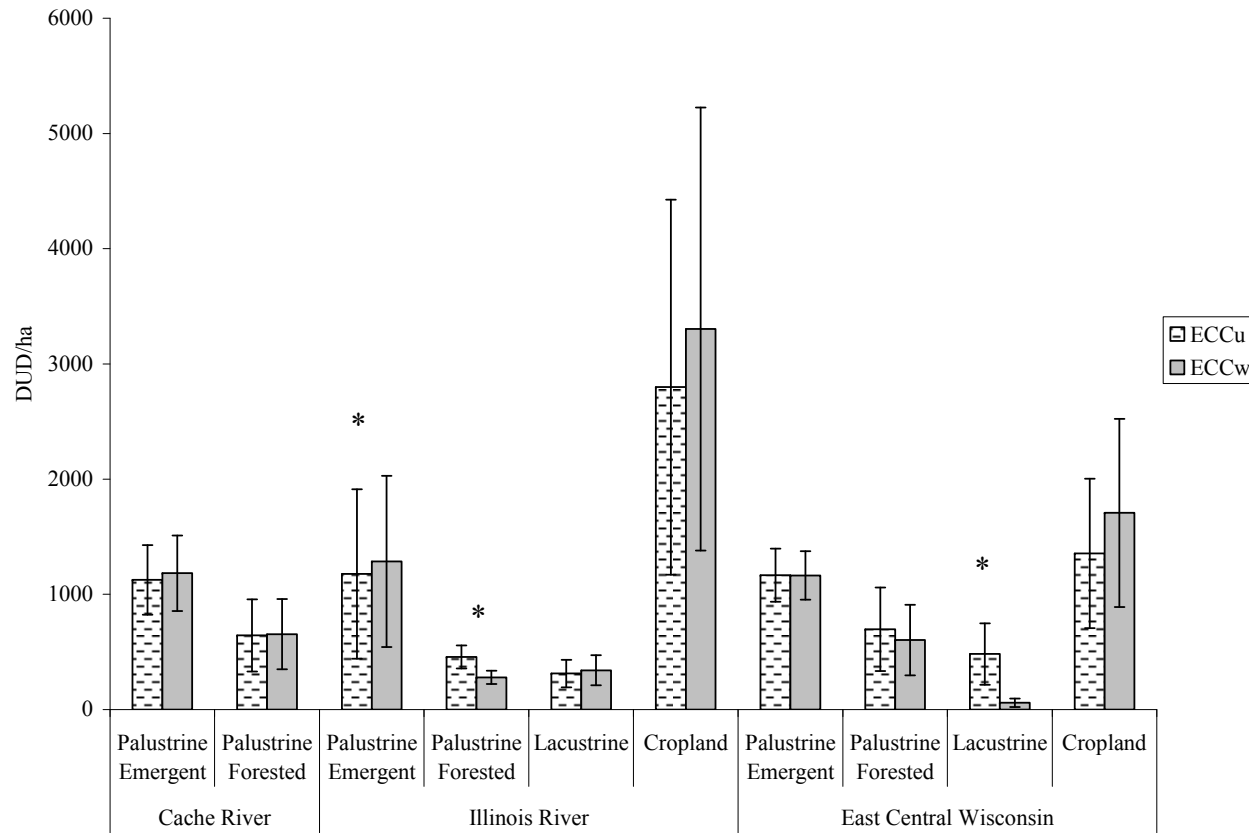
Figure 3.7. Energetic carrying capacity estimates (DUD/ha) +/- standard errors for ECC_u and ECC_w at the Cache River, Illinois River and East Central Wisconsin Study sites in wetland and cropland habitats during February-May 2006.
* = significant difference with paired t-test ($P < 0.05$)
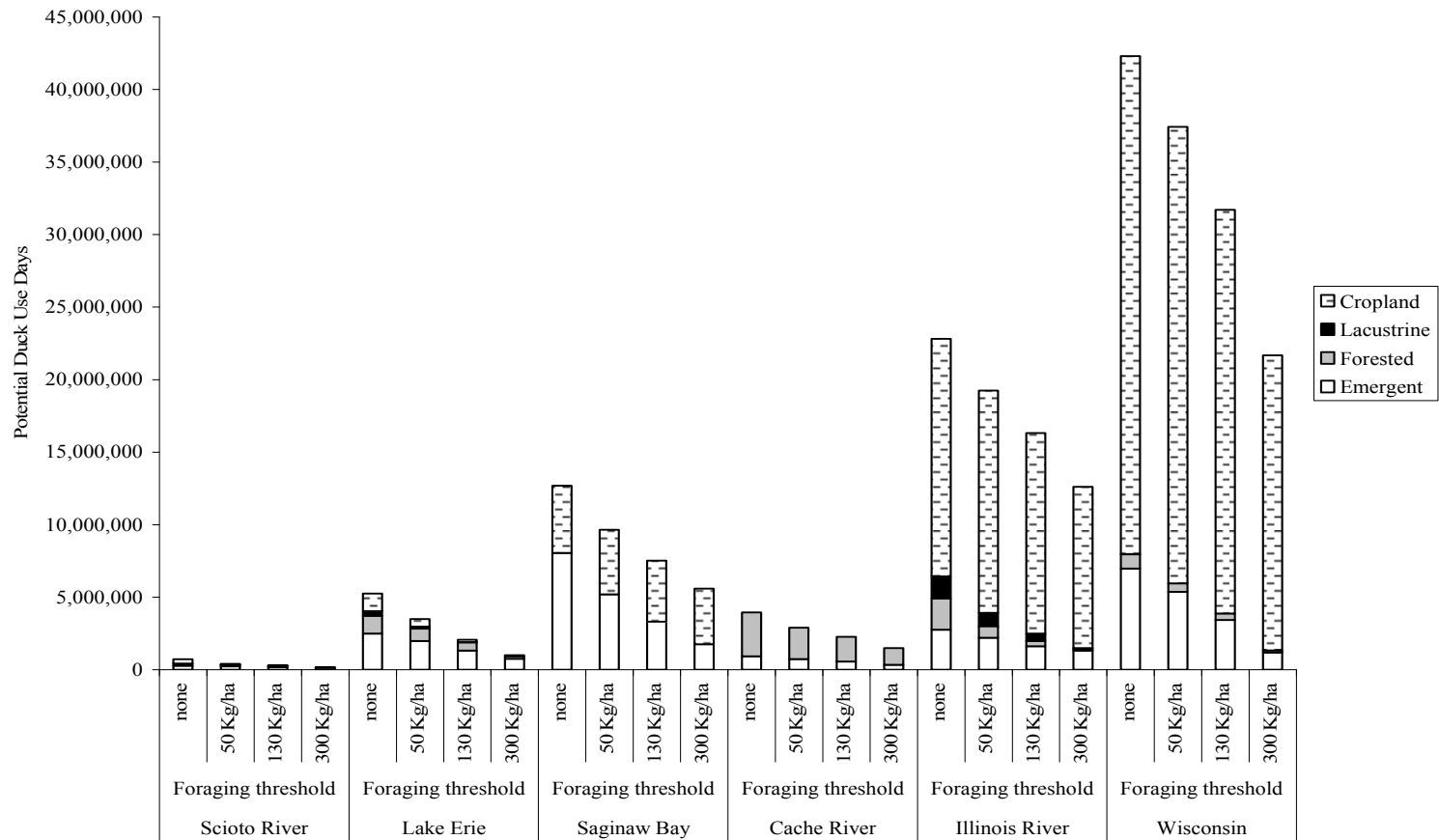
Figure 3.8. Contribution of cropland, lacustrine, palustrine forested, and palustrine emergent habitats to potential duck use days assuming no foraging threshold (none) and three theoretical thresholds at six study sites in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006. ECC_w estimates (Table 3.8) were multiplied by amount of habitat at a site (Table 1.1) to derive potential duck use days.
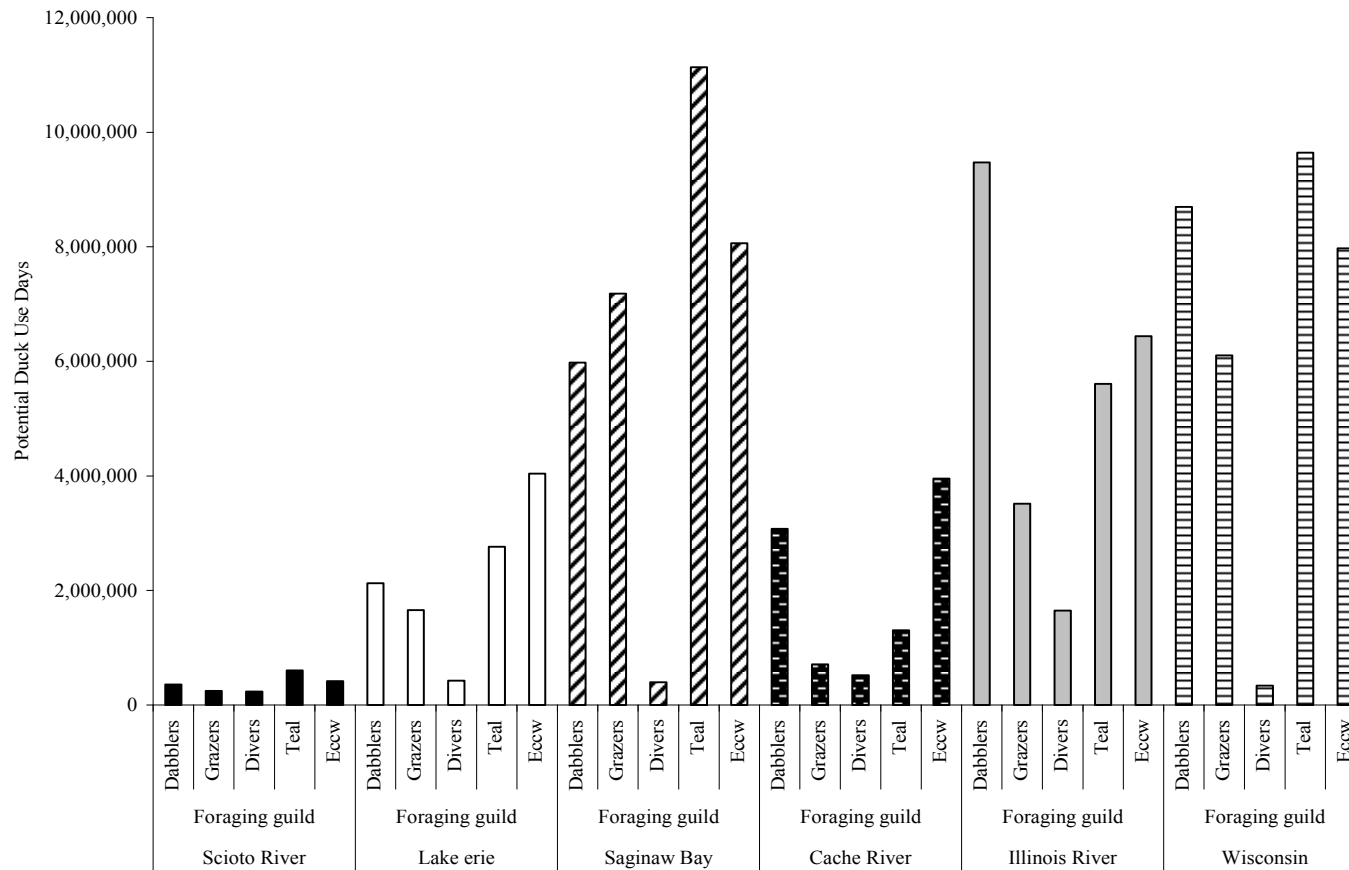
Figure 3.9. Total potential duck use days that wetlands habitats could support assuming energy, diet, and habitat requirements of dabbling, grazing, diving, and teal foraging guilds at six study sites in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006. Wetland estimates from ECC_{guild} (Appendix 9) and ECC_w (Table 3.8) were multiplied by amount of habitat at a site (Table 1.1) to derive potential duck use days.
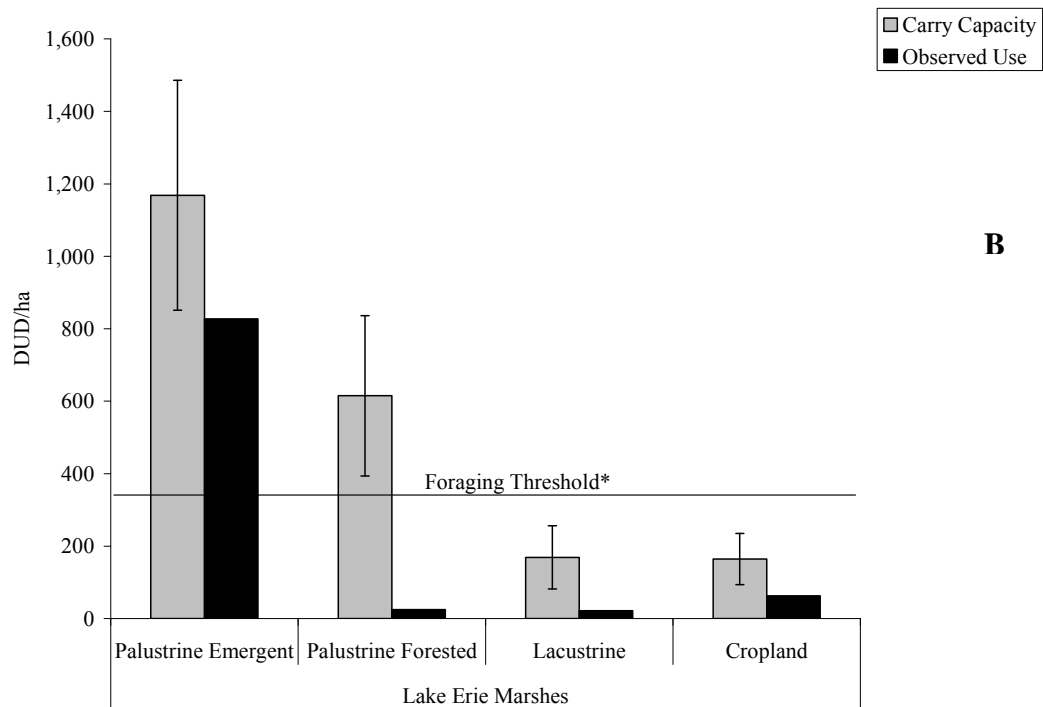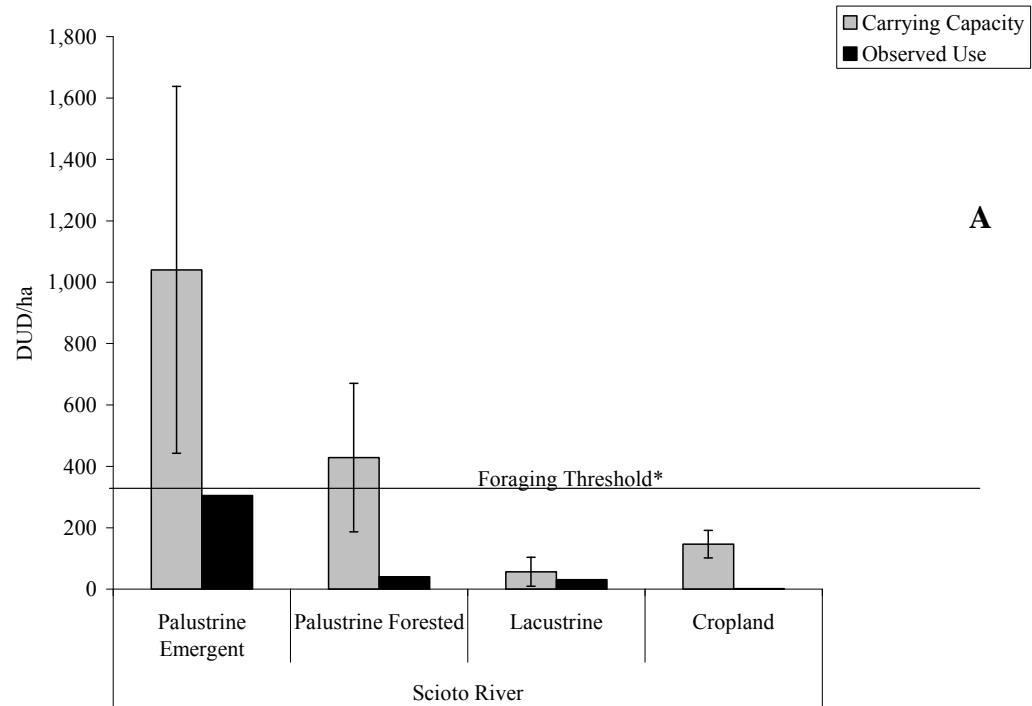
Figure 3.10. Energetic carrying capacity (weighted) +/- standard errors and mean observed waterfowl use/ha on palustrine emergent, palustrine forested, and lacustrine wetlands and croplands at Scioto River (A), Lake Erie (B) and Saginaw Bay (C) study sites during February-May 2006. Energetic foraging threshold is equivalent to 50 kg/ha food density.

Figure 3.10 continued
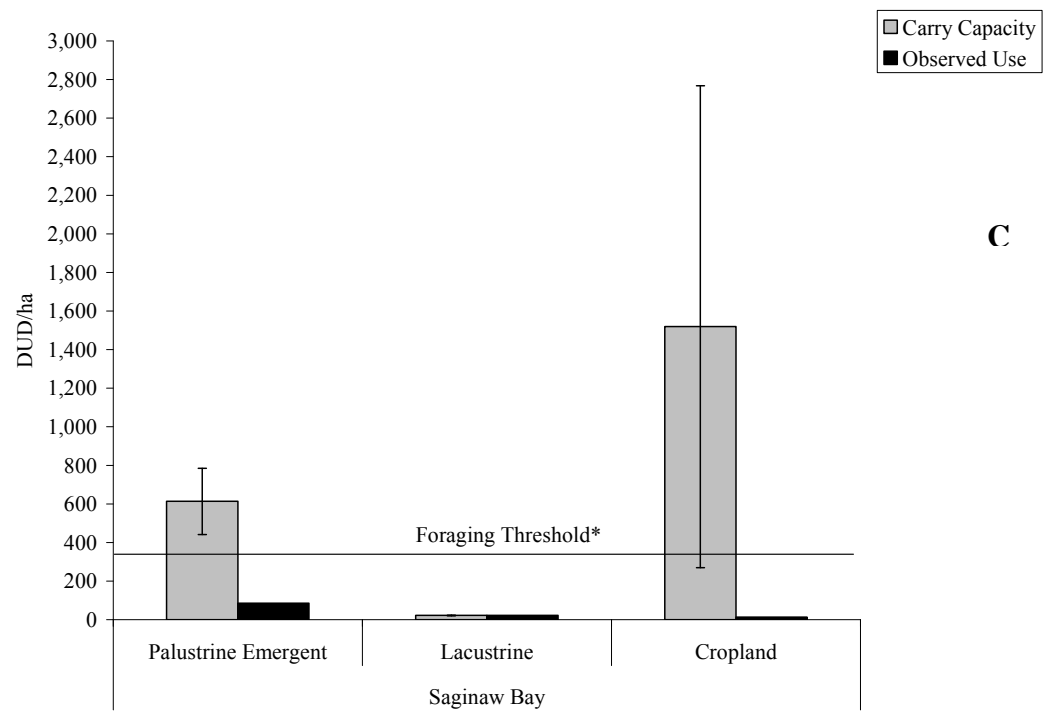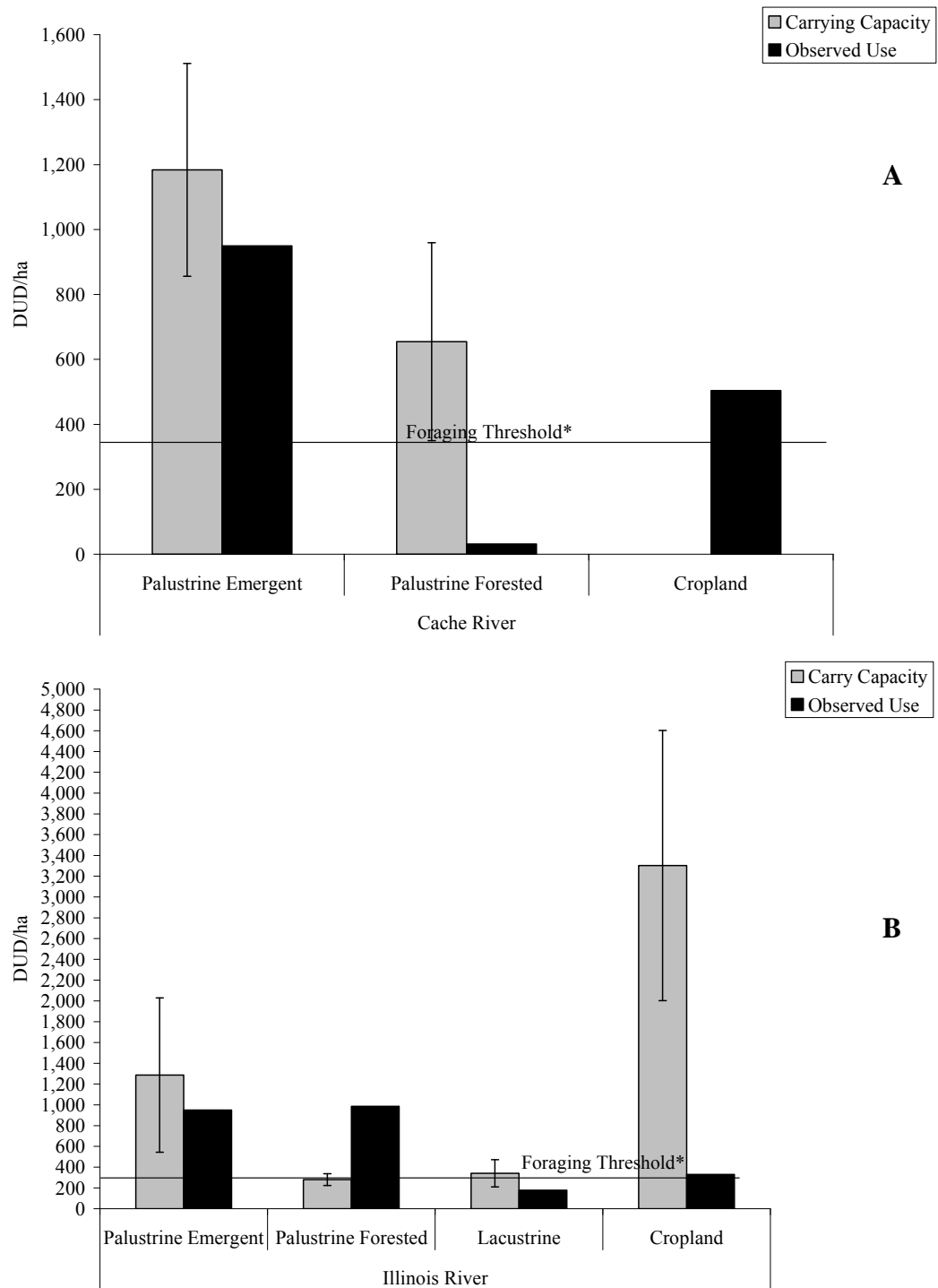
Figure 3.11. Energetic carrying capacity (weighted) +/- standard errors and mean observed waterfowl use/ha on palustrine emergent, palustrine forested, and lacustrine wetlands and croplands at Cache River (A), Illinois River (B) and East-central Wisconsin (C) study sites during February-May 2006. Energetic foraging threshold is equivalent to 50 kg/ha food density.

Figure 3.11 continued
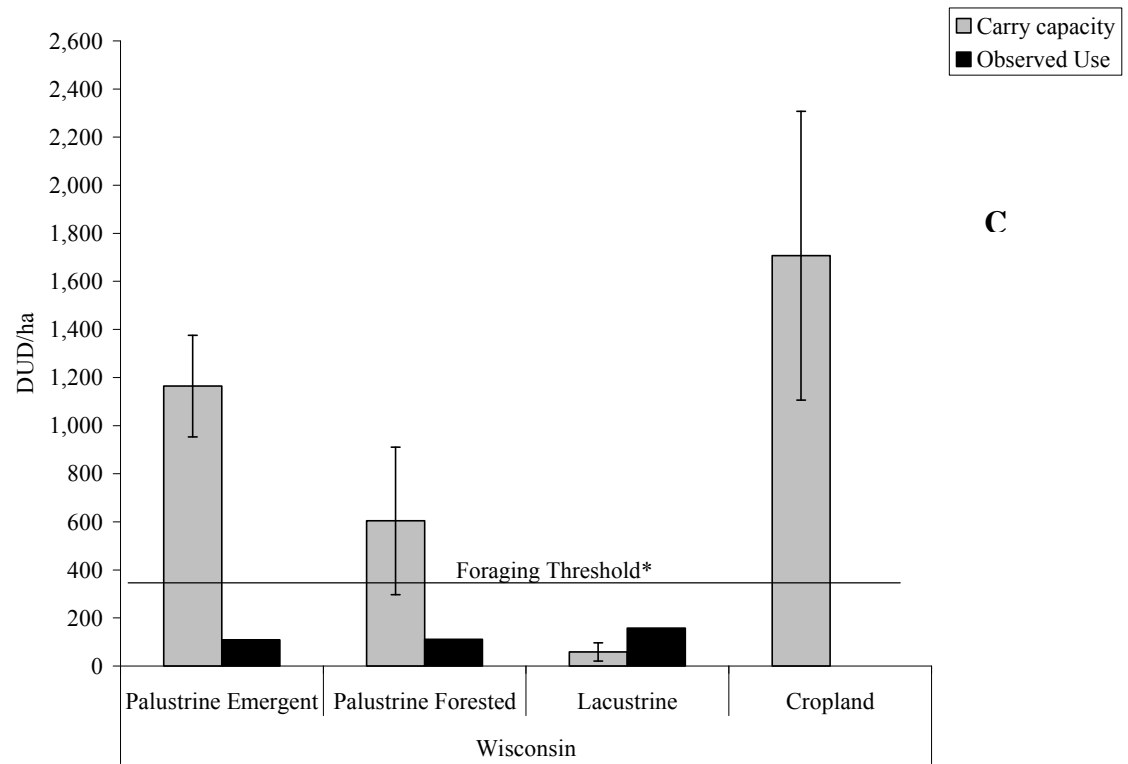
CHAPTER 4

DISCUSSION

In contrast to other NAWMP Joint Venture regions such as the Mississippi Alluvial Valley and the Central Valley of California, the UMRGLR contains a wide diversity of wetland types (Bookhout et al. 1989). Therefore, an attempt to quantify and compare food abundance among habitat types in the region has been challenging. Conservation planners need reliable food abundance estimates for croplands, marshes, natural lakes, rivers, impoundments, and riparian forests to effectively anticipate energetic and nutritional needs of spring-migrating waterfowl. These habitat types individually and collectively contribute to the total habitat resource that supports spring-migrating in the UMRGLR. My results provide a basis for understanding variation in food resource abundance along latitudinal and longitudinal gradients in the region.

Northern sites (i.e., Saginaw Bay and east-central Wisconsin) tended to have more food biomass in lacustrine, palustrine, forested and cropland habitats than southern sites (i.e., Scioto River and Cache River). Western sites tended to have more food biomass density in lacustrine and cropland habitats, compared to the eastern sites. Total food density varied among sites and habitat types. Palustrine emergent wetlands consistently had the highest food density (kg/ha) across study sites, followed by palustrine forested

wetlands, lacustrine wetlands, and finally croplands. Large differences among similar

habitat types suggest regional differences in site factors influence food abundance.

Plant seeds accounted for the majority of food biomass in all wetland types, but

species composition and biomass differed among wetland types. Plant food was

concentrated primarily on or within the substrate of wetlands, contributing >98% of total

food biomass. Similar to my results, Bartonek and Hickey (1969) reported few seeds

(<1% total food) in the water column and Baldassarre (1980) further corroborated this

pattern by finding the majority (>85%) of seeds in benthic samples.

My estimates of biomass density were generally similar to other estimates;

however, few studies of this type have been conducted during spring (Table 4.1).

Variability in estimates among studies likely resulted from site-specific influences or

different sampling and estimation methods. My benthic sampling method quantified

biomass density of food in the top 10cm of the substrate. The ability of waterfowl to

access food in the substrate likely differs among species. In fact, numerous studies have

demonstrated substantial differences in niche overlap in terms of foraging depth (Nudds

1983). Canvasbacks are known to consume sago pondweed (*Potamogeton pectinatus*)

tubers up to 20 cm below the substrate surface (Anderson and Low 1976). My estimates

of biomass in the substrate of wetlands were similar to Naylor (2002) and Dibona (2008)

who also sampled the top 10cm of the substrate during spring. However, my estimates

were substantially higher than Brasher et al. (2007) who sampled passive- and active-

managed wetlands in central and northern Ohio during springs 2000 – 2002. Brasher et

al. (2007) sampled only to the surface of the substrate using a stove-pipe sampler. Thus,

a likely reason why my estimates were higher is my sampling technique quantified

68

Food Type	Time Period	Habitat Type	Location	biomass (kg/ha)	Dud/ha	Reference
Seeds	autumn	actively managed wetlands	Illinois River Valley, IL	1454	12,444[a]	Bowyer et al. 2005
	autumn	actively managed wetlands	Texas	not reported	7,794	Anderson and Smith 1998
	autumn	actively managed wetlands	Mississippi Alluvial Valley	660	5,650[a]	Fredrickson and Taylor 1982
	autumn	actively managed wetlands	Illinois River Valley, IL	497	4,255	Bowyer et al. 2005
	autumn	actively managed wetlands	Mississippi Alluvial Valley	496	4,247[a]	Kross et al. 2008
	autumn	actively managed wetlands	Central Valley California	393	3,365[a]	Naylor 2002
	autumn	passively managed wetlands	Texas	not reported	1,806	Anderson and Smith 1998
	autumn	actively managed wetlands	Great Salt Lake Marshes, Utah	68	582[a]	Johnson 2008
	autumn	passively managed wetlands	Great Salt Lake Marshes, Utah	23	194[a]	Johnson 2008
	spring	tidal wetlands	New Jersey Meadowlands	201	1,721	Dibona 2008
	spring	actively managed wetlands	Central Valley California	194	1,661	Naylor 2002
	spring	passively managed wetlands	Central and Northern Ohio	not reported	191	Brasher et al. 2007
	spring	actively managed wetlands	Central and Northern Ohio	not reported	66	Brasher et al. 2007
	spring	**Palustrine emergent wetlands**	**UMRGLR**	**119**	**964**	**This study**
	spring	**Palustrine forested wetlands**	**UMRGLR**	**83**	**468**	**This study**
	spring	**Lacustrine wetlands**	**UMRGLR**	**28**	**106**	**This study**
Invertebrates	autumn	passively managed wetlands	Great Salt Lake Marshes, Utah	74	147[b]	Johnson 2008
	autumn	actively managed wetlands	Great Salt Lake Marshes, Utah	40	80[b]	Johnson 2008
	spring	non-tidal wetlands	New Jersey Meadowlands	181	360	Dibona 2008
	spring	tidal wetlands	New Jersey Meadowlands	24	48	Dibona 2008
	spring	rice fields	Louisiana	22	44[b]	Hohman et al. 1996
	spring	**Palustrine emergent wetland**	**UMRGLR**	**69**	**134**	**this study**
	spring	**Palustrine forested wetland**	**UMRGLR**	**28**	**48**	**this study**
	spring	**Lacustrine wetland**	**UMRGLR**	**18**	**24**	**this study**

Table 4.1. Published estimates of seed, invertebrate and waste grain biomass (kg/ha)) and energetic carrying capacity (duck use days [dud]/ha) in various geographic study locations in the United States.

Table 4.1 continued

Food Type	Time Period	Habitat Type	Location	biomass (kg/ha)	Dud/ha	Reference
Waste grains	autumn	cornfield	Iowa, Nebraska, Texas	321	4,034[c]	Frederick et al. 1984
	autumn	rice fields	Mississippi Alluvial Valley	78	892[d]	Stafford et al 2006a
	autumn	rice fields	Mississippi Alluvial Valley	66	755[d]	Kross et al. 2008
	spring	**corn and soybean fields**	**UMRGLR**	**33**	**474**	**this study**

[a] calculated for this table following methods of Reinecke et al. (1989) and using 2.5 kcal/g as true metabolizable energy value for moist-soil seeds.

[b] calculated for this table following methods of Reinecke et al. (1989) and using 0.58 kcal/g as true metabolizable energy value for invertebrates.

[c] calculated for this table following methods of Reinecke et al. (1989) and using 3.67 kcal/g as true metabolizable energy value for corn.

[d] calculated for this table following methods of Reinecke et al. (1989) and using 3.34 kcal/g as true metabolizable energy value for rice.

biomass from a larger portion of the substrate. I have no knowledge of the vertical

distribution of food resources within my substrate samples. If the majority of food

biomass I sampled was concentrated deep in the substrate, then I may have overestimated

biomass and ECC for species that feed only at or just below the wetland substrate surface.

Further research is needed to assess the depth into the substrate waterfowl are able to

access food resources and examine how this varies among species and substrate types.

Submerged aquatic vegetation (SAV) could be an additional source of food for

waterfowl in lacustrine habitats that I did not sample. Indeed, Winslow (2003) estimated

SAV biomass was 199 – 274 kg/ha in coastal impoundments in Louisiana during winter.

However, over-winter weather conditions in the UMRGLR typically cause SAV to

disappear before spring (Schloesser and Manny 1990, Wersal et al. 1996). Other studies

have documented the scarcity of SAV during spring (Brasher et al. 2007, Dibona 2008).

Concurrent studies showed that algae and duckweed (*Lemna* spp.) were important food

items for gadwalls (Jay Hitchcock SIUC unpublished thesis). My estimates do not

include these two potential food items. Thus, my estimates may be underestimated for

species that heavily rely on these food items.

I probably did not recover all food biomass during sampling. Reinecke and

Hartke (2005) recovered all but 12% of barnyard grass seeds from samples containing

known amounts of seeds. I sampled benthic biomass similar to Reinecke and Hartke

(2005) so I likely recovered a similar percentage of seeds of this size. However I may

have missed a higher percentage of small seeds (i.e., *Juncus* spp., *Eleocharis* spp.,

Amaranthus spp.). Although recovery efficiency of seeds from nektonic samples was

unknown, nektonic samples comprised < 2% of total food biomass.   Thus, even doubling

my nektonic estimates (i.e., assume 50% recovery efficiency) would only contribute about 10 kg/ha to total biomass.

The relative abundance of invertebrates was less in the substrate of wetlands than in the water column, especially at the end of spring migration. Surprisingly few studies have examined the abundance of invertebrates in relation to total food biomass (but see Cox and Kadlec 1995). Invertebrates are important sources of protein and have been shown to correlate with increased lipid reserves in waterfowl (Whyte and Bolen 1984, Miller 1986). Invertebrate-rich wetlands can attract large numbers of wintering waterfowl, including typically herbivorous species such as pintails (Euliss et al. 1991). In addition, female waterfowl are known to rely heavily on invertebrates on their breeding grounds (Swanson et al. 1979). Diet information during the spring is sparse and conflicting, so it is unclear whether waterfowl actively select invertebrates or simply consume food resources in proportion to local abundance. A concurrent diet study showed that invertebrate consumption by dabbling ducks increased from south to north across my study sites (Jay Hitchcock, Southern Illinois University, unpublished data).

My results indicate that invertebrates do not appear to contribute substantially to total food density in palustrine emergent and palustrine forested wetlands but they do so in open water lacustrine wetlands. My results showed that invertebrate biomass increased from south to north study sites as palustrine emergent wetlands at Saginaw Bay and lacustrine wetlands at east-central Wisconsin had 53% and 62% more invertebrate biomass, respectively, than any other wetland habitat sampled in the other 4 more southerly sites. However, relative abundance of benthic invertebrates between the early and late sampling period, showed no strong pattern along the south to north gradient.

72

There was a relatively strong pattern in nektonic invertebrate abundance whereby invertebrate relative abundance increased between early and late sampling period at all sites. Since these nektonic samples contributed minimally to overall biomass the importance of nektonic invertebrates to meeting food requirements of ducks is probably negligible. However, unlike plant food resources, the standing crop of invertebrates at any single point in time underestimates the total quantity of food resource available to supply energy and protein to spring-migrating waterfowl. Invertebrates are a continually renewed food resource during spring, whereas plant foods, particularly seeds, are finite resources that were produced during the preceding growing season. Therefore, my estimates of invertebrate abundance likely underestimated their total contribution to meeting dietary needs of spring-migrating waterfowl.

Invertebrates are known to have high turnover rates, especially in shallow wetlands (Jeffries 2006). Many factors influence the emergence and growth of invertebrate populations. The top model from my QAIC analysis for invertebrate abundance explained only 2% ($R^2 = 0.02$) of the variation compared to 17% ($R^2 = 0.17$) for plant food abundance. Factors such as temperature, pH, conductivity, and water clarity are important in explaining invertebrate growth and abundance in wetlands during spring all of which I did not measure.

Ducks rely on food at staging sites to fuel their migration flight (Ankney et al. 1991, Alisauskas and Ankney 1992). One theory of migration states that birds can optimize breeding success by migrating early to avoid competition with conspecifics for access to declining food resources (Alerstam and Hogstedt 1982). My results suggest that since plant and invertebrate food densities did not decline between early and late

spring there was no energetic advantage for waterfowl to migrate early, although the benefits of early arrival on breeding grounds are well-known (Alerstam and Högstedt. 1982, Baldassare and Bolen 2006, Devries et al. 2008).

The variability and highly skewed distribution of my data (Figure 4.1) raises several issues to consider. Only 19.5%, 14.4%, and 22.1% of samples exceed the mean for palustrine emergent, palustrine forested and lacustrine wetlands, respectively when combined across study sites and sampling periods,. Although multi-stage sampling (MSS) uses a weighted mean to compute unbiased estimates, the design is still sensitive to skewed distributions (Ernst 1980, Hidiroglou and Srinath 1981), producing higher measures of central tendency than other measures such as the median or geometric mean (see Figure 4.2). This raises the question, which measure of central tendency best expresses the overall level of food resource available to spring-migrating waterfowl? Each of the measures in figure 4.2 has validity under certain assumptions of how waterfowl distribute themselves across varying levels of food resource in their environment.

At least two theoretical distributions are relevant in considering the appropriate measure of central tendency. Ideal free distribution (IFD) theory (Fretwell 1972) predicts that animals distribute themselves among suitable habitats with densities that are proportional to the inherent quality (i.e. food energy) of those habitats. According to IFD, fitness is equal for all individuals, but habitats with lower inherent quality will support smaller densities of animals that occupy them. Simply stated in the context of my study, if wetland A contains twice as much food as wetland B, waterfowl utilization rates will be twice that of wetland B. The IFD assumes that animals correctly and

74
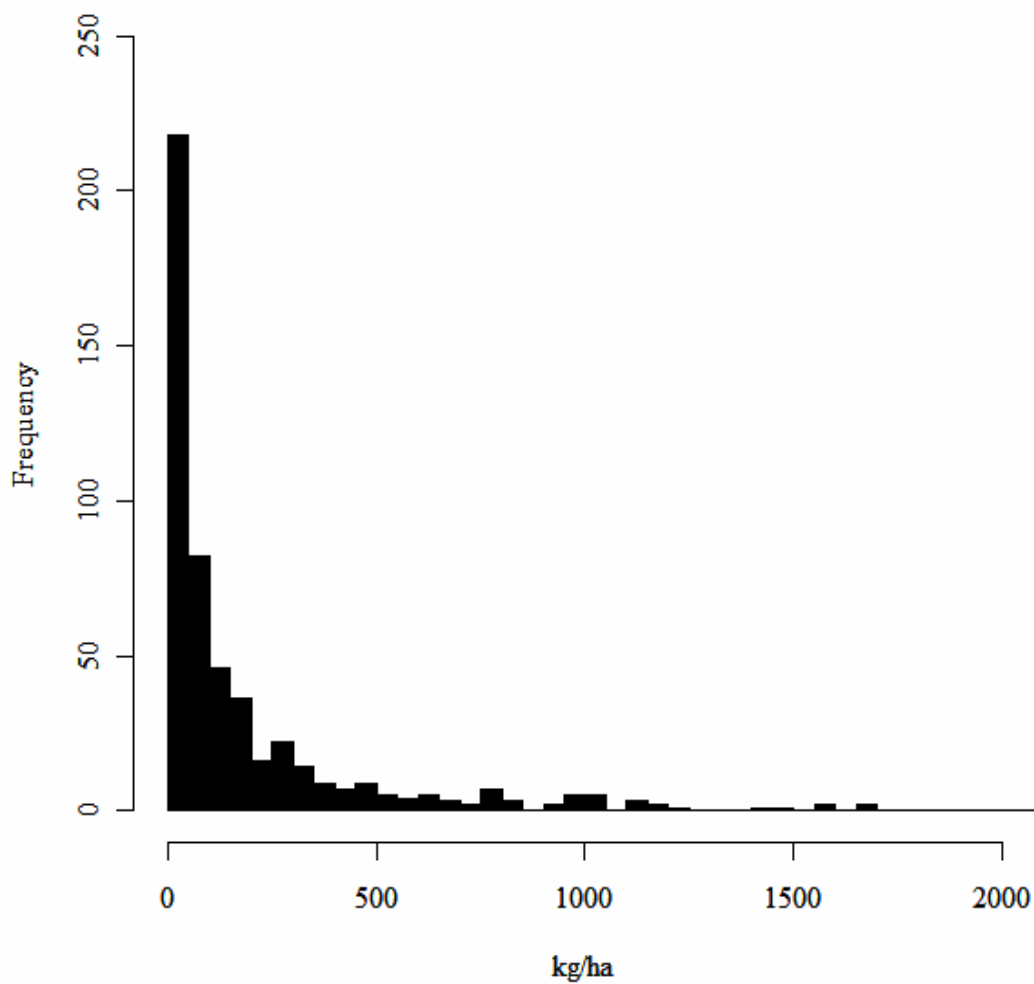
Figure 4.1. Frequency distribution of seeds, tubers, and invertebrates (kg/ha, dry mass) from a multistage sample of palustrine emergent, palustrine forested, and lacustrine wetland habitats at six study sites in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006
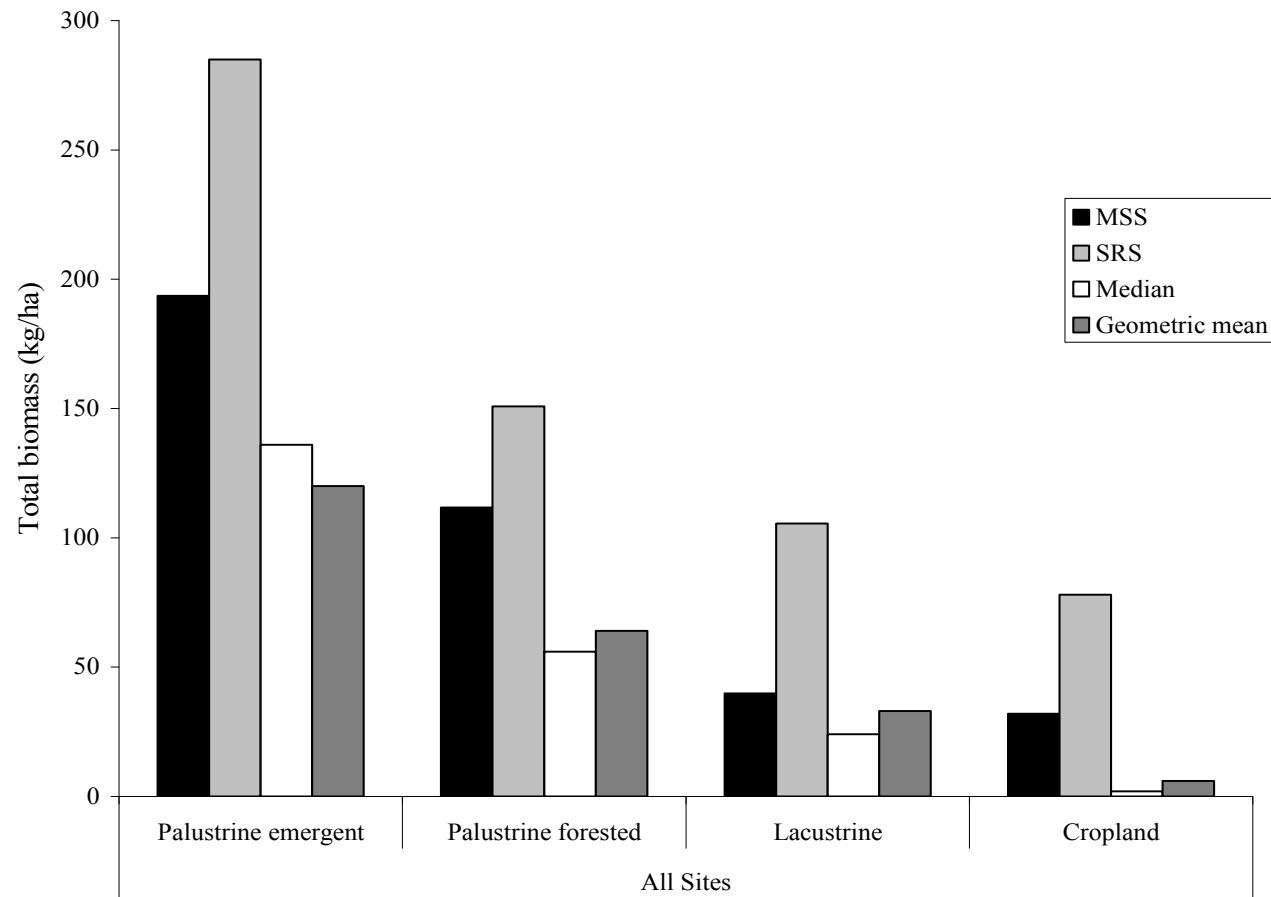
Figure 4.2. Total biomass (seeds + invertebrates + tubers) by habitat type combined across all sites using multi-stage sampling (MSS), simple random sampling (SRS), median, and geometric mean estimates.

immediately identify high quality food patches and are free to move unhindered among habitat patches to sustain the highest rates of food intake possible. Although similar to the IFD, in the ideal despotic distribution (IDD; Fretwell 1972) an individual's options for settling are constrained by the territorial behavior of already established individuals. In the IDD, territoriality limits species density, thus, resources in the preferred habitat would be underutilized. In this case, if wetland A contains twice as much food as wetland B, waterfowl utilization on wetland A will be influenced by the territorial nature of the despots. It is unreasonable to assume that free-living waterfowl behave in a perfectly ideal free, or despotic manner. However, in controlled experiments of captive flocks, waterfowl have been known to distribute themselves in both an ideal free and despotic manner (Harper 1982, Poysa 2002). Harper (1982) found that free-living, albeit tame mallards, distributed themselves proportionally to available food patches. In the same study, despotic behavior of dominant individuals forced some individuals to abandon feeding, even though there was food available. The relevance of these experiments to free living waterfowl may be limited since these birds are faced with more complicated foraging choices. Nonetheless, there is some evidence that free living waterfowl use wetlands with increasing proportion, relative to food abundance (Van Eerden 1984, Pehrsson 1984, Murkin and Kadlec 1986, Grabaskas 1993, Steckel 2005). There is also strong evidence of territoriality in waterfowl, especially when males are mate-guarding during spring (Mckinney et al. 1983, Davis 2002).

Selecting the best measure of food abundance that "typically" occurs within habitats has important ramifications for conservation planning strategies. If measures of food abundance are incorrectly estimated, it follows that habitat objectives will not

adequately reflect the need of anticipated waterfowl populations in the region. Specifically, the different distribution assumptions proposed here have direct implications to island biogeography theory (MacArthur and Wilson 1967) which is the basis for the debate over conserving single large versus several small areas (SLOSS) habitat areas for species conservation. This model has not worked well for many terrestrial species but it may have some application for migratory birds that depend on wetlands that can be conceived as islands of habitat embedded in a matrix (i.e., ocean) of largely unsuitable terrestrial areas that they must traverse during migration.

If spring-migrating waterfowl distribute themselves among available resource patches (i.e., wetlands) in a perfectly ideal free manner, then mean (arithmetic or MSS) estimates of food resources would better express the average quantity of total food resources available to the population. Under this scenario, waterfowl would distribute themselves among the most highly profitable food patches. Thus, conservation priority would be placed on maintaining and enhancing large wetland complexes, where management efforts can produce large quantities and densities of food resources. Conversely, if populations distribute themselves in a despotic manner (i.e., strong density dependence), then some waterfowl are forced into low quality food patches (assuming food is limiting). In this case, the median and geometric mean better express the quantity of resource that members of the population are likely to encounter during spring migration. Thus, conservation strategies whould emphasize ensuring small isolated wetlands have adequate food supplies in addition to large wetland complexes. More research is required to adequately understand how free-living waterfowl distribute

themselves among and within habitats, especially during spring migration, when density dependent factors may be at its highest.

Energetic carrying capacity

To effectively anticipate the needs of waterfowl, conservation planners use a biological approach that identifies the amount of habitat required (energetic carrying capacity; ECC) to meet NAWMP population objectives. This approach, first described by Reinecke et al. (1989), requires estimates of the amount of energy available to waterfowl in a particular habitat type. The simplest energetic approach assumes that all duck food items are available for consumption, ducks can forage at all water depths in all habitats, and all ducks require 292 kcal/day (typical female mallard). Since 1989, a plethora of research has come forth, allowing a more refined approach to estimating ECC including more precise TME estimates (Sherfy 1999, Kaminski et al 2003, Dugger et al. 2005) and typical daily energy requirements of ducks (Miller and Eadie 2006). Researchers now have the ability to make more sophisticated estimates of ECC. Therefore, I used my estimates of biomass to compute ECC using guild specific requirements, and compared results with estimates derived from the traditional approach. The UMRGLR Joint Venture habitat conservation strategy uses an approach similar to mine to derive migration and wintering habitat objectives. However, with limited information on availability of food energy, estimates from a small number of studies were pooled to generate the Joint Venture's ECC estimates. Few spring studies are available for comparison, but my estimates of ECC were generally similar to other published estimates during spring (Table 4.1).

The ECC_w estimates did not appear to substantially differ from ECC_u estimates. Several factors explain this result. First, dabbling ducks comprised the majority of use at all sites and habitats so daily energy requirements used in modeling were heavily weighted toward the requirements of dabblers (i.e., 300 kcal/day), which is similar to the traditional approach (292 kcal/day). Although I used guild-specific diet preferences from a concurrent study, this caused very little difference in estimates of total ECC because all four foraging guilds consumed diets largely consisting of the same food items. Although there were some differences in foods consumed, diet differences among foraging guilds were usually food items that did not contribute substantially to total biomass of samples. Diving ducks had the most restrictive habitat requirements as they do not feed in croplands or forested wetlands. However, since diving ducks comprised smaller proportions of use at most sites, their habitats requirements were not highly weighted in the ECC_w estimate. My results suggest that the traditional approach to estimating ECC first suggested by Reinecke (1989) is an adequate and reliable measure of what actual energy waterfowl may require. However when large dabbling ducks such as mallards do not comprise the majority of waterfowl it may actually overestimated energetic carrying capacity.

Although scrub shrub/forested wetlands provide seasonally important habitat for waterfowl in some regions (Heitmeyer 2006), there is insufficient research on the importance of these habitats in the UMRGLR. On the other hand, the importance of open water lakes and deep water (i.e., lacustrine habitats), especially to diving duck species, has been well documented (Thompson 1973, Korschgen et al. 1988). Not only do diving ducks require open water habitats they also typically rely heavily on invertebrates,

80

particularly as the breeding season approaches (Krapu and Swanson 1975, Krapu and

Reinecke 1992). My study indicates that although invertebrates contributed a larger

percentage of overall energy in lacustrine habitats, availability of food energy may be

insufficient for diving ducks during spring migration. This may especially true for lesser

scaup, which are typically more carnivorous compared to other ducks in this guild

(Wooten and Werner 2004, Badzinski and Petrie 2006). Consequently, quality of

lacustrine open water habitat during spring migration may limit waterfowl use, especially

for diving ducks which rely heavily on these habitats.

Although food energy appears to be more abundant in palustrine emergent

wetland habitats, the ability of waterfowl to exploit and assimilate that energy is

unknown. Research has shown that waterfowl abandon food patches when food densities

drop below a foraging threshold (Reinecke 1989, Naylor 2002). However, the proposed

theoretical foraging thresholds may differ from what waterfowl actually use during

spring. These proposed thresholds were conducted on habitats during winter. In spring,

time and feeding budgets of most species are more constrained as they must ultimately

make it to their breeding grounds. Therefore, ducks are more likely to abandon food

patches even though there is sufficient food, because they must fulfill other life-history

requirements. Not only do foraging thresholds likely vary among species, they likely

vary among individual food items. Further research is required during spring to assess

the idea of foraging thresholds and its relationship with available energy. Nevertheless, I

examined how my estimates from benthic samples compared to theoretical foraging

thresholds. Less than half (40%) of my point samples were above the least restrictive (50

kg/ha) foraging threshold, while less than 15% were above the most restrictive foraging

threshold (280 kg/ha). Assuming these foraging thresholds are realistic, my results imply most areas (>60%) within habitats may have limited or no energetic value to waterfowl during spring. If indeed these "giving up" densities are accurate, my results suggest that waterfowl may be energy limited in some habitats.

I estimated croplands could support millions of use days at some sites. Although croplands can be important sources of energy, morphological restrictions negate the value of these habitats for the majority of waterfowl species that use the UMRGLR during spring. A concurrent diet study indicated that corn and soybeans comprised less than 5% of aggregate percent mass of all food items consumed by species (mallard, gadwall, blue-winged teal, ring-necked duck, and lesser scaup; Jay Hitchcock SIUC unpublished thesis). In addition, use data from a concurrent study, indicated the majority of use is occurring in wetland habitats. Furthermore, predicted use days from croplands may be biased high because when modeling total use days, I assumed all croplands within my study sites were either corn or soybean fields. Other crop types (which I did not sample) likely existed in varying acreages across the sites I sampled. Though croplands may be locally significant in some areas in terms of meeting energy needs, my study suggests conservation priority be placed on restoring and enhancing wetland habitats for spring-migrating waterfowl. Specifically, emergent wetland habitats should receive the highest priority for restoration and enhancement since the have the greatest capability to support the most ducks.

CHAPTER 5

IMPLICATIONS FOR CONSERVATION MANAGEMENT

My estimates of energetic carrying capacity in wetlands, although not as low as what previous research has suggested (Brasher et al. 2007), are nonetheless still below what current conservation plans suggest. I compared my wetland estimates of ECC with those from the UMRGLR Joint Venture waterfowl conservation strategy. The current UMRGLR Joint Venture waterfowl habitat conservation strategy (Soulliere et al. 2007) presents estimates in raw energy (kilojoules/ha) and assumes 50% of available energy is accessible. To facilitate comparisons I converted the joint venture estimates to kcal/ha and reduced my estimates by 50%. My mean estimates of ECC for all four habitat types I sampled were below what the JV currently assumes habitats provide (Figure 5.1). The largest discrepancy was in lacustrine habits where my site- and habitat-specific estimates were 82 – 99% below the JV estimate. My estimates included seed, tuber, and invertebrate contributions to energy; whereas the joint venture strategy assumes plant food contributes to energy needs. My results imply that current habitat objectives put forth by the UMRGLR Joint Venture for forested wetlands and extensive open water, and to lesser extents emergent wetlands, may be underestimated.

I explored the implications of my estimates of energetic carrying capacity to proposed habitat objectives in the UMRGLR. Current habitat objectives set forth by the
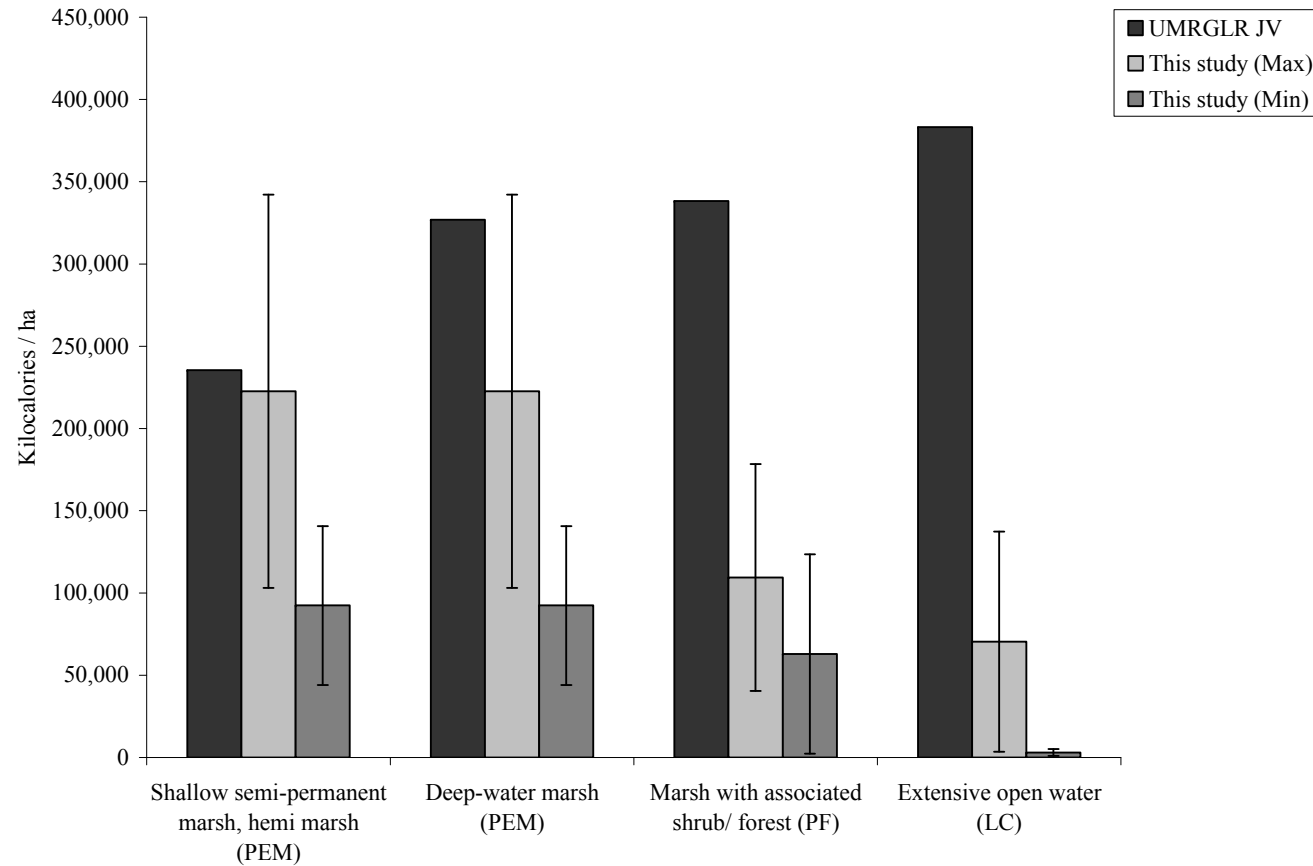
Figure 5.1. Energetic carrying capacity (kcal/ha) differences between the Upper Mississippi River Great Lakes Region Joint Venture's Habitat conservation strategy and my estimates (with 95% confidence intervals). Shown are the maximum and minimum for each individual habitat sampled across sites. My estimates are from wetland habitats in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006.

UMRGLR Joint Venture waterfowl conservation strategy are designed to meet the energetic demands of waterfowl populations that migrate and winter in the UMRGLR (Soulliere 2007). Derivation of habitat goals is a function of the estimated waterfowl population, energy density of habitat types (i.e., ECC), and the daily energy requirements of ducks. I compared how much spring habitat would be required to support mallard, lesser scaup, canvasback, blue-winged teal, northern pintail, and ring-necked duck populations in the UMRGLR, using my estimates of ECC with those of the current UMRGLR Joint Venture waterfowl habitat conservation strategy (Figure 5.2). According to my results, spring habitat objectives for individual species such as mallards need to be increased by only 5% to meet desired population objectives. However, spring habitat objectives for scaup and canvasback need to be increased by 82% to meet desired population objectives. My results suggest much more habitat is need for species that heavily rely on deep water, lacustrine wetland habitat to meet energetic demands during spring migration. For that reason, I recommend the UMRGLR JV adjust their habitat objectives, especially for species other than mallards.

I encourage waterfowl managers and conservation planners in the UMRGLR Joint Venture to reconsider assumed foraging values for habitats used by spring-migrating waterfowl. Specifically, I suggest the UMRGLR Joint Venture adopt my estimates of food energy abundance, as these estimates come from a sampling frame representing the diversity of habitats that exist in the region. Priorities for conservation effort at the national scale should recognize the importance preserving and enhancing habitats encountered by waterfowl during spring migration. My results show that it is during this
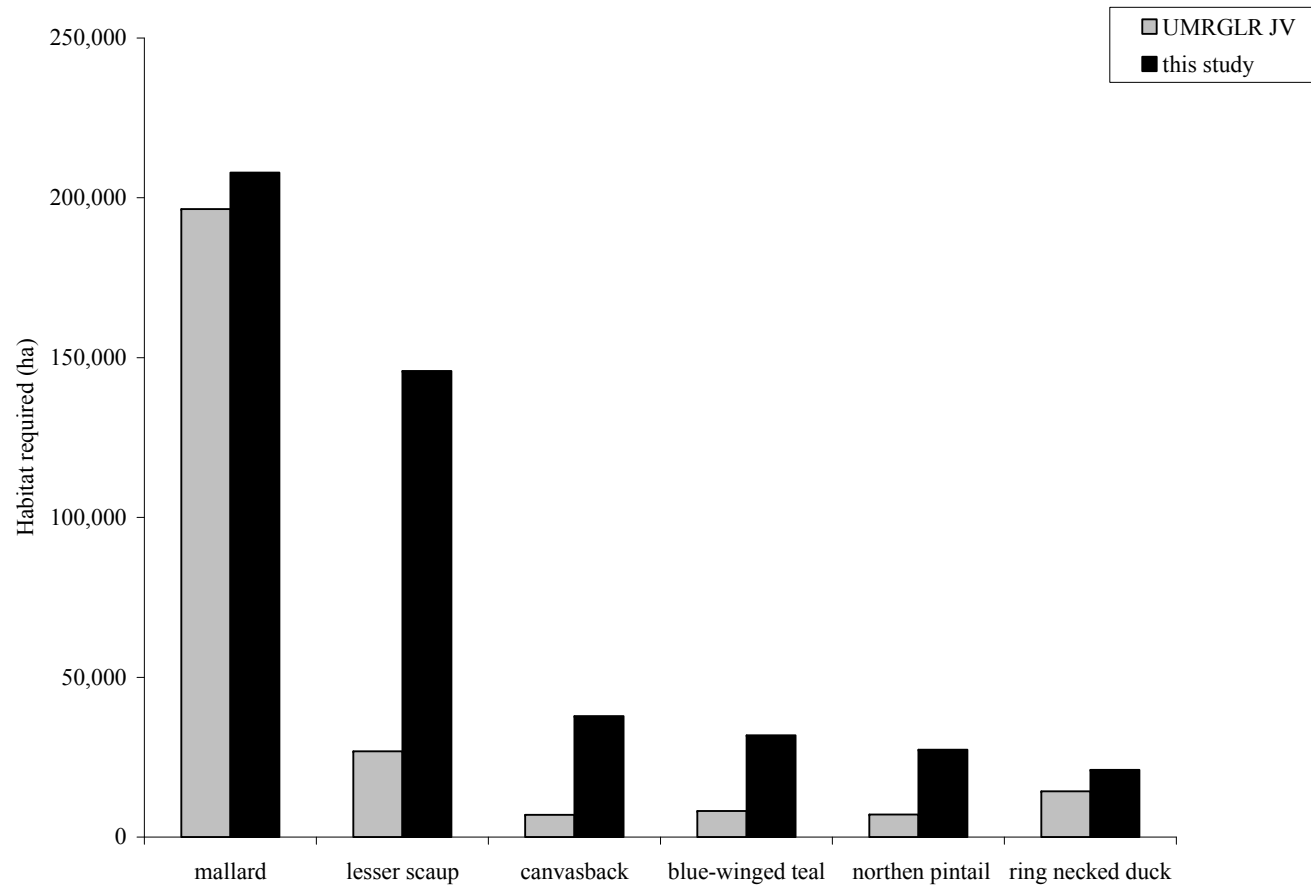
Figure 5.2. Habitat required to meet the desired species population objectives set forth by the Upper Mississippi River Great Lakes Region Joint Venture's Habitat conservation strategy. Habitat objectives for my study are from estimates of wetland habitats in the Upper Mississippi River and Great Lakes Region, USA, during February-May 2006

time, that these habitats have the least capability to support energetic demands of waterfowl. In addition, recent research has shown a strong link between the body condition of female mallards arriving on the breeding grounds, and numerous reproductive indicators (Devries et al. 2008). Without a doubt, factors such as food abundance and availability have a direct and immediate effect on body condition.

Food energy abundance appears be more limiting during spring compared to autumn migrations. Therefore, at a more local scale, wetland managers should consider flooding wetlands in late winter or early spring, as this has shown to increase spring food abundance (Greer et al. 2007). Though invertebrates did not contribute substantially to total energy they likely still play a significant role in meeting other dietary requirements, especially for female waterfowl. Hence, I suggest wetland managers ensure wetland habitats provide both an abundance of invertebrates and seeds during the spring. Future work should focus on the identifying the importance of invertebrates to spring migrating waterfowl, especially for primarily carnivorous species, and investigate the possibility of spring-migrating waterfowl being protein limited.

My study demonstrated differences among study sites in the UMRGLR in terms of their ability to support migrating waterfowl. Conservation planners should identify these areas where food density, energy, and habitat availability are comparatively low, then determine the feasibility to restore, or enhance these habitats. For instance, the Scioto River site had the least amount of overall habitat for spring migrating waterfowl, although food density estimates were similar to other study sites. The overall lack of habitat in the area likely reduced overall use of habitats even though they were capable of supporting high densities of waterfowl. Further research is required to determine if

patterns that I observed hold true over multiple years. In addition, more reliable

estimates of "giving up" densities (i.e., foraging thresholds) as well as information

regarding the manner in which waterfowl will distribute themselves in relation to

available energy resources at multiple scales will further strengthen the biological

approach to conservation management in the UMRGLR.

LITERATURE CITED

Afton, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. Auk 101:255–265.

Alerstam, T., and G. Högstedt. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. Ornis Scand 13:25–37.

Alisauskas, R. T., and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

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.

Anderson, J. T., and L. M. Smith. 1998. Protein and energy production in playas: implications for migratory bird management. Wetlands 18:437-446.

Ankney, C. D., and C.D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459–471.

Ankney, C. D. 1991. The role of nutrient reserves in limiting waterfowl reproduction. Condor 93:1029–1032.

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.

_____, and A. D. Afton. 2008. Amphipod densities and indices of wetland quality across the Upper-Midwest, USA. Wetlands 28:184–196.

Arzel, C., J. Elmberg, and M. Guillemain. 2006. Ecology of spring-migrating Anatidae: a review. Journal of Ornithology. 147:167–184.

_____,. Elmberg, M. Guillemain, P. Legagneux, F. Bosca, M. Chambouleyron, M. Lepley, C. Pin, A. Arnaud, and V. Schricke. 2007. Average mass of seeds encountered by foraging dabbling ducks in Western Europe. Wildlife Biology 13:328–336.

Badzinski, S. S., and S. A. Petrie. 2006. Diets of lesser and greater scaup during autumn and spring on the lower Great Lakes. Wildlife Society Bulletin 34:664–674.

Baldassare, G. A. 1980. Residual seeds as potential spring waterfowl foods in small, man-made impoundments. Prairie Naturalist 12:1–8.

_____ and E. G. Bolen. 2006. Waterfowl Ecology and Management. Second edition. Krieger Publishing Company, Malabar, Florida, USA.

Ballard, B. M., J. E. Thompson, M. J. Petrie, J. M. Checkett, and D. G. Hewitt. 2004. Diet and nutrition of northern pintails wintering along the southern coast of Texas. Journal of Wildlife Management 68:371–382.

Baranowski, T. E. 2007. Shorebird migration, habitat use and availability in the Lake Erie Marshes region. Thesis, The Ohio State University, Columbus, USA.

Bartonek, J. C., and J. J. Hickey. 1969. Selective feeding by juvenile diving ducks in summer. Auk 86:443–457.

Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. 1992. Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Bellrose, F. C. 1968. Waterfowl migration corridors east of the Rocky Mountains in the United States. Illinois Natural History Survey Biological Notes. No. 61. 24 pp.

_____ 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.

Bishop, C. T. 1990. Historical variation of water levels in Lakes Erie and Michigan-Huron. Journal of Great Lakes Research 16:406–425.

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, Texas, USA.

Boyer, M. W., J. D. Stafford., A. P.Yetter, C. S. Hine, M. M. Horath, and S. P. Havera. 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.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

California Health Interview Survey. 2002. CHIS 2001 Methodology Series: Report 5 – Weighting and Variance Estimation. Los Angeles, CA: UCLA Center for Health Policy Research.

Checkett, J. M., R. D. Drobney, M. J. Petrie, and D. A. Graber. 2002. True metabolizable energy of moist-soil seeds. Wildlife Society Bulletin 30:1113–1119.

Coluccy, J. M., T. Yerkes, R. Simpson, J. W. Simpson, L. Armstrong, J. Davis. 2008. Population dynamics of breeding mallards in the Great Lakes states. Journal of Wildlife Management 72:1181–1187.

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. U.S. Department of the Interior, Fish and Wildlife Service. FWS/OBS – 79/31.

Craven, S. R., and R. A. Hunt. 1984. Fall food habits of Canada geese in Wisconsin. Journal of Wildlife Management 48:169–173.

Dahl, T. E. 2006. Status and trends of wetlands in the conterminous United States 1998 to 2004. U.S. Department of the Interior; Fish and Wildlife Service, Washington, D.C. 112 pp.

Davis, E. S. 2002. Female choice and the benefits of mate guarding by male mallards. Animal Behaviour. 64 (4): 619-628.

Davis, L. W. 1993. Weed Seeds of The Great Plains: A handbook for identification. Lawrence, KS: University Press of Kansas. 145 p.

Davis T. J. 1994. The Ramsar Convention Manual. A guide to the Convention of
       Wetlands of International Importance especially as waterfowl habitat. Ramsar
       Convention Bureau, Gland, Switzerland.

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, Delaware, USA.

Delorit, R. J. 1970. An Illustrated Taxonomy Manual of Weed Seeds. Agronomy
       Publications, River Falls Wisconsin, USA.

Demarest, D. W., R. M. Kaminski, L. A. Brennan, and C. R. Boyle. 1997. Body-mass,
       survival, and pairing consequences of winter-diet restriction in wood ducks.
       Journal of Wildlife Management 61:822–832.

Demissie, M. T., W. Soong, R. Allgire, L. Keefer, and P. Makowski. 1990. Cache River
       basin: hydrology, hydraulics, and sediment transport, Vol. 1: background, data
       collection, and analysis. Illinois State Water Survey Contract Report, Champaign,
       Illinois, USA.

DeRoia, D. A., and T. A. Bookhout. 1989. Spring feeding ecology of teal on the Lake
       Erie marshes. Ohio Journal of Science 89:3

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 platyrhncos*). The
       Auk. 125 (3): 618-628.

Dobson, A. J. 1990. An introduction to generalized linear models. Chapman and Hall,
       London.

Dorge, C. L., W. J. Mitsch,. And J. R. Wiemhoff. 1984. Cypress wetlands in southern
       Illinois. Pages 393–404 *in* K. C. Ewel and H. T. Odum, editors. Cypress
       swamps. University of Florida Press, Gainesville, Florida, USA.

DuBowy, P. J. 1988. Waterfowl communities and seasonal environments: Temporal
       variability in interspecific competition. Ecology 69:1439–1453.

Ducks Unlimited. 2005a. Development of a potential wetland restoration layer for
       research and planning in the Great Lakes. Final Report. Submitted to the U.S.
       Fish and Wildlife Service, Upper Mississippi Great Lakes Joint Venture, 1
       Federal Drive, Fort Snelling, MN. 32p.
       <http://www.ducks.org/media/Conservation
       /GLARO/_documents/_library/_gis/GLPotentialWetland.pdf.> Accessed 16
       August, 2008.

Ducks Unlimited. 2005b. Updating the National Wetland Inventory (NWI) for the southern lower peninsula of Michigan. Final report submitted to the U.S. Fish and Wildlife Service Great Lakes Coastal Program Office. Ducks Unlimited's Great Lakes / Atlantic Regional Office, Ann Arbor, Michigan, USA 38pp. <http://ww w.ducks.org/media/Conservation/GLARO/_documents/_library/_gis/NWI_FinalR eport.pdf>. Accessed 15 August 15 2008.

Dugger, B. D., M. L. Moore, R. S. Finger, and M. J. Petrie. 2007. True metabolizeable energy for seeds of common moist-soil plant species. Journal of Wildlife Management 71:1964–1967.

Environmental Systems Research Institute. [ESRI]. 2001. ArcGIS Spatial Analyst Software, Version 9.0. ESRI 380 New York St., Redlands, California, USA.

Ernst, L. R. 1980. Variance of the estimated mean for several imputation procedures. Proceedings Survey Research: Methods Section. American Statistics. Association., pp. 716–720.

Euliss, N. H., Jr., and G. Grodhaus. 1987. Management of midges and other invertebrates for waterfowl wintering in California. California Fish and Game 73:238–243.

Euliss, N. H., Jr., R. L. Jarvis, and D. S. Gilmer. 1991. Feeding ecology of waterfowl wintering on evaporation ponds in California. Condor 93:582–590.

Farney, R. A. 1975. Fall foods of ducks in Lake Erie marshes during high water years. Thesis, The Ohio State University, Columbus, Ohio, USA.

Flather, C. H., and J. R. Sauer. 1996, Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77:28–35.

Frayer, W. E., T. J. Monahan, D. C. Bowden, and F. A. Graybill. 1983. Status and trends of wetlands and deepwater habitats of the conterminous United States, 1950's to 1970's. U.S. Fish and Wildlife Service, Washington, D.C. 33pp.

Frederick, R. B., E. E. Klass, G. A. Baldassarre, and K. J. Reinecke. 1984. A method for sampling waste corn. Journal of Wildlife Management 48:298–303.

Fredrickson, L. H., and R. D. Drobney. 1979. Habitat utilization by post-breeding waterfowl. Pages 119–131 *in* T. A. Bookhout, editor. Waterfowl and Wetlands – An Integrated Review. Proceedings of the 39th Midwest Fish and Wildlife Conference, Madison, Wisconsin, USA.

          and T. S. Taylor. 1982. Management of seasonally flooded impoundments for
          wildlife. Resource Publication 148. U.S. Dept. of Interior, Fish and Wildlife
          Service, Washington, D.C.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University
          Press.

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.

Gershunskaya, J., and L. Huff. 2004. Outlier Detection and Treatment in the Current
          Employment Statistics Survey. Proceedings of the Section on Survey Research
          Methods, American Statistical Association.

Galatowitsch, S. M., and A. G. van der Valk, 1996. The vegetation of restored and
          natural prairie wetlands. Ecological Applications 61:102–112.

Grabaskas, M. E. 1993. Aquatic vegetation and migratory waterfowl use of closed (non-
          hunted) and open (hunted) areas of Pools 4 and 5 of the Upper Mississippi River
          National Wildlife and Fish Refuge. Thesis, The Ohio State University,
          Columbus, Ohio, USA.

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 71:1561–1566.

Gruenhagen, N. M., and L. H. Fredrickson. 1990. Food use by migratory female
          Mallards in northwest Missouri. Journal of Wildlife Management 54:622–626.

Haig, S. M. 1998. Molecular contributions to conservation. Ecology 79:413–425.

Harper, D.G. 1982. Competitive foraging in mallards: 'ideal free' ducks. Animal
          Behavior. 30: 575-584.

Haukos, D. A., and L. M. Smith. 1993. Moist-soil management of playa lakes for
          migrating and wintering ducks. Wildlife Society Bulletin 21:288-298.

Havera, S. P. 1999. Waterfowl of Illinois: status and management. Illinois Natural
          Survey Special Publication 21. xliii+ 628 pp.

Heinrich, J. W., and S. R. Craven. 1992. The economic impact of Canada geese at the
          Horicon Marsh, Wisconsin. Wildlife Society Bulletin 20:364–371.

Heitmeyer, M. E. 1985. Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the upper Mississippi Delta. Dissertation, University of Missouri, Columbia, Missouri, USA.

_____ 1988. Body composition of female mallards in winter in relation to annual cycle events. Condor 90:669–680.

_____ 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.

_____ 2006. The importance of winter floods to mallards in the Mississippi Alluvial Valley. Journal of Wildlife Management 70:101–110.

Hepp, G. R. 1984. Dominance in wintering Anatinae: potential effects on clutch size and time of nesting. Wildfowl 35:132–134.

Hidiroglou, M., and K. P. Srinath. 1981. Some estimators of a population total from simple random samples containing large units. Journal of American statistics Association 76:690–695.

Hoekman, S. T., L. S. Mills, D. H. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of mid-continent mallards. Journal of Wildlife Management 66:883–900.

Hoffman, R. D., and T. A. Bookhout. 1985. Metabolizable energy of seeds consumed by ducks in Lake Erie marshes. Transactions of the North American Wildlife and Natural Resources Conference 50:557–565.

Hohman, W. L., T. S. Taylor, and M. W. Weller. 1988. Annual body weight change in ring-necked ducks (*Aythya collaris*). Pages 257–269 *in* M. W. Weller, editor. Waterfowl in Winter. University Minnesota Press, Minneapolis, Minnesota, USA.

Hooge P. N., and B. Eichenlaub. 1997. Animal movement extension to Arcview, version 1.1. U.S. Geological Survey, Anchorage, Alaska, USA.

Hutchison, M. D., 1987. The Lower Cache River basin of southern Illinois. Erigenia 9:1–54.

Illinois State Water Survey [ISWS]. 2008. ISWS home page. <http:www.sws.uiuc.edu>. Accessed 15 August 2008.

Jeffries, M. 2006. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology. 32(3): 603-612.

Johnson, A. M. 2007. Food abundance and energetic carrying capacity for wintering waterfowl in the Great Salt Lake wetlands. Thesis, Oregon State University, Corvallis, Oregon, USA.

Johnson, W. C., B. V. Millett, T. Gilmanvov, R. A Voldseth, B. R. Guntenspergen, and D. E. Naugle. 2005. Vulenerability of northern prairie wetlands to climate change. BioScience 55:863–872.

Johnston, C. A. 1984. Mapping Wisconsin's wetlands. Wisconsin Natural Resources, 8 4–6.

Jorde, D. G., and R. B. Owen, Jr. 1988. Efficiency of nutrient use by American black ducks wintering in Maine. Journal of Wildlife Management 52:209–214.

_____., M. Haramis, C. M. Bunck, and G. W. Pendleton. 1995. Effects of diet on rate of body mass gain by wintering canvasbacks. Journal of Wildlife Management 59:31–39.

Kaminski, R. M., J. B. Davis, H. W. Essig, P. D. Gerard, and K. J. Reinecke. 2003. True metabolizable energy for wood ducks from acorns compared to other waterfowl foods. Journal of Wildlife Management 67:542–550.

King, J. R. 1974. Seasonal allocation of time and resources in birds. Pages 4-85 in R. A. Paynter, editor. Avian energetics. Nuttall Ornithological Club 15, Cambridge, Mas- sachusetts, USA.

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, Minnesota, USA.

Koel, T. M., and R. E. Sparks. 2002. Historical patterns of river stage and fish communities as criteria for operations of dams on the Illinois River. River Research and Applications 18:2–19.

Krapu, G. L., and G. A. Swanson. 1975. Some nutritional aspects of reproduction in prairie nesting pintails. Journal of Wildlife Management 39:156–162.

_____ 1981. The role of nutrient reserves in mallard reproduction. Auk 98:29–38.

_____ and K. J. Reinecke. 1992. Foraging ecology and nutrition. Pages 1–29 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Kross, J., R. M. Kaminski, K. J. Reinecke, E. J. Penny, 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. 1985. Habitat use and nutrient reserves dynamics of spring migratory mallards in central Iowa. Thesis, Iowa State University, Ames, Iowa, USA.

_____ and J. J. Dinsmore. 1989. Habitat use by mallards during spring migration through central Iowa. Journal of Wildlife Management 53:1076–1081.

Lesaffre E, D. Rizopoulos, and R. Tsonaka. 2006. The logistic-transformation for bounded outcome scores. Biostatistics 2006.

Lovvorn, J. R. 1987. Behavior, energetics, and habitat relations of canvasback ducks during winter and early spring migration. Dissertation, University of Wisconsin, Madison, Wisconsin, USA.

MacArthur, R. H. and Wilson, E. O. 1967. The Theory of Island Biogeography. Princeton University Press. Princeton, New Jersey.

Martin, A. C., and F. M. Uhler. 1951. Food of game ducks in the United States and Canada. U.S. Fish and Wildlife Service Research Report 30. 308 pp.

_____ and W. D. Barkley. 1961. Seed identification manual. University of California Press, Berkeley, California, USA.

Manley, 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.

McKinney, F., S.R. Derrickson, and P. Mineau. 1983. Forced Copulation in Waterfowl. Behavior. 86: 250-293.

Midwestern Regional Climate Center [MRCC]. 2008. MRCC home page. <http://mcc. sws.uiuc.edu/climate_midwest>. Accessed 15 August 2008.

Miller, M. R. 1986. Northern Pintail body condition during wet and dry winters in the Sacramento Valley, California. Journal of Wildlife Management 50:189–198.

_____ and J. Eadie. 2006. The allometric relationship between resting metabolic rate and body mass in wild waterfowl (Anatidae) and an application to estimation of winter habitat requirements. Condor 108:166–177.

Montgomery, F. H. 1977. Seeds and fruits of plants of eastern Canada and northeastern United States. University of Toronto Press, Toronto, Canada.

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.

Nalepa, T. F., A. J. Wojcik, D. L., Fanslow, and G. A. Lang. 1995. Initial Colonization of the zebra mussel (Dreissena polymorpha) in Saginaw Bay, Lake Huron: population recruitment, density and size structure. Journal of Great Lakes Research 1:417–434.

National Wetlands Inventory (NWI). 1990. Photointrepretation conventions for the National Wetlands Inventory. U.S. Fish and Wildlife Service. National Wetlands Inventory Center, St. Petersburg, Florida, USA.

Naylor, L. W. 2002. Evaluating moist-soil seed production and management in Central Valley wetlands to determine habitat needs for waterfowl. Thesis, University of California, Davis, California, USA.

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 populations levels of birds? Journal of Ornithology. 147: 146-166.

Nudds, T. D. 1983. Niche dynamics and organization of waterfowl guilds in variable environments. Ecology 64:319–330.

Olson, T. M. 2003. Variation in use of managed wetlands by waterfowl, wading birds, and shorebirds in Ohio. Thesis, The Ohio State University, Columbus, Ohio, USA.

O'neal, B. J., E. J. Heske, and J. D. Stafford. 2008. Waterbird response to wetlands restored through the Conservation Reserve Enhancement Program. Journal of Wildlife Management 72:654–664.

Pederson, G. B., and R. L. Pederson. 1983. Feeding ecology of mallards and pintails in lower Klamath marshes. U.S. Fish and Wildlife Service final report. Humboldt State University Foundation, Arcata, California, USA. 89pp.

Pehrsson, O. 1984. Diving duck populations in relation to their food supplies. Pages 101–122 in P. R. Evans, J. D. Goss-Custard, and W. G. Hale, editors. Coastal Waders and Wildfowl in Winter. Cambridge University Press.

Petrie, M. J., R. D. Drobney, and D. A. Graber. 1998. True metabolizable energy estimates of Canada goose foods. Journal of Wildlife Management 62:1147–1152.

Poysa, H. 2001. Dynamics of habitat distribution in breeding mallards: assessing the applicability of current habitat selection models. Oikos. 94: 365-373.

Quinn G. P., and M. J. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, New York, Melbourne, Madrid, Cape Town, 537 pp.

R Development Core Team (version 2.5.1). 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, F. A., J. R. Kelley, T. S. Taylor, L. H. Fredrickson. 1989. Upper Mississippi Valley Wetlands- Refuges and Moist-Soil Impoundments. Pages 181–202 *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, Texas, USA.

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, Texas, USA.

_____,and K. M. Hartke. 2005. Estimating moist-soil seeds available to waterfowl with double sampling for stratification. Journal of Wildlife Management 69:794–799.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 *in* R. A Paytner, Jr., editor. Avian Energetics. Nuttall Ornithological. Cambridge, Massachusetts, USA.

Riley, T. Z., and T. A. Bookhout. 1993. Response of dabbling ducks to early-spring partial drawdown on Lake Erie marshes. Prairie Naturalist 25:13–18.

SAS Institute. 1999. SAS/STAT User's Guide. SAS Institute, Cary, North Carolina, USA.

Schloesser, D. W., and B. A. Manny. 1990. Decline of wild celery buds in the lower Detroit River, 1950–85. Journal of Wildlife Management 54:72–76.

Sherfy, M. H. 1999. Nutritional value and management of waterfowl and shorebird foods in Atlantic Coastal moist-soil impoundments. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Smith, H. I. 1901. Summary of the archeology of Saginaw valley, Michigan. American Anthropologist 3:286–293.

Smith, R. V. 2007. Evaluation of waterfowl habitat and spring food selection by mallard and lesser scaup on the Swan Lake Illinois Habitat Rehabilitation and Enhancement Project. Thesis, Southern Illinois University, Carbondale, Illinois, USA.

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.

Sparks, R. E., J. C. Nelson, and Y.Yin. 1998. Naturalization of the flood regime in regulated rivers. BioScience 48:706–720.

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.

_____, 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.

_____, M. M. Horath, A. P.Yetter, C. S. Hine, and S. P. Havera. 2007. Wetland use by mallards during spring and fall in the Illinois and central Mississippi River Valleys. Waterbirds 30:394–402.

Steckel, J. D. 2003. Food availability and waterfowl use on mid-migration habitats in central and northern Ohio. Thesis, The Ohio State University, Columbus, Ohio, USA.

Stollberg, B. P. 1950. Food habits of shoal-water ducks on Horicon Marsh, Wisconsin. Journal of Wildlife Management 14:214–217.

Sugden, L. G. 1971. Metabolizable energy of small grains for mallards. Journal of Wildlife Management 35:781–785.

Swanson, G. A., G. L. Krapu, and J. R. Serie. 1979. Foods of laying female dabbling ducks on the breeding grounds. Pages 59–70 *in* T. A. Bookhout, editor. Waterfowl and Wetlands – An Integrated Review, Proceedings of the 39th Midwest Fish and Wildlife Conference, Madison, Wisconsin, USA.

Taylor, T. S. 1978. Spring foods of migrating blue-winged teal on seasonally flooded impoundments. Journal of Wildlife Management 42:900–903.

The Nature Conservancy. 2008. Safeguarding the Scioto: Conservation Reserve Enhancement Program. <http://www.nature.org/wherewework/northamerica /states/ohio/preserves/art14378.html>. accessed 17 August 2008.

Thompson, D. 1973. Feeding ecology of diving ducks on Keokuk pool, Mississippi River. Journal of Wildlife Management 37:367–381.

Trauger, D. L., and J. H. Stoudt. 1978. Trends in waterfowl populations and habitats on study areas in Canadian parklands. Transactions of North American Wildlife and Natural Resources Conference 43:187–205.

Upper Mississippi River and Great Lakes Region [UMRGLR] 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.

U.S. Fish and Wildlife Service. 2004. Illinois River: National Wildlife and Fish Refuge Complex Comprehensive Conservation Plan Approval. http://www.fws.gov/ midwest/planning/IllinoisRiver/index.html Accessed 15 August, 2008.

Van Eerden, M. R. 1984. Waterfowl movements in relation to food stocks. Pages 84–100 *in* P. R. Evans, J. D. Goss-Custard, and W. G. Hale, editors. Coastal Waders and Wildfowl in Winter. Cambridge University Press.

Van Horn, K., K. Benton, and R. Gatti. 2006. Waterfowl breeding population survey for Wisconsin, 1973–2006. Wisconsin Department of Natural Resources, Bureau of Wildlife Management, Madison Wisconsin.

Weller, M. W., editor. 1988. Waterfowl in winter. University Minnesota Press, Minneapolis, Minnesota, USA.

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.

Winslow, C. J. 2003. Estimation of waterfowl food abundance in coastal freshwater marshes of Louisiana and Texas. Thesis, Louisiana State University, Baton Rouge, Louisiana, USA.

Wisconsin Department of Natural Resources. 2008. Wisconsin Waterfowl Strategic Plan 2008–2018. < http://prodwbin99.dnr.state.wi.us/org/land/wildlife/plan/plan2.pdf> Accessed 15 August 2008.

Wood, L. E. 1964. Bottom sediments of Saginaw Bay, Michigan. Journal of Sedimentary Research 34:173–184.

Wooten, D. E., and S. J. Werner. 2004. Food habits of lesser scaup aythya affinis occupying baitfish aquaculture facilities in Arkansas. Journal of the World Aquaculture Society 35:70–77.

Whyte, R. J., and E. G. Bolen. 1984. Variation in winter fat depots and condition indices of mallards. Journal of Wildlife Management 48:1370–1373.

Yerkes T., K. A. Hobson, L. I. Wassenaar, R. Macleod, and J. M. Coluccy. 2008. Stable isotopes (δD, δ^{13}C, δ^{15}N) reveal associations among geographic location and condition of Alaskan northern pintails. Journal of Wildlife Management 72:715–725.

Zimin V. B., A. V. Artemyev, and N. V. Lapshin. 2002. Survey of spring migrations and stopovers in the Olonets fields in Karelia. Pages 18–28 *in* G.A. Noskov, A. Czajkowski, and K. P. Fertikova, editors. Study of the status and trends of migratory bird populations in Russia, Fourth issue. OMPO special publication, St Petersburg, Worlds and Family.

APPENDICES

Study Site	Sampling Period	Dates	No. Survey days	Ag	PF benthic	PF nektonic	PEM benthic	PEM nektonic	L/R benthic	L/R nektonic	Total
Cache River	Pre-Migration	20 – 26 February	35	0	29	30	26	23	0	0	108
	Post-Migration	2 – 4 April		0	22	23	13	9	0	0	67
Illinois River	Pre-Migration	2 – 9, 15 March	35	9	17	18	9	9	12	12	77
	Post-Migration	12 – 15, 17 –19 April		9	24	22	10	11	15	14	96
Wisconsin	Pre-Migration	27 – 31 March	43	5	4	3	26	26	26	27	112
	Post-Migration	9 – 10, 12 – 13 May		9	4	3	29	27	26	23	112
Scioto River	Pre-Migration	17 – 20, 24 – 25 February	43	16	13	13	12	10	23	21	92
	Post-Migration	8 – 9 April		15	11	9	11	9	19	21	80
Lake Erie Marshes	Pre-Migration	2 – 6 March	53	15	13	8	15	17	11	12	76
	Post-Migration	25 – 28 April		15	11	12	15	15	5	6	64
Saginaw Bay	Pre-Migration	17 – 18, 23 – 25 March	40	12	0	0	20	23	11	11	65
	Post-Migration	2 – 4 May		12	0	0	22	22	5	5	54
Total				117	148	141	208	201	153	152	1120

A.1. Number of survey days and samples (benthic and nektonic) taken from cropland (Ag), palustrine forested wetlands (PF), palustrine emergent wetlands (PEM) and lacustrine wetlands (LC) in the Upper Mississippi River and Great Lakes Region during February-May 2006.

Food Item	TME	Source
Plant Foods		
Alismataceae		
Alisima spp.	3.06	TME value of *Sagittaria*
Sagittaria spp.	3.06	Hoffman and Bookhout 1985
Amaranthaceae		
Amaranthus spp.	2.97	Checkett et al. 2002
Asteraceae		
Ambrosia spp.	1.26	assigned using regression equation[1]
Ceratophyllaceae		
Ceratophyllum demersum	1.98	assigned using regression equation[1]
Chenopodiaceae		
Chenopodium spp.	2.52	Dugger et al. 2007
Compositae		
Bidens spp.	0.55	Sherfy 1999
Convolvulaceae		
Ipomoea lacunosa	2.30	assigned using regression equation[1]
Cornaceae		
Cornus spp.	0.89	assigned using regression equation[1]
Cyperaceae		
Carex spp.	1.36	mean for *Cyperaceae*
Cladium jamaicense	1.36	mean for *Cyperaceae*
Cyperus spp.	1.69	mean from Sherfy 1999 and Ballard et al. 2004
Eleocharis spp.	0.96	mean from Ballard et al. 2005 and Dugger et al. 2007
Rhynchospora corniculata	1.86	Checkett et al. 2002
Scirpus spp.	0.93	mean from Sherfy 1999, Ballard et al. 2005 and Dugger et al. 2007
Fagaceae		
Quercus spp.	2.75	Kaminski et al 2003.
Haloragaceae		
Myriophyllum spp.	0.61	assigned using regression equation[1]
Hydrocharitaceae		
Vallisneria americana	1.77	assigned using regression equation[1]
Juncaceae		
Juncus spp.	1.21	Sherfy 1999
Malvaceae		
Abutilon theophrasti	2.19	assigned using regression equation[1]
Sida spinosa	2.19	TME value of *Abutilon*
Najadaceae		
Najas spp.	2.26	assigned using regression equation[1]
Ruppia maritima	1.42	Ballard et al. 2004

Table A.2. TME values (kcal/g) used to calculate energetic carrying capacity for food items identified in benthic and nektonic samples in habitat types in the Upper Mississippi andGreat Lakes Region during February-May 2006.

Table A.2 continued

Food Item	TME	Source
Poaceae		
Digitaria spp.	3.10	Checkett et al. 2002
Echinochloa spp.	2.72	mean from Hoffman and Bookhout 1985 and Sherfy 1999
Leersia spp.	2.91	Hoffman and Bookhout 1985
Panicum spp.	2.45	mean from Sherfy 1999 and Checkett et al. 2002
Paspalum spp.	1.57	Checkett et al. 2002
Setaria spp.	2.88	Checkett et al. 2002
Sorghum	2.73	mean for Poaceae
spp.	2.73	mean for Poaceae
Polygonaceae		
Fagopyrum esculentum	1.45	mean for Polygonaceae
Polygonum pennsylvanicum	1.21	mean from Hoffman and Bookhout 1985 and Sherfy 1999
Polygonum spp.	1.59	Ballard et al. 2004
Rumex crispus	2.68	Checkett et al. 2002
Potamogetonaceae		
Potamogeton spp.	1.42	Ballard et al. 2004
Rubiaceae		
Cephalanthus occidentalis	0.78	assigned using regression equation[1]
Sparganiaceae		
Sparganium spp.	0.96	assigned using regression equation[1]
Vitaceae		
Vitis spp.	1.16	assigned using regression equation[1]
Zannichelliaceae		
Zannichellia palustris	3.20	assigned using regression equation[1]
Tubers	2.50	Petrie unpublished report
Invertebrates		
Arachnida	0.58	mean of published invertebrate TME estimates
Bivalvia	0.22	mean from Jorde and Owen 1988 and Ballard et al. 2004
Branchiopoda	0.82	Frederickson and Reid 1988
Chilopoda	0.58	mean of published invertebrate TME estimates
Clitellata	0.58	mean of published invertebrate TME estimates
Diplopoda	0.58	mean of published invertebrate TME estimates
Entognatha	0.58	mean of published invertebrate TME estimates
Gastropoda	0.29	mean from Sugden 1973 and Sherfy 1999
Hydozoa	0.58	mean of published invertebrate TME estimates
Insecta		
Diptera	0.27	Sherfy 1999
Coleoptera	0.38	mean of Insecta
Ephemeroptera	0.38	mean of Insecta
Hemiptera	0.48	Sherfy 1999
Hymenoptera	0.38	mean of Insecta
Lepidoptera	0.38	mean of Insecta
Megaloptera	0.38	mean of Insecta

Table A.2 continued

Food Item	TME	Source
Odonata	0.38	mean of Insecta
Plecoptera	0.38	mean of Insecta
Trichoptera	0.38	mean of Insecta
Malacostraca		
Amphipoda	2.33	mean from Sugden 1973 and Ballard et al. 2004
Decapoda	0.91	mean of Malacostraca
Isopoda	0.08	Sherfy 1999
Maxillopoda	0.58	mean of published invertebrate TME estimates
Ostracoda	0.58	mean of published invertebrate TME estimates
Nematoda	0.58	mean of published invertebrate TME estimates
Platyhelminthes	0.58	mean of published invertebrate TME estimates

[1] TME = (-0.0553* % fiber content) + 3.3361 (see figure 2.2)

Food Item	Source	% fiber	TME (kcal/g)
Amaranthus spp.	Checkett et al. 2002	16.6	2.97
Bidens spp.	Sherfy 1999	22.0	0.55
Chenopodium spp.	Dugger et al. 2006	16.9	2.52
Cyperus spp.	Sherfy 1999	14.5	1.96
Digitaria spp.	Checkett et al. 2002	10.0	3.10
Echinochloa spp.	Hoffman and Bookhout 1985	18.2	2.82
Eleocharis spp.	Ballard et al. 2004 and Dugger et al. 2006	32.9	0.96
Glycine max	Reineke et al. 1989	17.6	2.65
Leersia spp.	Hoffman and Bookhout 1985	9.3	2.82
Panicum spp.	Sherfy 1999	25.0	2.54
Paspalum spp.	Checkett et al. 2002	18.9	1.57
Polygonum pennsylvanicum	Sherfy et al. 2001	17.2	1.30
Polygonum spp.	Checkett et al. 2002	23.6	1.52
Potamogeton spp.	Ballard et al. 2004	46.5	1.42
Quercus spp.	Kaminski et al. 2003	17.2	2.77
Rumex crispus	Checkett et al. 2002	21.1	2.68
Ruppia maritima	Ballard et al. 2004	35.2	1.42
Sagittaria spp.	Hoffman and Bookhout 1985	23.0	3.06
Scirpus spp.	Hoffman and Bookhout 1985	16.2	0.99
Setaria spp.	Checkett et al. 2002	12.6	2.88
Zea mays	Reineke et al. 1989	7.1	3.67
Zizania spp.	Reineke et al. 1989	10.4	3.34

Table A.3. Seed taxa with sources, percent fiber and true metabolizeable energy (TME) used in regression equations which predicted seeds with no published TME value. Percent fiber values are from Havera (1999).

Species	Mean Body Mass (g)[a]	DER (kcal/day)[b]
Dabblers	**928**	**300**
Mallard	1,177	341
American black duck	1,182	342
Northern pintail	946	290
Wood duck	676	226
Grazers	**848**	**268**
Gadwall	901	280
American wigeon	794	255
Teal	**368**	**170**
Blue-winged teal	420	159
Green-winged teal	315	129
Northern shoveler	658	222
Divers	**883**	**274**
Canvasback	1,205	347
Redhead	1,039	311
Lesser scaup	787	253
Greater scaup	1,014	306
Ring-necked duck	708	234
Ruddy duck	542	192

Table A.4. Daily energetic requirements (DER) of species and guilds (bold) commonly found in wetland habitat in the Upper Mississippi River Great Lakes Region. Guild DER represents means of all species within a guild and used to calculate weighted and guild specific energetic carrying capacity.

[a] Bellrose (1980)
[b] DER migration = 3xBMR and DER wintering = 3xBMR (King 1974)

		% of total ducks			
Site	Habitat type	dabblers	divers	grazers	teal
Scioto River	Palustrine emergent	71.3	0.0	3.2	25.4
	Palustrine forested	76.4	0.0	0.7	22.9
	Lacustrine	98.9	0.0	0.0	1.1
	Cropland	72.0	0.0	0.0	28.0
Lake Erie Marshes	Palustrine emergent	67.9	11.8	13.0	7.3
	Palustrine forested	100.0	0.0	0.0	0.0
	Lacustrine	21.9	69.3	5.3	3.5
	Cropland	70.9	1.7	23.4	4.0
Saginaw Bay	Palustrine emergent	43.8	35.1	12.8	8.3
	Palustrine forested	not surveyed			
	Lacustrine	60.0	28.0	8.0	4.0
	Cropland	95.8	0.0	0.0	4.2
Cache River	Palustrine emergent	39.9	13.3	7.3	39.5
	Palustrine forested	83.1	0.0	0.0	16.9
	Lacustrine	not surveyed			
	Cropland	78.0	0.0	15.6	6.4
Illinois River	Palustrine emergent	67.6	12.8	5.6	14.0
	Palustrine forested	85.5	2.2	3.2	9.2
	Lacustrine	29.0	48.1	6.5	16.4
	Cropland	76.4	8.8	0.9	13.9
Wisconsin	Palustrine emergent	50.1	36.0	5.2	8.7
	Palustrine forested	100.0	0.0	0.0	0.0
	Lacustrine	97.0	0.0	0.0	3.0
	Cropland	no ducks observed in croplands			

Table A.5. Percent of total ducks observed by foraging guild during spring migration at six study sites in four habitat types in the Upper Mississippi and Great Lakes Region during February-May 2006.

Food Type	Common name	Foraging Guild			
		Dabblers	Divers	Grazers	Teal
Plant Foods					
Alismataceae					
Alisima spp.	water plantain	U		U	U
Sagittaria spp.	arrowhead	U	U	U	
Amaranthaceae					
Amaranthus spp.	pigweed	U	U	U	U
Asteraceae					
Ambrosia spp.	ragweed	U			
Ceratophyllaceae					
Ceratophyllum demersum	coontail		U		
Chenopodiaceae					
Chenopodium spp.	lambsquarters		U		U
Compositae					
Bidens spp.	beggarticks	U	U		U
Convolvulaceae					
Ipomoea lacunosa	morning glory		U		
Cornaceae					
Cornus spp.	dogwood	U			
Cyperaceae					
Carex spp.	sedge	U	U	U	U
Cyperus spp.	flatsedge	U	U	U	U
Eleocharis spp.	spikerush	U	U	U	U
Rhynchospora corniculata	beakrush				U
Scirpus spp.	bullrush	U	U	U	U
Fagaceae					
Quercus spp.	oak	U			
Haloragaceae					
Myriophyllum spp.	watermilfoil			U	
Hydrocharitaceae					
Vallisneria americana	eel grass		U		
Juncaceae					
Juncus spp.	rush		U		
Malvaceae					
Abutilon theophrasti	velvet leaf	U			
Najadaceae					
Najas spp.	waternymph	U	U	U	

Table A.6. Food items assumed to be consumed by foraging guilds. Data obtained from concurrent study that examined diets of mallard, lesser scaup, ring-necked duck, gadwall and blue-winged teal and were used to calculate weighted and guild specific energetic carrying capacity.

Table A.6 continued

Food Type	Common name	Foraging Guild			
		Dabblers	Divers	Grazers	Teal
Poaceae					
Digitaria spp.	crabgrass	U		U	U
Echinochloa spp.	millet	U	U	U	U
Leersia spp.	rice cut-grass	U	U	U	U
Panicum spp.	panic grass	U	U	U	U
Setaria spp.	bristlegrass	U			
spp.	grasses		U	U	
Polygonaceae					
Polygonum pennsylvanicum	pennsylvania smartweed	U	U	U	U
Polygonum spp.	smartweed	U	U	U	U
Rumex crispus	dock	U			U
Potamogetonaceae					
Potamogeton spp.	pondweed	U	U	U	U
Rubiaceae					
Cephalanthus occidentalis	buttonbush	U	U	U	U
Sparganiaceae					
Sparganium spp.	bur-reed	U			
Vitaceae					
Vitis spp.	grape	U			
Zannichelliaceae					
Zannichellia palustris	horned pondweed		U		
Tubers		U	U		
Invertebrates					
Bivalvia	mollusks, clams		U		U
Branchiopoda	fairy shrimp		U	U	U
Chilopoda	centipedes				U
Clitellata	earthworms, leaches	U	U	U	U
Entognatha	ametabolous arthropods			U	U
Gastropoda	snails	U	U	U	U
Insecta					
Diptera	flies	U	U	U	U
Coleoptera	beetles	U			U
Ephemeroptera	mayflies			U	
Hemiptera	aphids	U		U	
Hymenoptera	bees, wasps, ants				
Lepidoptera	butterflies	U		U	
Odonata	dragon flies, damselflies	U	U		U
Trichoptera	cadisflies	U	U		

Table A.6 continued

		Foraging Guild			
Food Type	Common name	Dabblers	Divers	Grazers	Teal
Malacostraca					
Amphipoda	fresh water shrimp	U	U	U	U
Isopoda	sowbugs	U	U	U	U
Maxillopoda	copepods	U		U	U
Ostracoda	seed shrimp		U	U	U
Nematoda	roundworms	U	U	U	
Gastropoda		U	U	U	U

		Foraging Guild			
Habitat Type	Foraging depth	Dabblers	Divers	Grazers	Teal
Palustrine Emergent	shallow	x		x	x
	deep		x		
Palustrine Forested	shallow	x		x	x
	deep				
Lacustrine	shallow	x	x	x	x
	deep		x		
Cropland	n/a	x		x	x

Table A.7. Habitat type and foraging depths assumed to be used by foraging guilds and used to calculate weighted and guild specific energetic carrying capacity.

Site	Habitat	$\bar{x}$ observed use
Scioto River	Palustrine Emergent	305.1
	Palustrine Forested	40.4
	Lacustrine	30.4
	Cropland	1.8
Lake Erie Marshes	Palustrine Emergent	827.2
	Palustrine Forested	24.9
	Lacustrine	21.9
	Cropland	62.8
Saginaw Bay	Palustrine Emergent	85.6
	Lacustrine	21.9
	Cropland	13.4
Cache River	Palustrine Emergent	949.7
	Palustrine Forested	31.5
	Cropland	504
Illinois River	Palustrine Emergent	949.6
	Palustrine Forested	985.3
	Lacustrine	178.3
	Cropland	330.1
Wisconsin	Palustrine Emergent	108.4
	Palustrine Forested	111.4
	Lacustrine	158.3
	Cropland	0

Table A.8. Mean observed waterfowl use (cumulative) per hectare (duck use days/ha) from observational surveys conducted on habitats at six sites in the Upper Mississippi and Great Lakes Region during February-May 2006. Surveys did not include geese.

Site	Habitat	Foraging guild (ECC$_{guild}$)			
		dabblers	divers	grazers	teal
SR	Palustrine Emergent	882	450	538	1461
	Palustrine Forested	367	n/a	328	619
	Lacustrine	58	269	40	101
	Cropland	121	n/a	135	213
LE	Palustrine Emergent	387	63	671	1121
	Palustrine Forested	578	n/a	75	131
	Lacustrine	75	156	41	60
	Cropland	155	n/a	173	273
SB	Palustrine Emergent	455	30	546	847
	Lacustrine	19	22	13	22
	Cropland	1472	n/a	1647	2597
CA	Palustrine Emergent	323	661	403	673
	Palustrine Forested	612	n/a	86	168
IR	Palustrine Emergent	712	82	433	689
	Palustrine Forested	976	n/a	250	398
	Lacustrine	93	331	148	238
	Cropland	2724	n/a	3049	4807
WI	Palustrine Emergent	1274	41	930	1451
	Palustrine Forested	644	n/a	318	569
	Lacustrine	87	503	54	84
	Cropland	1318	n/a	1476	2327

Table A.9. Duck use day/ha estimates of specific foraging guilds (ECC$_{guild}$) in habitats sampled in the Upper Mississippi and Great Lakes Region during February-May 2006. Estimates were calculated using multistage sampling and using guild specific daily energy, diet, and habitat requirements.