

12-10-2010

Winter food and waterfowl dynamics in managed moist-soil wetlands in the Mississippi Alluvial Valley

Heath Michael Hagy

Follow this and additional works at: <https://scholarsjunction.msstate.edu/td>

Recommended Citation

Hagy, Heath Michael, "Winter food and waterfowl dynamics in managed moist-soil wetlands in the Mississippi Alluvial Valley" (2010). *Theses and Dissertations*. 5026.
<https://scholarsjunction.msstate.edu/td/5026>

This Dissertation - Open Access is brought to you for free and open access by the Theses and Dissertations at Scholars Junction. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of Scholars Junction. For more information, please contact scholcomm@msstate.libanswers.com.

WINTER FOOD AND WATERFOWL DYNAMICS IN MANAGED MOIST-SOIL
WETLANDS IN THE MISSISSIPPI ALLUVIAL VALLEY

By

Heath Michael Hagy

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Forest Resources
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

December 2010

Copyright by
Heath Michael Hagy
2010

WINTER FOOD AND WATERFOWL DYNAMICS IN MANAGED MOIST-SOIL
WETLANDS IN THE MISSISSIPPI ALLUVIAL VALLEY

By

Heath Michael Hagy

Approved:

Richard M. Kaminski
Professor of Wildlife/Associate Dean
(Director of Dissertation)

Kenneth J. Reinecke
Wildlife Biologist
Patuxent Wildlife Research Center
(Committee Member)

Samuel K. Riffell
Associate Professor of Wildlife
(Committee Member)

Francisco J. Vilella
Professor of Wildlife
(Committee Member)

Eric D. Dibble
Professor of Wildlife
(Graduate Coordinator)

Bruce D. Leopold
Professor and Head of the Department
of Wildlife, Fisheries, and Aquaculture

George M. Hopper
Dean of the College of Forest Resources

Name: Heath Michael Hagy

Date of Degree: December 10, 2010

Institution: Mississippi State University

Major Field: Forest Resources

Major Professor: Richard M. Kaminski

Title of Study: WINTER FOOD AND WATERFOWL DYNAMICS IN MANAGED
MOIST-SOIL WETLANDS IN THE MISSISSIPPI ALLUVIAL
VALLEY

Pages in Study: 161

Candidate for Degree of Doctor of Philosophy

Moist-soil wetlands that are seasonally flooded provide important habitats for waterfowl in the Mississippi Alluvial Valley (MAV). These wetlands often contain tall and dense vegetation that may constrain waterfowl use before natural openings form. During winters 2006–2009, I estimated abundances of waterbirds, seeds and tubers, and invertebrates in response to autumn, pre-flooding treatments of light disking, mowing, and no manipulation (control) of vegetation in 26 moist-soil wetlands in the MAV. Seeds and tubers were most abundant in control and mowed plots in late autumn. Decomposition was least and invertebrate abundance was greatest in control plots during winter. Dabbling ducks were most abundant in mowed and disked plots during winter. Lightly disked plots contained ~30% fewer seeds and tubers than mowed and control plots. In late winter, ~260 kg[dry]/ha of seeds and tubers remained among mowed, disked, and control plots. Therefore, autumn mowing of robust moist-soil vegetation can be used to create an interspersed vegetation and open water attractive to waterfowl and conserve waterfowl foods. Additionally, I identified 6 seed taxa that may not be used for food by dabbling ducks (i.e., *Amaranthus* spp., *Cyperus odoratus*,

Eleocharis spp., *Ipomoea* spp., *Jacquemontia tamnifolia*, *Sesbania herbacea*) and estimated that removing these and other taxa not reported in diet literature in the MAV resulted in a ~31% reduction in estimated moist-soil food availability for ducks. In other experiments, I estimated that waterfowl reduced experimentally placed Japanese millet (*Echinochloa frumentacea*) to ~10 kg/ha and other natural seeds and tubers to ~170 kg/ha in experimental plots in mid-winter. However, waterfowl did not abandon wetlands or stop foraging when seed reduction ceased, suggesting residual abundances of seeds and tubers represented a food availability threshold (FAT). Using the median FAT value of 220 kg/ha from both experiments and removing 31% of seed mass that may not be consumed by dabbling ducks, results in a ~70% decrease in moist-soil seed availability in the MAV. Conservation planners should consider reducing the current estimates of seed and tuber availability and recommend increasing active management or implementation of additional managed, moist-soil wetlands in the MAV.

ACKNOWLEDGEMENTS

I am grateful to the Mississippi Department of Wildlife, Fisheries, and Parks for recognizing the need for waterfowl and wetlands research in Mississippi and the Lower Mississippi Alluvial Valley and providing the primary financial support for this research. Without the vision of Dr. Sam Polles, Larry Castle, Ed Penny, and the Mississippi Commission on Wildlife, Fisheries, and Parks, I would not have been able to undertake such an ambitious research project. Furthermore, I thank Ducks Unlimited; the Forest and Wildlife Research Center and Department of Wildlife, Fisheries, and Aquaculture at Mississippi State University; the Tennessee Wildlife Resources Agency; the U.S. Fish and Wildlife Service; the U.S. Geological Survey Patuxent Wildlife Research Center (Vicksburg, MS); Mr. James C. Kennedy and the James C. Kennedy Endowed Chair in Waterfowl and Wetlands Conservation; and Mr. Ralph D. Griffin for their financial, logistical, and in-kind support of my research. I especially thank all of the land managers and biologists that I had the pleasure to work with during this research project. Particularly, I thank, Sabrina Chandler, Steven Chandler, Mike Chouinard, Jimmy Drewery, Alejandro Galvan, Wayne Gordon, Jerry Hazelwood, David Linden, Landon Loveall, Joe McGowan, Rance Moring, David Richardson, Becky Rosamond, Henry Sansing, Bo Sloan, Jacob Tuttle, Brett Wehrle, Carl Wirwa, and many others who

showed great support for my project and went above and beyond their duties to assist with this research.

I especially thank Stephen Gard, Project Leader of the Sam D. Hamilton North Mississippi Refuge Complex, for driving to Coldwater National Wildlife Refuge late one Friday night after an unnamed road maintenance crew removed a culvert and 10 m of road which comprised the only accessible exit to the refuge where I was currently sampling. Similarly, I thank an unnamed federal conservation officer for not arresting my technician, Joe Lancaster, as he was unknowingly trying to conduct bird surveys at the same time as a federal, wildlife sting operation. I thank all my student technicians and the many volunteers who assisted during this project. Particularly, I thank my full-time technicians Justyn Foth and Joe Lancaster for their dedication to my project, willingness to sample at all times of the day and night, and friendship. I also am indebted to Josh Cheshier for the hundreds of volunteer hours he spent with me learning about ducks and taking core samples. I also thank James Callicutt for his dedicated service and for all the stories. Even when we were “lost as last year’s Easter egg,” James could always find humor in the situation and provide classic entertainment.

I thank my Dissertation committee, Drs. Ken Reinecke, Sam Riffell, and Francisco Vilella for their advice and encouragement during my years at Mississippi State University. I am grateful to have had the opportunity to work for and beside my Dissertation advisor Rick Kaminski. I thank Rick for his mentorship, “inviting” me to accompany him to the bench in front of Thompson Hall when it was necessary, his patience to let me pursue an occasional wild idea or project tangential to my research, and for making me part of his family. I thank all of my fellow graduate students, the faculty

and staff in the College of Forest Resources, and especially, Team Duck for support and friendship.

I thank my parents, Mike and Debra Hagy, for instilling in me the work ethic and stubbornness required to complete this Dissertation. Most importantly, I thank my wife, Erin, for her support and patience. Few people understand the stress of early mornings, late nights, and constant scrutiny that doctoral students endure. Thank you, Erin, for your support, patience, and for tolerating all the talk about ducks.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ii
LIST OF TABLES	viii
LIST OF FIGURES	xi
 CHAPTER	
I. WINTER WATERBIRD AND FOOD DYNAMICS IN AUTUMN- MANIPULATED MOIST-SOIL WETLANDS	1
Study Area	5
Methods.....	6
Experimental Design.....	6
Waterbird Abundance	7
Seed and Tuber Abundances and Decomposition	8
Washing Reagents.....	10
Invertebrate Abundance	10
Statistical Analyses	11
Waterbird Abundance and Diversity	11
Seed and Tuber Abundances.....	12
Existence Energy and Energy Removal.....	13
Invertebrate Abundance and Diversity	13
Seed Decomposition and Washing Reagents.....	14
Results	15
Waterbird Abundance and Diversity	15
Seed and Tuber Abundances.....	16
Existence Energy and Energy Removal.....	17
Invertebrate Abundance and Diversity	18
Seed Decomposition and Washing Reagents.....	19
Discussion.....	19
Waterbird Abundance and Diversity	19
Seed and Tuber Abundances.....	24
Invertebrate Abundance and Diversity	27
Management Implications.....	31
LITERATURE CITED	33

II.	SEED REDUCTIONS BY WATERFOWL AND DECOMPOSITION DURING WINTER IN MOIST-SOIL WETLANDS IN THE MISSISSIPPI ALLUVIAL VALLEY	56
	Study Area	58
	Methods.....	60
	Experimental Design.....	60
	Seed and Tuber Abundances.....	60
	Decomposition in Experimental Plots	61
	Decomposition at 2-week Intervals	61
	Sample Processing	62
	Statistical Analyses	63
	Decomposition	63
	Comparison of Predicted and Observed Seed Abundances.....	63
	Effect of Non-food Taxa on Abundance Estimates	66
	Results	66
	Decomposition	66
	Comparison of Predicted and Observed Seed Abundances.....	67
	Effect of Non-food Taxa on Abundance Estimates	68
	Discussion.....	68
	Management Implications.....	72
	LITERATURE CITED.....	73
III.	WINTER WATERFOWL RESPONSE TO SEED DENSITY AND A FOOD AVAILABILITY THRESHOLD IN MOIST-SOIL WETLANDS IN THE MISSISSIPPI ALLUVIAL VALLEY	84
	Study Area	89
	Methods.....	90
	Experimental Design.....	90
	Waterbird Abundance.....	91
	Seed and Tuber Abundances.....	91
	Pilot Experiment	92
	Principal Experiment	93
	Statistical Analyses	94
	Pilot Experiment	94
	Principal Experiment	95
	Waterbird Abundance.....	95
	Duck Energy Days.....	96
	Seed and Tuber Abundances.....	97
	Decomposition	97
	Existence Energy and Energy Removal.....	97
	Results	99
	Pilot Experiment	99
	Principal Experiment	100
	Waterbird Abundance.....	100

	Seed and Tuber Abundances.....	101
	Duck Energy Days	102
	Existence Energy and Energy Removal.....	102
	Decomposition	103
	Discussion.....	103
	Waterbird Abundance	103
	Seed and Tuber Abundances.....	104
	Management Implications.....	113
	LITERATURE CITED	115
IV.	SYNTHESIS.....	136
	LITERATURE CITED	143
APPENDIX		
A.	COMMON AND SCIENTIFIC NAMES OF PLANT TAXA.....	147
B.	LOCATIONS OF STUDY SITES IN EASTERN MISSISSIPPI, WESTERN TENNESSEE, AND THE MISSISSIPPI ALLUVIAL VALLEY	150
C.	DENSITIES OF SEEDS AND TUBERS IN CONTROL, LIGHTLY DISKED, AND MOWED PLOTS FROM NOVEMBER – FEBRUARY	153
D.	WATERBIRDS OBSERVED IN MANAGED MOIST-SOIL WETLANDS DURING NOVEMBER 2006–2008 THROUGH FEBRUARY 2007–2009	159

LIST OF TABLES

TABLE	Page
1.1 Mean (\bar{x} , SE) abundance (ducks/ha/site/survey) of mallards (<i>Anas platyrhynchos</i>) and other dabbling ducks (Anatini) and Shannon's diversity index (H') for all waterbirds and comparisons ^a of unmanipulated (control), lightly disked, and mowed plots (n) during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.....	45
1.2 Mean (\bar{x} , SE) combined seed and tuber abundances (kg[dry]/ha), excluding taxa not reportedly consumed by dabbling ducks (Chapter II), and comparisons ^a of unmanipulated (control), lightly disked, and mowed plots (n) during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley	46
1.3 Mean (\bar{x} , SE) abundances (kg[dry]/ha) of invertebrate taxa and Shannon's index of diversity by order (H') and comparisons ^a of unmanipulated (control), lightly disked, and mowed plots (n) during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.	47
2.1 Models of millet (<i>Echinochloa frumentaceae</i>) decomposition as a function of 2-week time intervals with coefficients of determination (R^2) from 6 moist-soil wetlands ^a during December 2008–February 2009 in western Tennessee and the Mississippi Alluvial Valley.....	80
2.2 Seeds recovered from core samples in the Mississippi Alluvial Valley during November 2006–2008 through February 2007–2009 and their mean adjusted percentage decomposition per day (\bar{x}), predicted (P) and observed (O) seed mass remaining as a percentage of November estimates, and statistics (n , P) from a repeated measures analysis of variance testing for differences in predicted and observed seed decline ($\alpha = 0.05$).	81

2.3	Seed taxa consumed by dabbling ducks in the Mississippi Alluvial Valley and references	83
3.1	Seeds and tubers recovered from moist-soil core samples and commonly consumed by waterfowl (Chapter II), their true metabolizable energy values (TME; kcal/g), and reference	126
3.2	Density of all dabbling ducks (Anatini; ducks/ha/site/survey; \bar{x} , SE; $n = 4$) and those feeding in 0.5-ha plots supplemented in mid-December 2008 with 50, 250, or 550 kg/ha of Japanese millet (<i>Echinochloa frumentacea</i>) observed from mid-December 2008 to late February 2009 and mid-December 2008 to early January 2009 (Late December) in 4 experimental wetlands in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley	129
3.3	Density of Japanese millet (<i>Echinochloa frumentacea</i> ; kg[dry]/ha; \bar{x} , SE; $n = 4$) plus other <i>Echinochloa</i> species and other seeds and tubers present in 4 experimental wetlands from mid-December 2008 to late-February 2009 in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley	130
3.4	Combined density of Japanese millet (<i>Echinochloa frumentacea</i> ; kg[dry]/ha; \bar{x} , SE; $n = 4$) and naturally occurring <i>Echinochloa</i> species in 0.5-ha plots supplemented in mid-December 2008 with 50, 250, or 550 kg/ha of Japanese millet before deposition of millet (Pre-treatment), in early and late January 2009, and in late February 2009 in 4 experimental, moist-soil wetlands in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.	132
A.1	Scientific and common names of plant taxa.....	148
B.1	Locations of study sites in U.S. Fish and Wildlife Service National Wildlife Refuges (NWR); Mississippi Department of Wildlife, Fisheries, and Parks Wildlife Management Areas (MWMA); Tennessee Wildlife Resources Agency Wildlife Management Areas (TWMA); and private lands in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley during November 2006–2008 through February 2007–2009	151

C.1	Density of seeds and tubers (kg[dry]/ha; \bar{x} , SE) naturally occurring in unmanipulated (control), lightly disked, and mowed plots (<i>n</i>) of robust vegetation in managed moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley	154
D.1	Waterbirds observed in managed moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley	160

LIST OF FIGURES

FIGURE	Page
1.1	Locations of 26 moist-soil wetlands (study sites) sampled during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley53
1.2	Mean dabbling duck abundance in unmanipulated (control), lightly disked, and mowed plots ($n = 62$) in moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley54
1.3	Existence energy (EE) of dabbling ducks for one day (Anatini; DED) and energy removed (ER) from unmanipulated (control), lightly disked, and mowed plots ($n = 62$) in moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley55
3.1	Locations of 2 study sites sampled during February 2008 and 7 study sites sampled from mid-December 2008 through February 2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley133
3.2	Density of total and feeding dabbling ducks (Anatini; ducks/ha/site) and estimated duck energy days (DED/ha \pm SE; Reinecke and Kaminski 2007) in 0.5-ha plots supplemented in mid-December with 50, 250, or 550 kg/ha of Japanese millet (<i>Echinochloa frumentacea</i>) in 4 experimental wetlands sampled from mid-December 2008 to late February 2009 in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley134

3.3 Existence energy (EE) and energy removed (ER) expressed as dabbling duck energy days (DED/ha; Anatini; Reinecke and Kaminski 2007) in 0.5-ha plots supplemented in mid-December with 50, 250, or 550 kg/ha of Japanese millet (*Echinochloa frumentacea*) in 4 experimental wetlands sampled from mid-December 2008 to late February 2009 in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.....135

CHAPTER I
WINTER WATERBIRD AND FOOD DYNAMICS IN AUTUMN-MANIPULATED
MOIST-SOIL WETLANDS

Agricultural producers and wildlife managers flood croplands and natural vegetation in autumn and winter to create seasonal wetlands for waterbirds and other wetland wildlife in the lower Mississippi Alluvial Valley (MAV) and elsewhere in North America (Reinecke et al. 1989, Smith et al. 1989, Manley et al. 2004, Baldassarre and Bolen 2006). Extensive wetland loss and flood control in the MAV have increased importance of managed seasonal wetlands to waterfowl and other waterbirds (Fredrickson and Taylor 1982, Reinecke et al. 1989, Mitsch and Gosselink 2000, Rewa 2005, Fleming 2010). Furthermore, these seasonal wetlands retain sediments and nutrients which improves water quality and provides other important ecosystem services (Tockner and Stanford 2002; Vymazal 2007; Kröger et al. 2007, 2008; Manley et al. 2009; Jenkins et al. 2010).

Although flooding of croplands provides extensive habitat (Reinecke et al. 1992, Uihlein 2000), recent studies have revealed reduced availability of waste agricultural seeds following harvest for wintering waterfowl in the MAV and Tennessee (Manley et al. 2004, Stafford et al. 2006, Greer et al. 2009, Foster et al. 2010). Seasonal flooding and management of natural vegetation (e.g., grasses, sedges, and forbs) in moist-soil

wetlands have been recommended to compensate for decreased seed abundance in harvested crop fields (Fredrickson and Taylor 1982, Reinecke et al. 1989, Stafford et al. 2006, Kross et al. 2008a, Foster et al. 2010). Thus, conservation planners depend on moist-soil wetlands to help meet carrying capacity goals for wintering waterfowl in the MAV (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986, Loesch et al. 1994). Moist-soil wetlands contain natural plants that produce abundant seeds, tubers, and aquatic invertebrates and provide structural habitat diversity for waterfowl (Fredrickson and Taylor 1982, Reinecke et al. 1989, Gray et al. 1999, Kross et al. 2008b). Moist-soil wetlands typically harbor greater diversities of plant and animal foods than harvested crop fields and subsequently, receive extensive waterfowl use (Bellrose and Anderson 1943, Smith et al. 1989, Reinecke et al. 1992, Twedt and Nelms 1999).

Moist-soil management entails dewatering wetland basins in spring or summer to expose mud flats and promote plant growth (Fredrickson and Taylor 1982, Nassar et al. 1993, Nelms 2007, Fleming 2010). Furthermore, periodic soil disturbance (e.g., ≤ 3 year intervals) helps promote growth of early-succession, annual vegetation (Fredrickson and Taylor 1982, Gray et al. 1999). In summer and autumn, dewatered moist-soil wetlands provide habitat for migratory grassland birds and resident wildlife (Fredrickson and Taylor 1982, Rewa 2005). In autumn and winter, managed moist-soil wetlands typically are shallowly flooded for migrating and wintering waterfowl and other wetland fauna (Fredrickson and Taylor 1982, Nelms 2007). Moist-soil management is cost-effective and can be implemented on idle croplands and aquaculture ponds, field margins, active crop fields after harvest, and public or private wildlife management areas to increase

habitat and food for wildlife and provide ecosystem services (Cross and Vohs 1988, Schultz et al. 1995, Marquez et al. 1998, Lyons et al. 2000, Dosskey 2001).

In addition to periodic spring or summer disking to promote early succession vegetation, managers may mow, disk, or otherwise manipulate moist-soil plants in autumn to create openings for waterfowl or control undesirable species (Gordon et al. 1989, Heitmeyer et al. 1989, Gray et al. 1999, Taylor and Smith 2003). Managed moist-soil wetlands often produce tall and dense (hereafter, robust) vegetation that may deter waterfowl use until vegetation naturally topples (Gray et al. 1999; R. M. Kaminski, Mississippi State University, personal communication). Waterfowl and other waterbirds may avoid use of wetlands when emergent vegetation is dense (Kaminski and Prince 1981, Smith et al. 2004, Moon and Haukos 2008) allowing decomposition to reduce food availability (Nelms and Twedt 1996). Gray et al. (1999) recommended that robust moist-soil vegetation be mowed in autumn if vegetation was in early seral stages. If perennial and woody vegetation exceeded density of annual plants, Gray et al. (1999) recommended autumn disking to create openings for waterfowl and stimulate production of early-succession plants in subsequent growing seasons. Autumn manipulation of robust moist-soil vegetation after seeds have matured can create food-rich openings and “hemi-marsh” conditions (i.e., approximate equal ratio of emergent vegetation and open water after flooding) attractive to waterfowl on breeding and wintering ranges (Kaminski and Prince 1981, Smith et al. 2004). However, large-scale evaluation of these management strategies in relation to waterfowl use and food abundance in moist-soil wetlands during winter is lacking.

Previous research has demonstrated that moist-soil wetlands in the MAV contain an average of 556 kg[dry]/ha of seeds and tubers in late autumn (Kross et al. 2008b); however, no previously published research has documented dynamics of seeds and tubers and corresponding waterfowl use in these wetlands during winter. Reinecke et al. (1992) reported that mallard (*Anas platyrhynchos*) use of moist-soil wetlands varied among monthly surveys during winter, possibly attributable to availability of other foraging habitats. Gray et al. (1999) sampled aquatic macroinvertebrates in Mississippi moist-soil wetlands in winter but did not present monthly biomass estimates and reported invertebrate densities less than those in forested and emergent wetlands (Krull 1970, Wehrle et al. 1995, De Szalay and Resh 2000, Batema et al. 2005). Several researchers have examined effects of manipulating moist-soil vegetation on waterfowl food production and availability (Gray et al. 1999, Taylor and Smith 2003, Smith et al. 2004, Kostecke et al. 2005); however, few have simultaneously monitored winter food dynamics and waterfowl use (cf. Greer et al. 2009, Havens et al. 2009). Therefore, my objectives were to concurrently estimate winter abundances of 1) waterfowl and other waterbirds, 2) seeds and tubers, and 3) invertebrates in response to autumn pre-flooding treatments of light disking, mowing, and no manipulation (control) of robust moist-soil vegetation in the MAV. Additionally, I estimated 4) seed decomposition during winter and 5) abundance of residual moist-soil seeds and tubers remaining after waterfowl abandoned or stopped foraging in experimental plots.

Study Area

The MAV is a 10 million-ha alluvial plain of the Mississippi River that stretches from southern Missouri to the gulf coast of Louisiana and is an important ecoregion for migrating and wintering waterfowl (Reinecke et al. 1988, 1989; Fredrickson 2005). Historically, the MAV regularly flooded from overflow of the Mississippi River and its tributaries and was composed mostly of mature bottomland hardwood forests (King et al. 2005, Schoenholtz et al. 2005). Presently, approximately 70% of the MAV has been cleared for row-crop agriculture and other human uses, and flood control along major rivers and streams has partially replaced seasonal and temporary wetlands with small permanent basins or networks of ditches to remove water rapidly (Reinecke et al. 1988, 1989; Havera 1999; Fredrickson 2005; King et al. 2005; Manley et al. 2009).

I selected and sampled managed moist-soil wetlands within federal, state, and private waterfowl management complexes in Arkansas, Mississippi, and Tennessee. Eighteen study sites were located in the MAV; however, I selected 5 sites in eastern Mississippi within the Tombigbee River Basin and 2 sites in western Tennessee in the Lower Hatchie River Watershed of the Lower Mississippi River Basin because of close proximity to, similar plant communities to, and similar waterfowl use as the MAV (Boulton 2005, Keck and Etnier 2005; Fig. 1.1; Appendix B). I selected managed moist-soil wetlands using the following criteria: 1) visual presence of continuous, robust stands of moist-soil vegetation; 2) adequate area for placement of a 2.5 ha treatment block; 3) surrounding habitat and landscape composition that provided access to wetlands, vantage points for waterbird observations, and isolation from human disturbance; and 4)

availability from cooperators. I selected wetlands containing continuous stands of grasses (e.g., wild millets [*Echinochloa* spp.], panicgrass [*Panicum* spp.]), sedges (*Carex* spp., *Cyperus* spp.), and forbs (e.g., smartweeds [*Polygonum* spp.], teaweed [*Sida spinosa*]) that produce seeds and tubers consumed by waterfowl (Bellrose and Anderson 1943, Chapter II). However, wetlands also contained other plants that contributed to robustness of vegetation (e.g., coffeeweed [*Sesbania herbacea*], cocklebur [*Xanthium strumarium*]; Chapter II) and had little or unknown nutritional value for waterfowl.

Methods

Experimental Design

During autumns 2006–2008, I established plots of mowed, disked, and unmanipulated vegetation in 26 moist-soil wetlands in the MAV (i.e., sites; Fig. 1.1; Appendix B). I cooperated with wetland managers who mowed (~8–15 cm high), lightly disked (i.e., a single pass at a shallow depth), and did not manipulate vegetation (control) in 0.8-ha treatment plots within 2.5 ha blocks prior to flooding at each site. I chose 2.5 ha as the block size because that was the size of the smallest wetland impoundment I typically observed being managed for moist-soil in my study area. Each treatment was applied randomly and separated by a 10-m buffer of standing vegetation and all blocks were located within waterfowl sanctuaries in U.S. Fish and Wildlife Service National Wildlife Refuges, state Wildlife Management Areas, and private lands. Managers and cooperators mowed and disked treatment plots in late October or early November and then flooded (3–45 cm) areas typically by mid to late November. After plots were

flooded, I measured water depths at 10 locations along 2 randomly placed transects in each treatment plot and erected a water depth gauge so that mean depths for each treatment could be inferred from the single depth gauge.

Waterbird Abundance

I enumerated waterfowl and other waterbirds by species from elevated blinds and obtained water depths twice weekly from initial flooding in late November to late February when waterfowl migrated from study areas. I conducted diurnal scan surveys at sites from approximately sunrise – 3 hrs post sunrise or from 3 hrs before sunset – sunset and alternated morning or afternoon surveys among visits to sites (Arzel and Elmberg 2004, Amano et al. 2006, Greer et al. 2009). During each scan survey, I scanned all birds in mowed and disked plots and recorded species and behavior of each individual (i.e., aggression, foraging, resting, swimming). After counting all waterbirds in the mowed and disked plots, I entered control plots to flush and count waterbirds because standing vegetation often obscured partially my view from blinds. I assumed that all birds present in plots were detected because vision from elevated blinds was unobstructed in mowed and disked plots, I entered control plots to flush birds and ensure all were detected, and 3 observers practiced counts together and conducted all surveys (Anderson and Smith, Smith et al. 2004). During each morning or afternoon, I surveyed 1–3 sites, depending on travel distances. I did not conduct counts when winds exceeded 30 kph.

I observed waterfowl using wetlands after dusk, but was unable to conduct systematic nocturnal surveys due to dense vegetation in the control treatments, distances from blinds to study plots, and logistical constraints (Anderson and Smith 1999, Brasher

2010). Brasher (2010) estimated that nocturnal use of moist-soil wetlands was less than diurnal use by ducks, and Euliss and Harris (1987) reported wintering ducks preferred dense emergent wetlands nocturnally, making passive observations difficult. Moon and Haukos (2008) reported that female northern pintail (*Anas acuta*) used playa wetlands with differing proportions of emergent cover similarly diurnally and nocturnally; thus, I assumed diurnal surveys provided representative data of relative diurnal and nocturnal use of experimental wetlands.

Seed and Tuber Abundances and Decomposition

I collected 10 core samples containing soil, vegetation, seeds, and tubers (10 cm in diameter and depth) from each treatment plot immediately after flooding but before waterfowl used wetlands (i.e., late November 2006–2008) and monthly thereafter until late February 2007–2009 (Stafford et al. 2006, Kross et al. 2008b, Havens et al. 2009). I collected core samples along a randomly placed transect within each plot. I selected a random distance (0–25 m) to the first sample location and then located each subsequent sample location at a fixed interval predetermined to span the treatment plot (Greer et al. 2007).

I estimated seed decomposition by placing 10 porous, fiberglass envelopes (30 x 30 cm; 0.12 mm aperture mesh) containing 100 g (dry mass) of Japanese millet (*Echinochloa frumentacea*) in each treatment plot immediately after flooding (Neely 1956). I was unable to obtain a mixture of harvested moist-soil seeds for use as a decomposition control and, thus, used millet as a surrogate. Japanese millet is similar to naturally occurring millets and is planted commonly in wetlands managed for waterfowl

(Michael 1983, Yabuno 1983, Nelms 2007, Strickland et al. 2009, Schummer et al. 2011). I placed envelopes along a transect located in the center of each treatment plot and randomly selected the distance (0–25 m) to the first sample location. After selecting the first location, I placed envelopes at fixed intervals predetermined to span each plot. I spread seed evenly within envelopes before each was submerged and placed beneath vegetation and atop substrate. I covered envelopes with 10 mm aperture wire mesh and staked them in place to deter predators. I collected all envelopes in late February of each winter. I stored core samples and seed envelopes at -15°C until processed.

I processed soil core and decomposition samples in a random sequence by site and month to account for possible bias associated with the duration samples were frozen. I thawed core samples in warm water; added a solution of 3% hydrogen peroxide (H₂O₂), sodium bicarbonate, and water for 1–3 hours to disperse soil (Bohm 1979); and washed cores through sieves (i.e., mesh sizes #50 [0.03 mm], #10[1.65 mm], and #4[4.75 mm]; Kross et al. 2008*b*). I recovered and air dried seeds and other material from each sieve separately for 24–48 hrs. I homogenized materials retained by the small sieve (#50) and separated a random one-quarter subsample by mass (hereafter, small portion). Using forceps, I removed seeds and tubers from the small portion and from materials retained by 2 large sieves (#s 4 and 10; hereafter, large portion; Kross et al. 2008*b*; H. M. Hagy, Mississippi State University, unpublished data). I dried seeds and tubers at 80°C for 24 hrs to dry mass and enumerated and weighed seeds by genus or species (Seed Images 2008, Bryson and DeFelice 2009, Schummer et al. 2011). I multiplied seed and tuber masses from the small portion by 4 and added each to the large portion to estimate total

seeds and tubers per core sample (H. M. Hagy, Mississippi State University, unpublished data). To process decomposition envelopes, I thawed envelopes in warm water, rinsed mud and debris from envelopes, washed seeds into a #50 sieve and rinsed thoroughly to remove inorganic and organic matter, and dried seed at 80°C for 24–48 hrs to constant mass. I estimated decomposition of millet seeds by subtracting the ending mass from the original mass and divided by number of days each envelope was in each plot to standardize rates among years and sites. I weighed all seeds and tubers to the nearest 0.1 mg immediately after removal from the drying oven.

Washing Reagents

To test the assumption that clay-dispersing reagents did not affect mass of moist-soil seeds, I soaked 10 10-g samples (dry mass) of Japanese millet in each of 4 different solutions used to wash core samples for 3 hours (water [control], H₂O₂, H₂O₂ + sodium bicarbonate, and water + H₂O₂ + sodium bicarbonate). After 3 hrs, I rinsed each sample with water in a #50 sieve, dried at 80°C for 24–48 hrs to constant mass, and weighed to the nearest 0.1 mg.

Invertebrate Abundance

I collected nektonic and benthic invertebrates at each sample location and time period of soil cores using a 500 µm rectangular sweep net (46 x 20 cm; $n = 10$ samples/plot/month; Wehrle et al. 1995). I pushed the net through vegetation and along and in contact with substrate for 1.1 m to sample a 0.5-m² area (Cheal et al. 1993, Gray et al. 1999). I preserved invertebrate samples on ice during transportation and stored at

-15°C until processed. I quantified invertebrate abundance by removing invertebrates from debris using forceps and enumerated by order (Pennak 1989, Thorp and Covich 1991, McCafferty 1998, Voshell 2002). I dried each taxa to constant mass at 60°C for 24 hrs and weighed to the nearest 0.1 mg (Salonen and Sarvala 1985, Murkin et al. 1994).

Statistical Analyses

Waterbird Abundance and Diversity

Because numbers and timing of bird surveys varied among years due to timing of flooding and among weeks because of vagaries of weather, I standardized repeated waterbird observations by averaging surveys within the same 7-day calendar period of each winter (i.e., weeks). I calculated Pearson correlation coefficients between waterbird guilds to reduce number of dependent variables for analyses (i.e., all dabbling ducks [Anatini], mallards, dabbling ducks other than mallards [hereafter, other dabbling ducks], and all waterbirds combined). I selected 2 density metrics (duck/ha) as dependent variables for individual analyses: 1) density of mallards, because it was correlated with dabbling ducks ($r = 0.95$, $n = 679$) and all waterbirds ($r = 0.95$, $n = 679$); and 2) density of other dabbling ducks, because it was not highly correlated with mallards ($r = 0.35$, $n = 679$). I excluded diving ducks (Aythyini), waterbirds other than ducks, and geese (Anserini) from analyses as these groups represented a small portion of observed waterbirds. Additionally, I calculated Shannon's index of species diversity for each treatment during each week (Hair 1980, Zar 2009).

In separate analyses, I used repeated measures ANOVA to test effects of autumn mowing, disking, and no treatment of moist-soil vegetation on densities of mallards, dabbling ducks other than mallards, and Shannon's index of diversity using the MIXED procedure (PROC MIXED; SAS Institute 2008). I designated treatment, water depth, and their interaction as fixed effects; year and site as random effects; and week as the repeated measure.

Seed and Tuber Abundances

Similarly, I assessed treatment effects on seed and tuber and invertebrate abundances (kg[dry]/ha) using previously described modeling procedures. Instead of week, I used month as the repeated measure. I did not analyze combined potential waterfowl foods (i.e., seeds, tubers, and invertebrates) because it was correlated with seed and tuber abundance ($r = 0.99$, $n = 261$). I included only seed taxa that have been reported as potential food of dabbling ducks in analyses (Chapter II, Olmstead 2010) and adjusted seed mass using seed size-class correction factors to account for negative bias associated with core sample processing (H. M. Hagy, Mississippi State University, unpublished data). I used one-way ANOVA to test for an effect of treatment on late-autumn seed abundance (kg[dry]/ha) with year and site as random effects (PROC MIXED, SAS Institute 2008). Additionally, I assessed treatment effects on seed abundance from December – February using repeated measures ANOVA with site and year as random effects and month as a repeated measure. I included month, treatment, seed abundance in the previous month, and the interaction between treatment and month

as fixed effects (Havens et al. 2009). Additionally, I converted seed masses to duck energy days (DEDs) following methods described in Chapter III (Reinecke et al. 1989).

Existence Energy and Energy Removal

I used repeated measures ANOVA to model effects of potential energy requirements of dabbling ducks (i.e., existence energy [EE]) on energy reduction (ER) from experimental plots using PROC MIXED. I calculated existence energy by estimating dabbling duck abundance per month in each treatment plot and multiplying it by the daily energetic requirements of dabbling ducks in the MAV (294.35 kcal/day; Reinecke and Uihlein 2006, Reinecke and Kaminski 2007, Murray et al. 2009, Chapter III). I calculated energy reduction by multiplying the difference in seed and tuber abundance (kg[dry]/ha) between subsequent months in each treatment plot by the mean true metabolizable energy value for moist-soil seeds (2.5 kcal/gram; Reinecke et al. 1989, Kaminski et al. 2003, Chapter III). If a difference between 2 months was negative (i.e., a slight increase in seed and tuber abundance occurred), I attributed this phenomenon to sampling error and assumed 0 energy reduction for that month. The dependent variable was ER; EE, treatment, sampling period, interaction of sampling period and EE, and interaction of treatment and EE were fixed effects; site was a random effect; and sampling period was the repeated measure.

Invertebrate Abundance and Diversity

I assessed treatment effects on invertebrate abundance (kg[dry]/ha) and Shannon's index of diversity using repeated measures ANOVA (PROC MIXED; SAS

Institute 2008). I calculated Shannon's index of diversity by order for each treatment plot and month (Hair 1980, Lyons 1981, Gray et al. 1999, Zar 2009). I designated treatment and depth and their interaction as fixed effects, year and site as random effects, and month as the repeated measure and a fixed effect.

Seed Decomposition and Washing Reagents

I used a general linear model to test for a treatment effect on Japanese millet decomposition using percentage decomposition per day as the dependent variable, treatment as the fixed effect, and site and year as random effects (PROC MIXED, SAS Institute 2008). Additionally, I used a one-way ANOVA to test for an effect of washing reagent (fixed effect) on dry mass of Japanese millet (dependent variable; PROC GLM, SAS Institute 2008).

For all analyses, I examined histograms, variances of independent variables, plots of residuals, and used recommended data transformations to ensure data met assumptions of analyses (Littell et al. 2006, Zar 2009). When using repeated measures analysis of variance (ANOVA), I used Akaike's Information Criterion to select an appropriate covariance structure and specified restricted maximum likelihood estimation of fixed effects (Littell et al. 2006). I designated $\alpha = 0.05$ a priori. Additionally, I performed Tukey's pair-wise multiple comparisons tests of means among treatments when $P < 0.05$. I calculated means and standard errors from untransformed data.

Results

Waterbird Abundance and Diversity

I conducted waterbird surveys on 26 sites in winters 2006–2009, but did not analyze data from 5 sites because treatment plots were flooded inconsistently, human-related activities caused bird disturbances, and other factors potentially biased data. Among sites, treatments, and surveys, most waterbirds observed were dabbling ducks (92%, $n = 679$ surveys), including mallard (68%), northern shoveler (11%; *A. clypeata*), northern pintail (9%), gadwall (7%; *A. strepera*), American green-winged teal (5%; *A. crecca*), and other species (< 1%). Diving ducks accounted for 2% of all waterbirds observed and were mostly ring-necked ducks (65%; *Aythya collaris*) and hooded mergansers (34%; *Lophodytes cucullatus*). I rarely observed geese or other waterbirds using experimental plots, except American coot (4% of all waterbirds; *Fulica americana*).

I detected a treatment effect on mallard ($F_{2, 329} = 3.89$, $P = 0.021$) and other dabbling duck abundances ($F_{2, 227} = 6.83$, $P = 0.001$) among winters 2006–2009. Mallards were approximately twice more abundant on mowed ($t_{156} = 2.73$, $P = 0.018$) and disked plots ($t_{156} = 2.86$, $P = 0.012$) than control plots, but their use of mowed and disked plots did not differ ($t_{154} = 0.08$, $P = 0.997$; Table 1.1; Fig. 1.2). Mallard abundance was not related to water depth ($F_{1, 331} = 1.35$, $P = 0.245$) or the interaction between treatment and water depth ($F_{2, 338} = 1.89$, $P = 0.152$); however, 90% of mallards used plots with a mean depth of ≤ 15 cm ($\bar{x} = 10.8$ cm, SE = 0.1, range = 3–15 cm, $n = 679$). Similarly, other dabbling ducks were approximately three times more abundant in mowed ($t_{134} =$

4.64, $P < 0.001$) and disked plots ($t_{134} = 4.08$, $P < 0.001$) than control plots, but their use of mowed and disked plots did not differ ($t_{132} = 0.63$, $P = 0.802$). Other dabbling duck abundance varied inversely with water depth ($F_{1, 271} = 6.27$, $P = 0.001$). Ninety percent of other dabbling ducks used plots with a mean depth of ≤ 16 cm ($\bar{x} = 10.9$ cm, SE = 0.1, range = 4–16 cm, $n = 679$), but there was no interaction between treatment and water depth ($F_{2, 209} = 2.05$, $P = 0.131$).

Waterbird species diversity differed among treatments ($F_{2, 102} = 9.42$, $P < 0.001$) and was approximately 0.8 times greater in mowed ($t_{31.8} = 5.00$, $P < 0.001$; Table 1.1) and disked plots ($t_{31.5} = 4.22$, $P < 0.001$) than control plots. Waterbird diversity was similar in mowed and disked plots ($t_{31.7} = 0.86$, $P = 0.664$) and was not related to water depth ($F_{1, 291} = 3.34$, $P = 0.068$) or the interaction of depth and treatment ($F_{2, 357} = 2.37$, $P = 0.094$).

Seed and Tuber Abundances

I sampled seeds and tubers on 26 sites in winters 2006–2009; however, I did not analyze data from 4 sites because treatment plots were flooded inconsistently or I did not observe ducks in plots. At one site, I was unable to mow vegetation and samples from 1 additional mowed plot were inadvertently destroyed. Combined seed and tuber abundance in late November 2006–2008 differed among treatments ($F_{2, 40.2} = 8.48$, $P < 0.001$) and was approximately 1.4 times greater in control ($t_{40} = 3.90$, $P = 0.001$) and mowed plots ($t_{40.3} = 3.04$, $P = 0.011$) than disked plots, but not different between control and mowed plots ($t_{40.3} = 0.72$, $P = 0.751$; Table 1.2). Seed and tuber abundance from December 2006–2008 through February 2007–2009 were related to month ($F_{2, 69.9} =$

10.59, $P < 0.001$), but did not vary by treatment ($F_{2, 34.9} = 0.12$, $P = 0.891$), seed abundance in the previous month ($F_{1, 45.6} = 0.53$, $P = 0.471$), or the interaction between treatment and month ($F_{4, 77.8} = 0.47$, $P = 0.760$). Among sites, treatments, and years, seeds and tubers declined 38% (SE = 3.9, $n = 60$) from late November to December, 22% (SE = 3.1, $n = 60$) from December–January, and 18% (SE = 2.8, $n = 65$) from January – February. Among all treatments and sites in late February 2007–2009, an average of 258.6 kg/ha (SE = 14.3, median = 232.3 kg/ha, $n = 66$) of seeds and tubers remained after waterfowl abandoned wetlands.

Existence Energy and Energy Removal

Energy reduction in plots from late November 2006–2008 through February 2007–2009 varied among months ($F_{2, 131} = 10.14$, $P < 0.001$), but was not related to existence energy ($F_{1, 130} = 2.11$, $P = 0.149$; Fig. 1.3), treatment ($F_{2, 68.6} = 2.27$, $P = 0.111$), or the interactions of EE and month ($F_{2, 141} = 0.19$, $P = 0.828$), or EE and treatment ($F_{2, 102} = 0.03$, $P = 0.966$). Energy reduction was 3.6 times greater from late November – late December than from late December – late January ($t_{104} = 4.95$, $P < 0.001$) and 5 times greater than from late January – late February ($t_{119} = 4.68$, $P < 0.001$). Energy reduction from late December – late January did not differ from reduction during late January – late February ($t_{122} = 0.53$, $P = 0.595$). Furthermore, existence energy always exceeded energy removal from plots (Fig. 1.3).

Invertebrate Abundance and Diversity

I sampled invertebrates on 26 sites in winters 2006–2009. However, I did not process samples from 8 randomly selected sites because of financial limitations.

Additionally, I processed and analyzed only 5 invertebrate samples per treatment plot from an additional 5 sites due to financial limitations. Throughout winter, invertebrate abundance differed among treatments ($F_{2, 29.8} = 7.35$, $P = 0.003$) and was 1.6 times greater in control than mowed ($t_{30} = 3.04$, $P = 0.013$) and twice greater in control than disked plots ($t_{29.5} = 3.52$, $P = 0.004$; Table 1.3). I did not detect differences in invertebrate abundance between mowed and disked plots ($t_{30} = 0.39$, $P = 0.919$).

Invertebrate abundance declined from late November – late January and then increased in February ($F_{3, 117} = 5.88$, $P < 0.001$) similarly among treatments ($F_{6, 122} = 0.72$, $P = 0.632$). Diversity of invertebrate Orders differed among treatments ($F_{2, 27.8} = 11.83$, $P < 0.001$) and was approximately 1.3 times greater in control than disked ($t_{27.3} = 3.86$, $P = 0.002$) and mowed plots ($t_{28.1} = 4.47$, $P < 0.001$), but was similar in mowed and disked plots ($t_{28.1} = 0.69$, $P = 0.770$). Invertebrate diversity did not differ among months ($F_{3, 123} = 0.47$, $P = 0.702$) or the interaction of month and treatment ($F_{6, 126} = 0.77$, $P = 0.592$).

Among treatments, months, and years, Classes Malacostraca, Insecta, and Gastropoda accounted for most mass (57.8%, 15.7%, 12.4%, respectively) in invertebrate samples ($n = 1,561$). Orders Isopoda (34.3%), Decapoda (19.8%), Pulmonata (11.6%), Podocopida (6.5%), Amphipoda (4.6%), Hemiptera (4.4%), Coleoptera (3.6%), Cladocera (3.3%), and Odonata (2.6%) accounted for 90% of total mass in invertebrate

samples. However, invertebrates composed only 0.5% (SE = 0.07%, $n = 167$ plots; dry mass) of potential waterbird foods throughout winter.

Seed Decomposition and Washing Reagents

Percentage decomposition of Japanese millet in envelopes varied by treatment ($F_{2, 39} = 5.68$, $P = 0.007$). Decomposition was greater in mowed ($t_{39} = 2.94$, $P = 0.015$; $\bar{x} = 0.55\%$ decline/day, SE = 0.07) and disked plots ($t_{39} = 2.94$, $P = 0.001$; $\bar{x} = 0.55\%$ decline/day, SE = 0.07) than control plots ($\bar{x} = 0.53\%$ decline/day, SE = 0.07), but did not differ between disked and mowed plots ($t_{39} = 0.01$, $P = 0.999$). Additionally, different washing reagents did not affect variation in dry mass of Japanese millet seeds ($F_{3, 39} = 1.33$, $P = 0.28$).

Discussion

Waterbird Abundance and Diversity

Dabbling ducks used mowed and disked plots more than control plots diurnally in moist-soil wetlands during winter consistent with other studies of nonbreeding waterfowl (Smith et al. 2004, Havens et al. 2009). Dense, standing vegetation may have deterred waterbird use of control plots until emergent vegetation naturally toppled and created openings (Weller and Fredrickson 1974, De Szalay and Resh 2000, Smith et al. 2004). Although I did not measure interspersed vegetation and open water in control plots, proportional use of control plots by dabbling ducks increased during winter. This increase may have been due to formation of natural openings in control plots during

winter. Similarly, Moon and Haukos (2008) reported that female northern pintails in Texas diurnally and nocturnally used playa lakes with $\leq 50\%$ emergent cover more than areas that were more densely vegetated. However, pintail use of areas with $\geq 50\%$ emergent vegetation was greater in mid and late winter than in late autumn (Moon and Haukos 2008).

Waterbird diversity also was greatest in mowed and disked plots, but some waterbirds only were observed in control plots, such as American bittern (*Botaurus lentiginosus*) and sora (*Porzana carolina*). These species are often associated with wetlands containing more dense vegetation than open water in an interspersed arrangement (Rehm and Baldassarre 2007). In contrast, dabbling ducks and American coot selected wetlands in Manitoba, Canada with approximately 50% and $>50\%$ open water, respectively (Murkin et al. 1997). Individual species and feeding guilds of waterbirds select habitats along a continuum of differing vegetation densities and water depths, and structural habitat diversity may increase niche diversity (Fredrickson and Taylor 1982, Murkin et al. 1997). Interspersion of vegetation and open water increases structural complexity, amount of edge, and has been associated with greater use and diversity in regions used by breeding and nonbreeding waterfowl (Kaminski and Prince 1981, Smith et al. 2004). Created or natural openings in robust emergent vegetation can provide hemi-marsh conditions attractive to waterbirds which appear to increase overall wetland use and species diversity (Kaminski and Prince 1981, Solberg and Higgins 1993, Linz et al. 1996, Smith et al. 2004).

Waterbirds other than ducks respond positively to increased interspersed (i.e., extent of edge) of open water and emergent vegetation or land (Kaminski and Prince 1981, 1984; Pearse 2007; Rehm and Baldassarre 2007). Ducks forming pair bonds in winter may be attracted to wetlands where hemi-marsh conditions provide visual isolation from conspecifics (Kaminski and Prince 1981, Murkin et al. 1982), although ducks remain gregarious during winter (Baldassarre and Bolen 2006, Legagneux et al. 2009). Hemi-marsh conditions may be a proximate cue for waterfowl for a combination of factors which may increase overall fitness prospects (Kaminski and Prince 1981). Although individual treatment plots alone may not have represented hemi-marsh configurations, the combination of all plots and buffers within experimental wetlands provided open water and standing vegetation and may have corresponded to proximate cues of waterfowl.

Although there is evidence that waterfowl select structurally diverse emergent wetlands (Weller and Fredrickson 1974, Kaminski and Prince 1981, Smith et al. 2004), few studies have documented causal mechanisms. Diurnal use of plots by ducks did not appear to be related only to food densities and was likely related to other unknown factors (Kaminski and Prince 1981). Light disking resulted in lesser seed and tuber abundance than mowing; however, there was no difference in the abundance of dabbling ducks between manipulated plots. Similarly, control plots contained the greatest abundance of seeds and tubers, but were least used by dabbling ducks. From late December – late February, dabbling ducks continued to use and forage in all plots, but

did not reduce seeds and tubers faster than decomposition rates or remove sufficient seeds and tubers to account for daily energy expenditures (Fig. 1.2).

Kaminski and Prince (1981) hypothesized that invertebrate production might be greater in emergent wetlands with a 50:50 interspersion of open water and emergent vegetation, but they and other researchers did not find support consistent with this hypothesis (Murkin et al. 1982, Solberg and Higgins 1993, Murkin et al. 1997).

Conversely, Voights (1976) showed that nesting waterfowl used marshes with the greatest invertebrate abundance during nesting and Pöysä (2001) showed that breeding mallards used lakes of greater habitat quality more than lower quality lakes in Finland (Pöysä et al. 1998). I did not find overwhelming evidence to suggest that diurnal dabbling duck use of moist-soil wetlands was related only to food availability. If this was the case, foraging waterfowl would have been most abundant in control plots, followed by mowed and disked plots until food abundance was equalized. Furthermore, after food was reduced to equal abundances among plots in December, waterfowl should have been equally distributed among treatment plots. However, I did not observe these patterns. Thus, waterfowl may select habitats using a combination of proximate cues for ultimate factors and preferences depend on many endogenous and exogenous factors (Arengo and Baldassarre 1995, Pöysä et al. 1998, Gawlik 2002, Arzel and Elmberg 2004).

Waterfowl use of moist-soil wetlands decreased during winter with most use occurring in late November and December (Fig. 1.3). As experimental wetlands were located on waterfowl management areas and often were artificially flooded, I suspect that waterbird use in early winter was related to wetland availability in my study area.

Reinecke et al. (1992) observed greater use by waterfowl of managed habitats than unmanaged, naturally flooded habitats in early winter and attributed the difference to increased wetland availability in late winter. Additionally, Reinecke et al. (1992) observed an increase in proportion of mallards using moist-soil wetlands compared to croplands from early December – early January. In mid January, I did observe an increase in use of all plots which may have been related to arrival of migrating waterfowl in the MAV (Reinecke et al. 1992, Pearse et al. 2007). Increased wetland availability from natural flooding during winter (Reinecke et al. 1992) and rapid food reduction in my experimental wetlands may have been related to the overall trend of decreased waterfowl use of moist-soil wetlands during winter.

I managed water depths in experimental wetlands within ranges often used by dabbling ducks (i.e., ≤ 45 cm; Fredrickson and Taylor 1982, Baldassarre and Bolen 2006); however, depths varied slightly among treatment plots and wetlands due to natural topography and dynamic hydrology. I detected an inverse relationship between other dabbling duck use and water depth consistent with suggestions to provide shallowly flooded wetlands for dabbling ducks (Fredrickson and Taylor 1982). I observed 90% mallards and other dabbling ducks using plots averaging < 16 cm in depth. When water was near these depths, I observed mostly dabbling ducks using plots, but when plots were more deeply flooded, I observed increasing numbers of ring-necked ducks, American coot, and pied-billed grebe (*Podilymbus podiceps*). Similarly, Euliss and Harris (1987) observed wintering northern pintail and American green-winged teal commonly foraging in 17 and 11 cm of water, respectively, and Fredrickson and Taylor (1982) indicated that

American coot commonly use water depths of approximately 30 cm. Waterfowl may more easily obtain submerged foods when water depths do not require tips-ups (Euliss and Harris 1987, Nolet et al. 2006) and dabbling ducks may not be able to obtain foods in or on top of the soil when water depths exceed 50 cm (Fredrickson and Taylor 1982).

Seed and Tuber Abundances

Assuming that all seeds and tubers present in late November 2006–2008 were available for consumption by waterfowl, control and mowed plots contained 6,421 and 6,070 Duck Energy Days/ha (DED), respectively (Murray et al. 2009). Lightly disked plots contained ~30% fewer seeds and tubers than mowed and control plots and thus provided 4,357 DED/ha in late autumn. Unmanipulated moist-soil wetlands on public lands in the MAV in autumns 2002–2004 provided approximately 4,760 DED/ha (556,000 g/ha x 2.5 kcal/g x 1 DED/294 kcal; Reinecke and Uihlein 2006, Kross et al. 2008*b*, Murray et al. 2009). Therefore, control and mowed plots provided more potential DEDs than areas sampled by Kross et al. (2008*b*), but autumn disking in these wetlands produced similar DEDs as estimated by Kross et al. (2008*b*). Although equipment was calibrated so light disking would topple vegetation rather than incorporate it into soil, slight soil disturbance may have buried seeds below depths of core samplers in disked plots (Taylor and Smith 2003). As mowing and disking of vegetation preceded flooding ($\bar{x} = 37$ days, SE = 1.9, $n = 9$ sites), decomposition before flooding, granivory, or other factors also might have reduced seed and tuber abundances in disked plots (Stafford et al. 2006, Greer et al. 2007). Autumn disking is useful to set-back plant succession when vegetation composition has advanced beyond early seral stages (Fredrickson and Taylor

1982, Gray et al. 1999), control undesirable species (Fredrickson and Taylor 1982), and increase seed production in subsequent years, but may result in significant seed and tuber loss and slightly increased decomposition (Baldassarre and Bolen 1984, Gray et al. 1999, Taylor and Smith 2003).

Waterfowl used densely vegetated control plots diurnally approximately 50% less than mowed and disked plots until late winter, but seed abundances declined to similar levels in all plots by mid-winter. Therefore, different consumption rates by waterfowl among treatments, nocturnal foraging, a foraging threshold, or other factors may explain differences in waterfowl use and seed and tuber reduction in experimental wetlands. Researchers in other wintering regions have observed waterfowl using and foraging in densely vegetated portions of moist-soil wetlands nocturnally (Euliss and Harris 1987, Anderson and Smith 1999). I observed waterfowl landing in mowed and disked plots at dusk and swimming into control plots beginning in mid-December; thus, waterfowl may have foraged on seeds and tubers in control plots at night from mid December–February.

Differences in seed abundance among treatment plots were detected only in late autumn and no differences occurred subsequently through late February. Initially, foods were reduced in mowed and control plots more than disked plots. By early January, dabbling ducks and decomposition decreased foods in all treatment plots equally suggesting foraging profitability among treatments may have been equalized. Furthermore, reduction of seeds and tubers from late December–February did not proceed faster than would be predicted by decomposition rates of Japanese millet (Chapter II, Table 2.1). Similarly, Olmstead (2010) reported ducks did not reduce moist-soil seeds

and tubers from November–January in Arkansas and seeds reported previously as “beneficial” to waterfowl remained at approximately 150 kg/ha. Therefore, waterfowl may have removed undetectable abundances of seeds and tubers between late December–February, and residual abundances might indicate a foraging profitability threshold (i.e., giving-up density [GUD]; Reinecke et al. 1989, Brown and Kotler 2007, Greer et al. 2009).

My estimate of seeds and tubers remaining at the end of winter (~260 kg/ha [dry mass]) was approximately 5 times greater than the GUD estimate for harvested rice (50 kg/ha) and 17 times greater than residual corn estimates after waterfowl stopped feeding in dry fields (~15 kg/ha; Baldassarre and Bolen 1984, Reinecke et al. 1989, Barney 2008, Greer et al. 2009). As washing reagents did not affect mass of millet seeds and I adjusted seed estimates for recovery bias, these estimates should be unbiased. Residual moist-soil seed and tuber abundances varied among experimental plots from 91–563 kg/ha similar to variability reported in California (30–163 kg/ha; Naylor 2002). Straub (2008) estimated that palustrine emergent wetlands in the Upper Mississippi River and Great Lakes Region contained 126 kg/ha of seeds and tubers and that abundance did not differ before and after waterfowl used wetlands in spring. Greer et al. (2007) indicated that moist-soil seeds declined by 79% during winters of 2000–2001 and 2001–2002 in northern Missouri wetlands to approximately 459 and 235 kg/ha, respectively. Brasher et al. (2007) reported carrying capacity of actively and passively managed wetlands in spring in northern Ohio before waterfowl arrived (\bar{x} = 66–242 DED/ha) was below a theoretical energy profitability threshold calculated from rice fields (572 DED/ha;

Reinecke et al. 1989). Therefore, variation in seed abundance, distribution, and metabolizable energy in moist-soil wetlands may result in different foraging profitability thresholds compared to agricultural fields (Kaminski et al. 2003, Kross et al. 2008*b*, Greer et al. 2009, Foster et al. 2010, Chapter III).

Greer et al. (2009) speculated that GUD in seasonal emergent wetlands was likely different from rice fields due to different true metabolizable energy of moist-soil seeds and rice grains (Kaminski et al. 2003). However, greater GUD in moist-soil than agricultural wetlands would reduce current carrying capacity estimates for moist-soil wetlands and diminish potential for these wetlands to mitigate decreased quantity of foods in harvested agricultural fields (Stafford et al. 2006, Foster et al. 2010). Furthermore, experiments should be conducted to determine if winter seed and tuber abundances represent a foraging threshold in my moist-soil wetlands (e.g., Chapter III) or if food abundances were sufficient in my study areas or elsewhere so waterfowl did not reach a critical food density (van Gils et al. 2004). Future experimentation using marked birds and night-vision optics to study individual habitat use and relative to foraging behavior and survival might help further identify foraging thresholds.

Invertebrate Abundance and Diversity

Invertebrate abundance was greatest in control plots each sampling period and greater in mowed than disked plots in all months except late February. Similarly, invertebrate diversity was greater in control plots during winter than disked or mowed plots. Gray et al. (1999) reported similar findings of greater invertebrate diversity during winter in Mississippi in unmanipulated moist-soil vegetation than in areas manipulated in

autumn. Kostecke et al. (2005) reported greatest invertebrate biomass in unmanipulated emergent vegetation, but greater diversity in burned, disked, and grazed vegetation in Kansas during autumn. De Szalay and Resh (2000) estimated that invertebrate diversity was greater in unmanipulated than mowed patches in coastal wetlands in California, but mowed patches with low emergent coverage contained greater biomass in late winter. Similarly, Gray et al. (1999) reported greater invertebrate biomass in mowed than unmanipulated moist-soil vegetation, suggesting that a combination of mowed and unmanipulated patches of moist-soil vegetation may increase invertebrate abundance and diversity in winter.

Previous studies have attributed similar findings to abundance of detritus (Gray et al. 1999, Anderson and Smith 2000, Kostecke et al. 2005). Although I did not quantify detritus, different treatments of vegetation likely created different amounts and structural complexities of emergent vegetation and submerged detritus (Neckles 1990, Gray et al. 1999). Detritus is an important component of aquatic food webs and may be associated with invertebrate biomass and diversity (Murkin et al. 1982, Gray et al. 1999, De Szalay and Resh 2000). Voigts (1976) reported that abundance of aquatic invertebrates differed with amount of floating and submerged vegetation and was greatest when submerged and emergent vegetation were highly interspersed. Standing and toppled detritus in control plots may have increased habitat complexity and invertebrate diversity and abundance. However, small biological effect sizes among treatments (<0.8 kg/ha) may have been influenced by invertebrates moving among treatment plots within experimental wetlands. However, De Szalay and Resh (2000) erected barriers between differently manipulated

vegetation in brackish marshes in California and reported rapid colonization by insects and similar patterns of abundance among their treatments of vegetation.

Invertebrates comprised a small portion (<1% dry mass) of potential waterbird foods in my experimental plots and abundances were less than in forested wetlands and flooded rice fields in the MAV (Wehrle et al. 1995, Manley et al. 2004, Batema et al. 2005). Although aquatic invertebrate abundance was less than seeds and tubers, invertebrates contribute to protein demands of wintering waterfowl in late winter and may be an important diet component (Heitmeyer 1988, Reid et al. 1989, Reinecke et al. 1989). In late winter, waterfowl may begin to consume a greater proportion of invertebrates compared to seeds to meet nutritional requirements (Miller 1987, Heitmeyer 1988, Ballard et al. 2004). Other researchers have reported that increased flooding duration in seasonal wetlands results in increased invertebrate colonization and reproduction rates throughout winter (Batzer et al. 1993, Anderson and Smith 2000, Manley et al. 2004) and greater biomass in spring (Davis and Smith 1998). Invertebrate abundances were greatest in late winter in my study wetlands (Table 1.3) which corresponds to increased use of invertebrates by dabbling ducks (Miller 1987, Heitmeyer 1988, Ballard et al. 2004, Baldassarre and Bolen 2006). Continual invertebrate reproduction in winter may replace individuals consumed by waterfowl, thus sustaining invertebrate abundance during winter. Nonetheless, dabbling ducks occurring commonly in my experimental wetlands consume mostly seeds during winter (Glasgow and Bardwell 1962, Miller 1987, Gruenhagen and Fredrickson 1990) and even continual

invertebrate reproduction may not have accounted for significant increases of food biomass for ducks.

A possible explanation for lesser overall invertebrate abundance in moist-soil wetlands compared to other wetlands may be dynamic seasonal hydrology. Managed moist-soil wetlands are typically completely dewatered in spring and summer to allow moist-soil plants to grow (Fredrickson and Taylor 1982, Anderson and Smith 2000). Therefore, invertebrates must recolonize wetlands in fall and winter or survive drawdown periods by aestivating or other adaptations (Wiggins 1980, Anderson et al. 1999, Dietz-Brantley et al. 2002). Long drawdowns during summer may be detrimental to invertebrate survival (Kadlec 1962, Nelson and Kadlec 1984). Managed moist-soil wetlands often are wholly or partially surrounded by levees which may temporarily promote retention of soil moisture after precipitation events and result in frequent wet-dry cycles. While wet and dry periods are both important for invertebrate production (Neckles et al. 1990), frequent and short hydroperiods may reduce invertebrate abundance and production (Nelson and Kadlec 1984, Whiles and Golowitz 2001). Periodic soil disturbance also may result in reduced survival of aestivating invertebrates (De Szalay and Resh 1997, 2000; Anderson and Smith 2000, 2004; Dietz-Brantley et al. 2002). Additionally, I did not remove benthic invertebrates from core samples as few remained intact following dissolution of soils and sieving. Therefore, my invertebrate abundance estimates are based on nektonic invertebrates and benthic invertebrates occurring at or near the soil surface and may be conservative.

Another explanation for comparatively low invertebrate biomass is potential weight loss from freezing samples. Murkin et al. (1994) indicated freezing results in weight loss which cannot be standardized readily because rates vary among taxa (Salonen and Sarvala 1985). Martin (2001) reported 11–21% weight loss in frozen gastropods whereas Salonen and Sarvala (1985) reported 10–54% carbon loss of several aquatic invertebrate taxa. Because of the volume of invertebrate samples collected, I was unable to process samples in the field or use formalin as a recommended preservative (Salonen and Sarvala 1985). Thus, my invertebrate samples may have experienced some weight loss due to freezing; however, loss of up to 50% of dry mass still would not produce a biologically meaningful increase in invertebrate abundance compared to seed estimates. Furthermore, because samples were processed in random order, any other biases were likely uniform among treatments. My results are likely comparable with other studies that also froze invertebrate samples before processing (Gray et al. 1999, Anderson and Smith 2000) and provide an index of invertebrate abundance relative to fall disking, mowing, or no manipulation of moist-soil vegetation in the MAV.

Management Implications

Because seeds, tubers, and invertebrates were most abundant in control plots, decomposition was least in control plots, and ducks were most abundant in mowed plots during winter, I recommend partial autumn mowing of robust vegetation in moist-soil wetlands to create interspersions of emergent vegetation and open water after flooding and preserve waterfowl foods. Managers may attempt to create hemi-marsh configurations with approximately equal interspersions of open water and emergent

vegetation which is attractive to breeding and nonbreeding waterfowl (Kaminski and Prince 1981, Smith et al. 2004). Partial autumn mowing may provide foraging and resting areas and potentially increase accessibility of seeds, tubers, and invertebrates in early winter; dabbling duck abundance; and waterbird diversity (Kaminski and Prince 1981, DuBowy 1988, Anderson and Smith 1999, Smith et al. 2004). Patches of emergent vegetation not mowed in late autumn may serve as dense cover for secretive or roosting waterbirds and substrate for algae and invertebrates (Gray et al. 1999). I cannot suggest a threshold stem density or plant height when autumn manipulation may be necessary because plant senescence and toppling depend on many factors (e.g., morphology, taxa, water depth, weather events, etc.). However, mowing may be considered when vegetation grows ≥ 1 m tall, is continuous and dense, and would protrude above water after wetlands are shallowly flooded (≤ 16 cm) and obscure water visibility of waterbirds and possibly constrain landing. Furthermore, unlike fall manipulation of unharvested agricultural crops which create “baited” conditions when hunted for migratory waterfowl, natural moist-soil and naturalized vegetation can be hunted legally after manipulation (Code of Federal Regulations 2009). Further research should be conducted to determine if other methods of creating hemi-marsh configurations (e.g., burning, rolling, crushing, etc.) benefit waterfowl and what factors other than food availability determine GUD and influence waterfowl use of moist-soil wetlands.

LITERATURE CITED

- Amano, T., K. Ushiyama, G. Fujita, and H. Higuchi. 2006. Foraging patch selection and departure by non-omniscient foragers: a field example in white-fronted geese. *Ethology* 112:544–553.
- Anderson, C. R., B. L. Peckarsky, and S. A. Wissinger. 1999. Tinajas of southeastern Utah: invertebrate reproductive strategies and the habitat template. Pages 791–810 *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. John Wiley and Sons, New York, USA.
- Anderson, J. T., and L. M. Smith. 1999. Carrying capacity and diel habitat use of managed playa wetlands by non-breeding waterbirds. *Wildlife Society Bulletin* 27:281–291.
- Anderson, J. T., and L. M. Smith. 2000. Invertebrate response to moist-soil management of playa wetlands. *Ecological Applications* 10:550–558.
- Anderson, J. T., and L. M. Smith. 2004. Persistence and colonization strategies of playa wetlands invertebrates. *Hydrobiologia* 513:77–86.
- Arengo, F. A., and G. A. Baldassarre. 1995. Effects of food density on the behavior and distribution of nonbreeding American flamingos in Yucatan, Mexico. *Condor* 97:325–334.
- Arzel, C., and J. Elmberg. 2004. Time use, foraging behavior and microhabitat use in a temporary guild of spring-staging dabbling ducks (*Anas* spp.). *Ornis Fennica* 81:157–168.
- Baldassarre, G. A., and E. G. Bolen. 1984. Field feeding ecology of waterfowl wintering on the southern high plains of Texas. *Journal of Wildlife Management* 48:63–71.
- Baldassarre, G. A., and E. G. Bolen. 2006. *Waterfowl ecology and management*. Second edition. Krieger, 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.
- Batema, D. L., R. M. Kaminski, and P. A. Magee. 2005. Wetland invertebrate communities and management of hardwood bottomlands in the Mississippi Alluvial Valley. Pages 173–199 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Barney, E. S. 2008. Change in availability and nutritional quality of post-harvest waste corn on waterfowl staging areas near Long Point, Ontario. Thesis, University of Western Ontario, London, Canada.
- Batzer, D. P., M. McGee, and V. H. Resh. 1993. Characteristics of invertebrates consumed by mallards and prey response to wetlands flooding schedules. *Wetlands* 13:41–49.
- Bellrose, F. C., and H. G. Anderson. 1943. Preferential rating of duck food plants. *Illinois Natural History Survey Bulletin* 22:417–433.
- Bohm, W. 1979. *Methods of studying root systems*. Springer-Verlag, Berlin, Germany.
- Boulton, M. A. D. 2005. Spatio-temporal patterns of geomorphic adjustment in channelized tributary streams of the Lower Hatchie River Basin, West Tennessee. Dissertation, University of Tennessee, Knoxville, USA.
- Brasher, M. G. 2010. Duck use and energetic carrying capacity of actively and passively managed wetlands in Ohio during autumn and spring migration. Dissertation, The Ohio State University, Columbus, USA.
- Brasher, M. G., 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.
- Brown, J. S., and B. P. Kotler. 2007. Foraging and ecology of fear. Pages 437–480 *in* *Foraging behavior and ecology*, D. W., Stephens, J. S. Brown, and R. C., Ydenberg, editors. University of Chicago Press, Chicago, Illinois, USA.
- Bryson, C. T., and M. S. DeFelice. 2009. *Weeds of the south*. University of Georgia Press, Athens, USA.

- Canadian Wildlife Service and U.S. Fish and Wildlife Service. 1986. North American waterfowl management plan. Canadian Wildlife Service and U.S. Fish and Wildlife Service. Washington, D.C., USA.
- Cheal, F., J. A. Davis, J. E. Grows, J. S. Bradley, and F. H. Whittles. 1993. The influence of sampling method on the classification of wetland invertebrate communities. *Hydrobiologia* 257:47–56.
- Code of Federal Regulations. 2009. Migratory Bird Hunting. Title 50, Part 20.21. U. S. National Archives and Records Administration, College Park, Maryland, USA.
- Cross, D., and P. Vohs, editors. 1988. Waterfowl management handbook. U. S. Fish and Wildlife Service, Fort Collins, Colorado, USA.
- Davis, C. A., and L. M. Smith. 1998. Ecology and management of migrant shorebirds in the playa lakes region of Texas. *Wildlife Monographs* 140:1–45.
- De Szalay, F. A., and V. H. Resh. 1997. Responses of wetland invertebrates and plants important in waterfowl diets to burning and mowing of emergent vegetation. *Wetlands* 17:149–156.
- De Szalay, F. A., and V. H. Resh. 2000. Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. *Freshwater Biology* 45:295–308.
- Dietz-Brantley, S. E., B. E. Taylor, D. P. Batzer, and A. E. DeBiase. 2002. Invertebrates that aestivate in dry basins of Carolina bay wetlands. *Wetlands* 22:767–775.
- Dosskey, M. G. 2001. Toward quantifying water pollution abatement in response to installing buffers on cropland. *Environmental Management* 28:577–598.
- DuBowy, P. J. 1988. Waterfowl communities and seasonal environments: temporal variability in interspecific competition. *Ecology* 69:1439–1453.
- Euliss, N. H., and S. W. Harris. 1987. Feeding ecology of northern pintails and green-winged teal wintering in California. *Journal of Wildlife Management* 51:724–732.
- Fleming, K. S. 2010. Effects of management and hydrology on vegetation, winter waterbird use, and water quality on Wetlands Reserve Program lands, Mississippi. Thesis, Mississippi State University, Mississippi State, USA.

- Foster, M. A., M. J. Gray, and R. M. Kaminski. 2010. Agricultural seed biomass for migrating and wintering waterfowl in the southeastern United States. *Journal of Wildlife Management* 74:489–495.
- Fredrickson, L. H. 2005. Contemporary bottomland hardwood systems: structure, function and hydrologic condition resulting from two centuries of anthropogenic activities. Pages 19–35 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally-flooded impoundments for wildlife. U. S. Fish and Wildlife Service Resource Publication 148, Washington, D.C., USA.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72:329–346.
- Glasgow, L. L., and J. L. Bardwell. 1962. Pintail and teal foods in south Louisiana. *Proceedings of the Annual Conference of Southeast Association of Game and Fish Commissioners* 16:175–184.
- Gordon, D. H., B. T. Gray, R. D. Perry, M. B. Prevost, T. H. Strange, and R. K. Williams. 1989. South Atlantic coastal wetlands. Pages 57–92 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, USA.
- Gray, M. J., R. M. Kaminski, G. Weerakkody, B. D. Leopold, and K. C. Jensen. 1999. Aquatic invertebrate and plant responses following mechanical manipulations of moist-soil habitat. *Wildlife Society Bulletin* 27:770–779.
- 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.
- Greer, D. M., B. D. Dugger, K. J. Reinecke, and M. J. Petrie. 2009. Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 73:1125–1133.
- Gruenhagen, N. M., and L. H. Fredrickson. 1990. Food use by migratory female mallards in northwest Missouri. *Journal of Wildlife Management* 54:622–626.

- Hair, J. D. 1980. Measurement of ecological diversity. Pages 269–275 in Schemnitz, S. D., editor. Fourth edition. Wildlife management techniques manual. The Wildlife Society, Washington D.C., USA.
- Havens, J. H., R. M. Kaminski, J. B. Davis, and S. K. Riffell. 2009. Winter abundance of waterfowl and waste rice in managed Arkansas rice fields. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 63:41–46.
- Havera, S. P. 1999. Waterfowl of Illinois: status and management. Illinois Natural History Survey Special Publication 21.
- Heitmeyer, M. E. 1988. Protein costs of prebasic molt in female mallards. Condor 90:263–266.
- Heitmeyer, M. E., D. P. Connelly, and R. L. Pederson. 1989. The Central, Imperial, and Coachella Valleys of California. Pages 475–505 in L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, USA.
- Jenkins, W. A., B. C. Murray, R. A. Kramer, and S. P. Faulkner. 2010. Valuing ecosystem services from wetlands restoration in the Mississippi Alluvial Valley. Ecological Economics 69:1051–1061.
- Kadlec, J. A. 1962. Effects of a drawdown on a waterfowl impoundment. Ecology 43:267–281.
- 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.
- Kaminski, R. M., and H. H. Prince. 1981. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. Journal of Wildlife Management 45:1–15.
- Kaminski, R. M., and H. H. Prince. 1984. Dabbling duck-habitat associations during spring in Delta Marsh, Manitoba. Journal of Wildlife Management 48:37–50.
- Keck, B. P., and D. A. Etnier. 2005. Distributional changes of the fishes of the Hatchie River system in western Tennessee and northern Mississippi. Southeastern Naturalist 4:597–626.

- King, S. L., J. P. Shepard, K. Ouchley, J. A. Neal, and K. Ouchley. 2005. Bottomland hardwood forests: past, present, and future. Pages 1–17 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Kostecke, R. M., L. M. Smith, and H. M. Hands. 2005. Macroinvertebrate response to cattail management at Cheyenne Bottoms, Kansas, USA. *Wetlands* 25:758–763.
- Kröger, R., M. M. Holland, M. T. Moore, and C. M. Cooper. 2007. Plant senescence: a mechanism for nutrient release in temperate agricultural wetlands. *Journal of Environmental Pollution* 146:114–119.
- Kröger, R., M. M. Holland, M. T. Moore, and C. M. Cooper. 2008. Agricultural drainage ditches mitigate phosphorus loads as a function of hydrological variability. *Journal of Environmental Quality* 37:107–113.
- Kross, J., R. M. Kaminski, K. J. Reinecke, and A. T. Pearse. 2008*a*. Conserving waste rice for wintering waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:1383–1387.
- Kross, J., R. M. Kaminski, K. J. Reinecke, E. J. Penny, and A. T. Pearse. 2008*b*. Moist-soil seed abundance in managed wetlands in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:707–714.
- Krull, J. N. 1970. Aquatic plant-macroinvertebrate associations and waterfowl. *Journal of Wildlife Management* 34:707–718.
- Legagneux, P., C. Blaize, F. Latraube, J. Gautier, and V. Bretagnolle. 2009. Variation in home-range size and movements of wintering dabbling ducks. *Journal of Ornithology* 150:183–193.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. *SAS for Mixed Models*. Second edition. SAS Institute, Inc. Cary, North Carolina, USA.
- Linz, G. M., D. C. Blixt, D. L. Bergman, and W. J. Bleier. 1996. Response of ducks to glyphosate-induced habitat alterations in wetlands. *Wetlands* 16:38–44.
- Loesch, C. R., K. J. Reinecke, and C. K. Baxter. 1994. Lower Mississippi Valley Joint Venture evaluation plan. North American Waterfowl Management Plan, U. S. Fish and Wildlife Service, Vicksburg, Mississippi, USA.

- Lyons, N. I. 1981. Comparing diversity indices based on counts weighted by biomass or other importance values. *The American Naturalist* 118:438–442.
- Lyons, J., S. T. Trimble, and L. K. Paine. 2000. Grass versus trees: managing riparian areas to benefit streams of central North America. *Journal of the American Water Resources Association* 36:919–930.
- 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.
- Manley, S. W., R. M. Kaminski, P. B. Rodrigue, J. C. Dewey, S. H. Schoenholtz, P. D. Gerard, and K. J. Reinecke. 2009. Soil and nutrient retention in winter-flooded rice fields with implications for watershed management. *Journal of Soil and Water Conservation* 64:173–182.
- Marquez, C., C. Cambardella, T. Isenhardt, and R. Schultz. 1998. Assessing soil quality in a riparian buffer by testing organic matter fractions in central Iowa, USA. *Agroforestry Systems* 44:133–140.
- Martin, P. R. 2001. Effect of freezing preservation on dry weights of freshwater snails. *Journal of Molluscan Studies* 67:124–128.
- McCafferty, W. P. 1998. *Aquatic entomology: the fishermen's and ecologists' illustrated guide to insects and their relatives*. Jones and Bartlett Publishers, Sudbury, Massachusetts, USA.
- Michael, P. W. 1983. Taxonomy and distribution of *Echinochloa* species with special reference to their occurrence as weeds of rice. Pages 291–306 in *Proceedings of the Conference on Weed Control in Rice*, International Rice Research Institute, Los Baños, Laguna, Philippines.
- Miller, M. R. 1987. Fall and winter foods of northern pintails in the Sacramento Valley, California. *Journal of Wildlife Management* 51:405–414.
- Mitsch, W. J., and J. G. Gosselink. 2000. *Wetlands*. Third edition. John Wiley and Sons, New York, USA.
- Moon, J. A., and D. A. Haukos. 2008. Habitat use of female northern pintails in the playa lakes region of Texas. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 62:82–87.

- Murkin, H. R., R. M. Kaminski, and R. D. Titman. 1982. Responses by dabbling ducks and aquatic invertebrates to an experimentally manipulated cattail marsh. *Canadian Journal of Zoology* 60:2324–2332.
- Murkin, H. R., E. J. Murkin, and J. P. Ball. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. *Ecological Applications* 7:1144–1159.
- Murkin, H. R., D. A. Wrubleski, and F. A. Reid. 1994. Sampling invertebrates in aquatic and terrestrial habitats. Pages 349–369 *in* T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. The Wildlife Society, Bethesda, Maryland, USA.
- Murray, B. C., W. A. Jenkins, R. A. Kramer, and S. P. Faulkner. 2009. Valuing ecosystem services from wetlands restoration in the Mississippi Alluvial Valley. Report No. 09-02, Nicholas Institute for Environmental Policy Solutions, Duke University. <<http://www.nicholas.duke.edu/institute/msvalley.pdf>>. Accessed 14 Aug. 2010.
- Nassar, J. R., W. E. Cohen, and C. R. Hopkins. 1993. *Waterfowl habitat management handbook for the lower Mississippi Alluvial River Valley*. Mississippi State University Extension Publication 1864.
- 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, USA.
- Neckles, H. A., H. R. Murkin, and J. A. Cooper. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetlands habitats. *Freshwater Biology* 23:311–322.
- Neely, W. W. 1956. How long do duck foods last underwater? *Transactions of the North American Wildlife and Natural Resources Conference* 21:191–198.
- Nelms, K. D. 2007. *Wetland management for waterfowl: a handbook*. Mississippi River Trust, Stoneville, Mississippi, USA.
- Nelms C. O., and D. J. Twedt. 1996. Seed deterioration in flooded agriculture fields during winter. *Wildlife Society Bulletin* 24:85–88.
- Nelson, J. W., and J. A. Kadlec. 2004. A conceptual approach to relating habitat structure and macroinvertebrate production in freshwater wetlands. *Transactions of the North American Wildlife and Natural Resources Conference* 49:262–270.

- Nolet, B. A., V. N. Fuld, and M. E.C. van Rijswijk. 2006. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos* 112:353–362.
- Olmstead, V. G. 2010. Evaluation of management strategies on moist-soil seed availability and depletion on Wetland Reserve Program sites in the Mississippi Alluvial Valley. Thesis, Arkansas Tech University, Russellville, USA.
- Pearse, A. T. 2007. Design, evaluation, and applications of an aerial survey to estimate abundance of wintering waterfowl in Mississippi. Dissertation, Mississippi State University, Mississippi State, USA.
- Pennak, R. W. 1989. Freshwater invertebrates of the United States. Third edition. John Wiley and Sons, New York, USA.
- Pöysä, H. 2001. Dynamics of habitat distribution in breeding mallards: assessing the applicability of current habitat selection models. *Oikos* 94:365–373.
- Pöysä, H., J. Elmberg, K. Sjöberg, and P. Nummi. 1998. Habitat selection rules in breeding mallards (*Anas platyrhynchos*): a test of two competing hypotheses. *Oecologia* 114:283–287.
- Rehm, E. M., and G. A. Baldassarre. 2007. The influence of interspersed marsh on marsh bird abundance in New York. *Wilson Journal of Ornithology* 119:648–654.
- Reid, F. A., J. R. Kelley, Jr., T. S. Taylor, and L. H. Fredrickson. 1989. Upper Mississippi Valley-refuges and moist-soil impoundments. Pages 203–247 in L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, USA.
- Reinecke, K. J., R. C. Barkley, and C. K. Baxter. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. Pages 325–337 in M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.
- Reinecke, K. J., M. W. Brown, and J. R. Nassar. 1992. Evaluation of aerial transects for counting wintering mallards. *Journal of Wildlife Management* 56:515–525.
- Reinecke, K. J., and R. M. Kaminski. 2007. Lower Mississippi Valley Joint Venture, waterfowl working group memorandum. U.S. Fish and Wildlife Service, Vicksburg, Mississippi, 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, USA.
- Reinecke, K. J., and W. B. Uihlein. 2006. Lower Mississippi Valley Joint Venture, Waterfowl working group memorandum. U.S. Fish and Wildlife Service, Vicksburg, Mississippi, USA.
- Rewa, C. 2005. Wildlife benefits of the Wetlands Reserve Program. Pages 133–146 *in* J. B. Haufler, editor. Fish and wildlife benefits of Farm Bill conservation programs: 2000–2005 update. The Wildlife Society Technical Review 05–2, Bethesda, Maryland, USA.
- Salonen, K., and J. Sarvala. 1985. Combination of freezing and aldehyde fixation: a superior preservation method for biomass determination of aquatic invertebrates. *Fundamental and Applied Limnology* 103:217–230.
- SAS Institute, Inc. 2008. SAS® 9.2 Enhanced Logging Facilities, SAS Institute, Inc., Cary, North Carolina, USA.
- Schoenholtz, S. H., J. A. Stanturf, J. A. Allen, and C. J. Schweitzer. 2005. Afforestation of agricultural lands in the Lower Mississippi Alluvial Valley: the state of our understanding. Pages 413–431 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Schultz, R. J., Colletti, T. Isenhardt, W. Simpkins, C. Mize, and M. Thompson. 1995. Design and placement of a multi-species riparian buffer strip system. *Agroforestry Systems* 29:201–226.
- Schummer, M. L., H. M. Hagy, K. S. Fleming, J. C. Cheshier, and J. T. Callicutt. 2011. Moist-soil wetland plants of the Mississippi Alluvial Valley. University Press of Mississippi, Jackson, USA. In Press.
- Seed Images. 2008. Discover Seeds. Colorado State University. Fort Collins, USA. <<http://www.seedimages.com>>. Accessed 24 Feb. 2009.
- Smith, L. M, R. L. Pederson, and R. M. Kaminski, editors. 1989. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, Texas, USA.

- Smith, L. M., D. A. Haukos, and R. M. Prather. 2004. Avian responses to vegetative pattern in playa wetlands during winter. *Wildlife Society Bulletin* 32:474–480.
- Solberg, K. L., and K. F. Higgins. 1993. Effects of glyphosate herbicide on cattails, invertebrates, and waterfowl in South Dakota wetlands. *Wildlife Society Bulletin* 21:299–307.
- Stafford, J. D., R. M. Kaminski, K. J. Reinecke, and S. W. Manley. 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:61–69.
- Straub, J. N. 2008. Energetic carrying capacity of habitats used by spring migrating waterfowl in the Upper Mississippi and Great Lakes Region during spring migration. Thesis, The Ohio State University, Columbus, USA.
- Strickland, B. K., R. M. Kaminski, K. D. Nelms, and A. Tullos, editors. 2009. Waterfowl habitat management handbook. Mississippi State University Extension Service Publication 1864, Mississippi State, USA.
- Taylor, J. P., and L. M. Smith. 2003. Chufa management in the middle Rio Grande Valley, New Mexico. *Wildlife Society Bulletin* 31:156–162.
- Thorp, J. H., and A. P. Covich, editors. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, California, USA.
- Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29:308–330.
- Twedt, D. J., and C. O. Nelms. 1999. Waterfowl density on agricultural fields managed to retain water in winter. *Wildlife Society Bulletin* 27:924–930.
- Uihlein, W. B. 2000. Extent and distribution of waterfowl habitat managed on private lands in the Mississippi Alluvial Valley. Dissertation, Mississippi State University, Mississippi State, USA.
- van Gils, J. A., P. Edelaar, G. Escudero, and T. Piersma. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104:197–204.
- Voigts, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. *American Midland Naturalist* 95:313–322.
- Voshell, J. R., Jr. 2002. A guide to common freshwater invertebrates of North America. McDonald and Woodward Publishing Company, Blacksburg, Virginia, USA.

- Vymazal, J. 2007. Removal of nutrients in various types of constructed wetlands. *Science of the Total Environment* 380:48–65.
- Wehrle, B. W., R. M. Kaminski, B. D. Leopold, and W. P. Smith. 1995. Aquatic invertebrate resources in Mississippi forested wetlands during winter. *Wildlife Society Bulletin* 23:774–783.
- Weller, M. W., and L. H. Fredrickson. 1974. Avian ecology of a managed glacial marsh. *Living Bird* 12:269–291.
- Whiles, M. R., and B. S. Golowitz. 2001. Hydrologic influences on insect emergence production from central Platte River wetlands. *Ecological Applications* 11:1829–1842.
- Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv für Hydrobiologie Supplement* 58:197–206.
- Yabuno, T. 1983. Biology of *Echinochloa* species. Pages 307–318 in *Proceedings of the conference on weed control in rice*, International Rice Research Institute, Los Baños, Laguna, Philippines.
- Zar, J. H. 2009. *Biostatistical analysis*. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Table 1.1. Mean (\bar{x} , SE) abundance (ducks/ha/site/week) of mallards (*Anas platyrhynchos*) and other dabbling ducks (Anatini) and Shannon's diversity index (H') for all waterbirds and comparisons^a of unmanipulated (control), disked, and mowed plots (n) during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

Taxon / Diversity	Control			Disk			Mow		
	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE
Mallards	21	19.1A	3.2	21	36.3B	6.2	20	36.9B	5.1
Other dabbling ducks	21	9.1A	2.6	21	25.3B	2.6	20	24.7B	2.8
H'	21	0.13A	0.04	21	0.21B	0.04	20	0.22B	0.04

^a Means within rows followed by unlike capital letters differ ($P < 0.05$) by Tukey pairwise multiple comparison test.

Table 1.2. Mean (\bar{x} , SE) combined seed and tuber abundances (kg[dry]/ha), excluding taxa not reportedly consumed by dabbling ducks (Chapter II), and comparisons^a of unmanipulated (control), lightly disked, and mowed plots (n) during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

Survey	Control			Disk			Mow		
	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE
November	22	750.7A	105.7	22	509.8B	66.3	20	709.7A	132.2
December	19	351.7A	40.0	20	389.2A	46.4	19	382.2A	61.8
January	20	331.5A	54.6	20	317.1A	33.3	19	282.7A	38.1
February	21	257.7A	25.3	21	264.6A	22.2	19	253.8A	27.8

^aMeans within rows followed by unlike capital letters differ ($P < 0.05$) by Tukey pairwise multiple comparison test.

Table 1.3. Mean (\bar{x} , SE) abundances (kg[dry]/ha) of invertebrate taxa and Shannon's index of diversity by order (H') and comparisons^a of unmanipulated (control), lightly disked, and mowed plots (n) during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

Month	Class	Order	Control			Disk			Mow		
			n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE
November	Total		13	2.54	0.71	13	0.92	0.13	12	1.27	0.46
	Arachnida			0.04	0.02		tr ^d	0		0.01	0.01
		Araneae		0.04	0.02		0	0		0.01	0.01
		Ixodida		0	0		0	0		0	0
	Branchiopoda			0	0		tr	0		0	0
		Anostraca		0	0		0	0		0	0
		Cladocera		0	0		0	0		0	0
	Clitellata	Oligocheata ^b		0	0		0.01	0		0.02	0.01
	Gastropoda	Pulmonata ^c		0.91	0.49		0.16	0.08		0.38	0.26
	Insecta			0.30	0.11		0.31	0.09		0.19	0.07
		Coleoptera		0.22	0.11		0.09	0.05		0.12	0.06
		Diptera		0.01	0.01		0.03	0.02		0.01	0
		Hemiptera		0.04	0.01		0.14	0.05		0.05	0.02
		Hymenoptera		0.01	0		0.01	0.01		0.01	0
		Lepidoptera		tr	0		tr	0		tr	0
		Odonata		0.02	0.01		0.02	0.02		tr	0

Table 1.3. Continued.

		Orthoptera	0.00	0.00		0.02	0.01		0.00	0.00	
		Plecoptera	0	0		0	0		0	0	
	Malacostraca		1.04	0.49		0.36	0.13		0.53	0.35	
		Amphipoda	0.03	0.02		0.03	0.02		0.01	0.00	
		Decapoda	0.26	0.16		0.13	0.08		0.24	0.22	
		Isopoda	0.75	0.36		0.20	0.09		0.28	0.15	
	Maxillopoda	Eucopepoda	tr	0		0	0		0	0	
	Ostracoda	Podocopida	0.17	0.12		0.06	0.03		0.11	0.08	
	Other		0.10	0.03		0.03	0.01		0.04	0.02	
		Unknown	0.08	0.02		0.02	0.01		0.03	0.01	
		Vertebrates	0.02	0.01		0.01	0.01		0.01	0.01	
	H'		13	0.34	0.03	13	0.27	0.03	12	0.22	0.02
December	Total		15	1.56	0.32	15	0.81	0.24	14	1.02	0.32
	Arachnida			tr	0		0	0		tr	0
		Araneae		tr	0		0	0		tr	0
		Ixodida		0	0		0	0		0	0
	Branchiopoda		0.08	0.04		0.08	0.03		0.09	0.03	
		Anostraca		0	0		0.03	0.03		0.03	0.03
		Cladocera		0.08	0.04		0.05	0.02		0.06	0.02
	Clitellata	Oligocheata ^b		tr	0		tr	0		0	0
	Gastropoda	Pulmonata ^c		0.32	0.13		0.08	0.03		0.08	0.04
	Insecta			0.18	0.12		0.08	0.02		0.07	0.02

Table 1.3. Continued.

		Coleoptera	0.12	0.10		0.01	0		0.01	0	
		Diptera	tr	0		tr	0		tr	0	
		Hemiptera	0.03	0.01		0.06	0.02		0.05	0.02	
		Hymenoptera	tr	0		0	0		tr	0	
		Lepidoptera	0	0		0	0		tr	0	
		Odonata	0.01	0.00		0.01	0.00		0.01	0.00	
		Orthoptera	0.02	0.02		0	0		0	0	
		Plecoptera	0	0		0	0		0	0	
	Malacostraca		0.72	0.29		0.41	0.23		0.63	0.32	
		Amphipoda	0.04	0.02		0.03	0.01		0.03	0.01	
		Decapoda	0.25	0.12		0.14	0.11		0.25	0.15	
		Isopoda	0.42	0.19		0.24	0.12		0.35	0.18	
	Maxillopoda	Eucopepoda	0.01	0		0.02	0.01		0.01	0.01	
	Ostracoda	Podocopida	0.22	0.10		0.13	0.07		0.12	0.06	
	Other		0.01	0.01		0.01	0		0.02	0.01	
		Unknown	0.01	0.01		0.01	0		0.02	0.01	
		Vertebrates	0	0		0	0		0	0	
	H'		15	0.35	0.02	15	0.26	0.02	14	0.26	0.02
January	Total		16	0.84	0.21	16	0.45	0.09	15	0.77	0.30
	Arachnida			tr	0		0	0		tr	0
		Araneae		tr	0		0	0		tr	0
		Ixodida		0	0		0	0		0	0

Table 1.3. Continued.

Branchiopoda		0.06	0.03	0.05	0.02	0.04	0.01
	Anostraca	0.00	0.00	0.00	0.00	0.01	0.01
	Cladocera	0.06	0.03	0.05	0.02	0.04	0.01
Clitellata	Oligocheata ^b	0	0	0	0	0	0
Gastropoda	Pulmonata ^c	0.04	0.02	0.04	0.02	0.05	0.03
Insecta		0.04	0.01	0.06	0.02	0.04	0.02
	Coleoptera	0.01	0	tr	0	0	0
	Diptera	0.01	0	0	0	0	0
	Hemiptera	0.02	0.01	0.04	0.02	0.04	0.01
	Hymenoptera	tr	0	0	0	0	0
	Lepidoptera	0	0	0	0	0	0
	Odonata	tr	0	tr	0	tr	0
	Orthoptera	0	0	0	0	0	0
	Plecoptera	0	0	0	0	0	0
Malacostraca		0.63	0.24	0.26	0.10	0.56	0.30
	Amphipoda	0.05	0.02	0.03	0.01	0.04	0.02
	Decapoda	0.15	0.10	0.08	0.05	0.20	0.12
	Isopoda	0.44	0.18	0.15	0.07	0.33	0.18
Maxillopoda	Eucopepoda	0.01	0.00	0.01	0	0.01	0
Ostracoda	Podocopida	0.05	0.03	0.03	0.01	0.05	0.03
Other		0.01	0.01	0	0	0	0
	Unknown	0.01	0	tr	0	tr	0
	Vertebrates	tr	0	0	0	0	0

Table 1.3. Continued.

	H'	16	0.33	0.03	16	0.27	0.03	15	0.28	0.02
February	Total	17	2.23	0.58	17	1.48	0.67	16	1.22	0.44
	Arachnida		tr	0		0	0		tr	0
	Araneae		tr	0		0	0		tr	0
	Ixodida		0	0		0	0		0	0
	Branchiopoda		0.05	0.03		0.04	0.03		0.06	0.05
	Anostraca		0	0		0	0		0.02	0.02
	Cladocera		0.05	0.03		0.04	0.03		0.05	0.04
	Clitellata									
	Oligocheata ^b		tr	0		0	0		tr	0
	Gastropoda									
	Pulmonata ^c		0.16	0.06		0.08	0.03		0.06	0.02
	Insecta		0.35	0.24		0.15	0.05		0.11	0.03
	Coleoptera		0.02	0.01		0.01	0.01		0.02	0.02
	Diptera		0.01	0		0.01	0		0.01	0
	Hemiptera		0.04	0.02		0.11	0.05		0.06	0.02
	Hymenoptera		tr	0		0	0		tr	0
	Lepidoptera		0	0		0	0		0	0
	Odonata		0.27	0.24		0.02	0.01		0.02	0.01
	Orthoptera		0	0		0	0		0	0
	Plecoptera		tr	0		0	0		0	0
	Malacostraca		1.52	0.57		1.17	0.62		0.95	0.42

Table 1.3. Continued.

		Amphipoda	0.18	0.05		0.10	0.02		0.09	0.03	
		Decapoda	0.33	0.15		0.75	0.61		0.14	0.08	
		Isopoda	1.01	0.40		0.32	0.14		0.71	0.34	
	Maxillopoda	Eucopepoda	0.01	0		0.01	0		0.01	0	
	Ostracoda	Podocopida	0.12	0.08		0.03	0.02		0.02	0.01	
	Other		0.03	0.01		0.01	0.01		0.02	0.01	
		Unknown	0.02	0.01		0.01	0		0.01	0	
		Vertebrates	tr	0		0.01	0		0.01	0.01	
	H'		17	0.36	0.02	17	0.27	0.02	16	0.23	0.02
Nov. - Feb.	Combined		61	1.79A	0.37	61	0.91B	0.21	57	1.06B	0.11
	H'		61	0.34A	0.01	61	0.26B	0.01	57	0.25B	0.01

^aMeans within rows followed by unlike capital letters differ ($P < 0.05$) by Tukey pairwise multiple comparison test.

^bOligocheata is typically used taxonomically as a subclass of Clitellata. However, there is little agreement regarding taxonomic grouping of Phylum Annelida and taxonomic Orders are presently not available (Thorp and Covich 2001).

^cPulmonata is an informal group, but was previously classified as an Order and contains families Physidae and Planorbidae which were common in samples (Pennak 1989, Thorp and Covich 2001).

^d“tr” indicates that there were trace amounts (<0.01 kg [dry] /ha) of mass present.

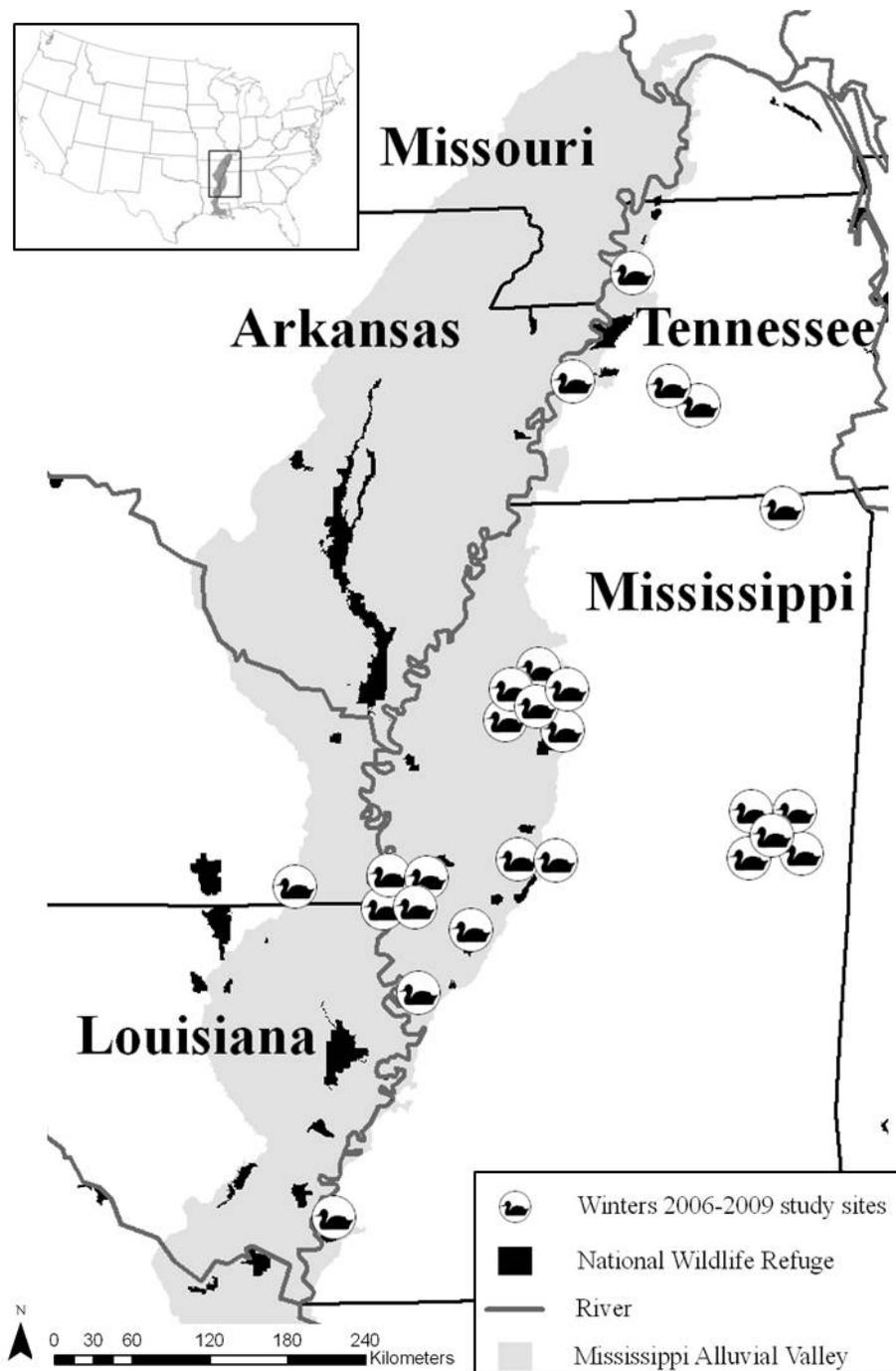


Figure 1.1. Locations of 26 moist-soil wetlands (study sites) sampled during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

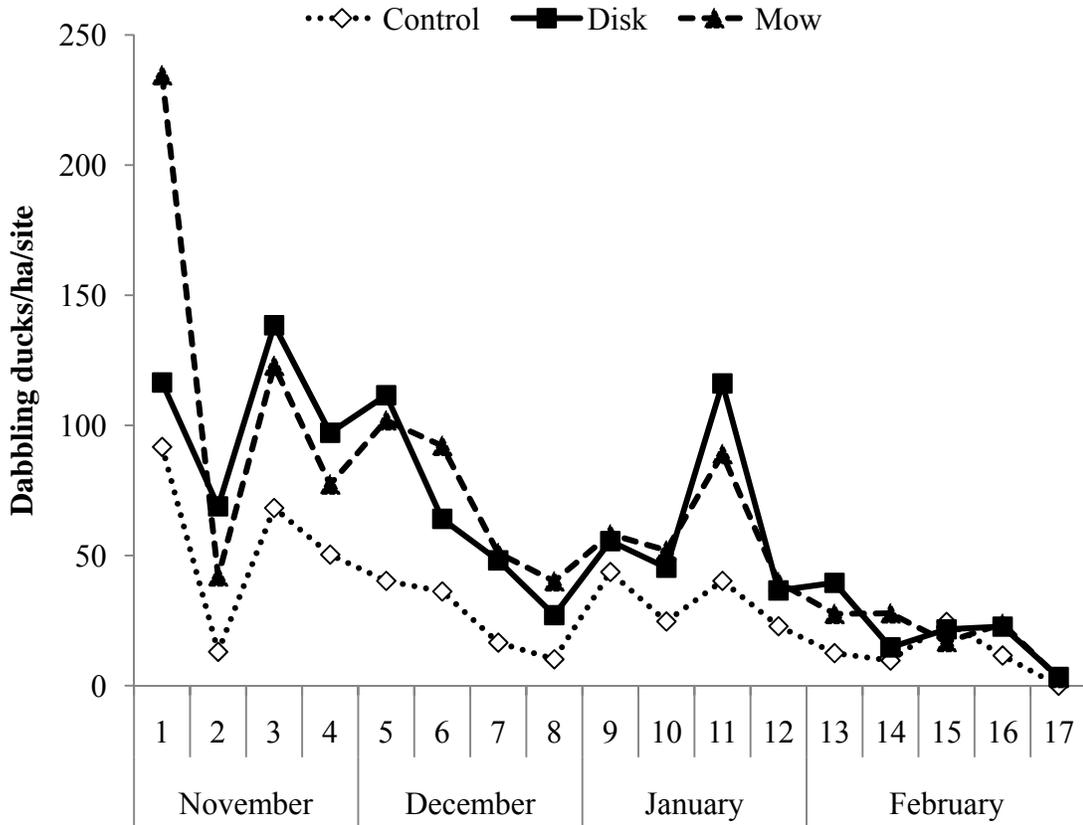


Figure 1.2. Mean dabbling duck abundance in unmanipulated (control), lightly disked, and mowed plots ($n = 62$) in moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

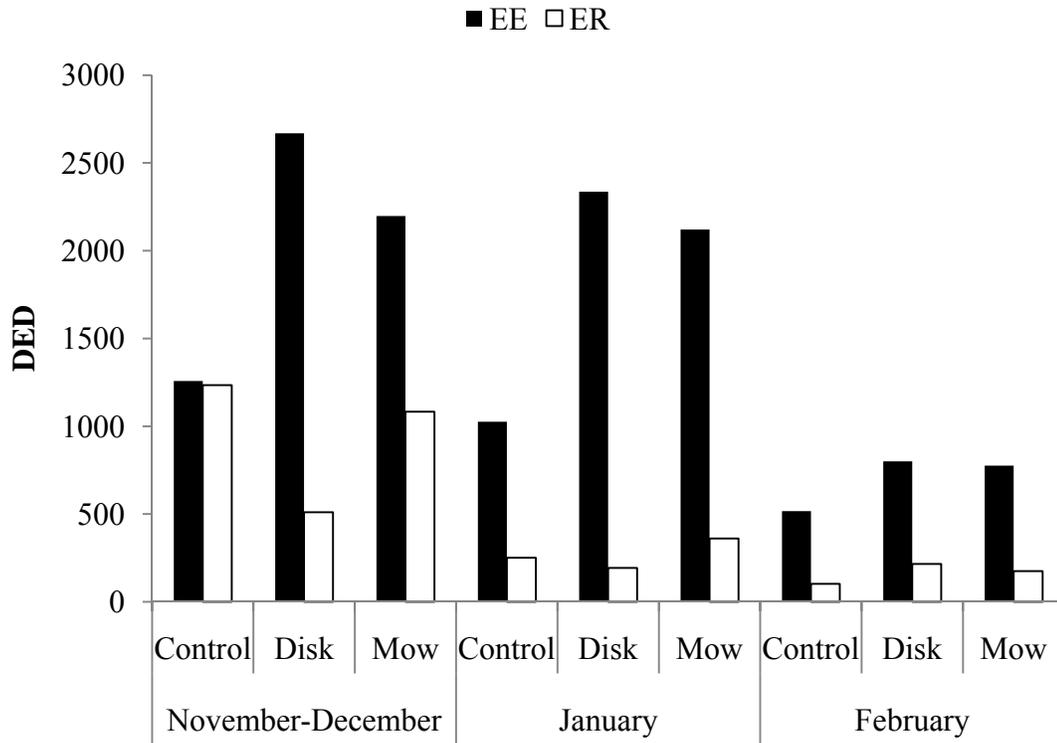


Figure 1.3. Existence energy (EE) of dabbling ducks for one day (Anatini; DED) and energy removed (ER) from unmanipulated (control), lightly disked, and mowed plots ($n = 62$) in moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

CHAPTER II
SEED REDUCTIONS BY WATERFOWL AND DECOMPOSITION DURING
WINTER IN MOIST-SOIL WETLANDS IN THE
MISSISSIPPI ALLUVIAL VALLEY

Scientists and conservation planners estimate energetic carrying capacity for wintering waterfowl in North America and seek to provide sufficient foraging habitat (Reinecke et al. 1989, Miller and Eadie 2006). Currently, conservation planners in some wintering regions assume food energy limits carrying capacity and influences regional abundance of migrating and wintering waterfowl (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986, Loesch et al. 1994, Williams et al. 1999). The food-limitation hypothesis assumes increasing available energy in wintering habitat will support additional waterfowl and possibly influence population demographics (Heitmeyer and Fredrickson 1981, Sutherland and Anderson 1993, Dubovsky and Kaminski 1994, Greer et al. 2009). However, patterns of use and energetic profitability of foods (i.e., seeds and tubers) must be known to estimate carrying capacity accurately and provide sufficient waterfowl foraging habitat (Prince 1979, Reinecke et al. 1989, Taylor and Smith 2005).

Waterfowl consume a variety of natural and agronomic seeds from diverse habitats in fall and winter (Anderson 1959, Delnicki and Reinecke 1986, Combs and Fredrickson 1996, Havera 1999, Ballard et al. 2004). In winter, dabbling ducks (Anatini)

commonly use moist-soil wetlands that may contain >50 species of seeds (Fredrickson and Reid 1988, Havera 1999, Pearse 2007) with different metabolizable energy (Checkett et al. 2002, Kaminski et al. 2003, Dugger et al. 2007, Kross et al. 2008). Variable morphology and energy values among species of moist-soil seeds may influence ducks to exploit some taxa preferentially to maximize foraging efficiency (Miller 1987, Gurd 2005) or influence habitat selection (van Eerden and Munsterman 1997, Fritz et al. 2001, Klaassen et al. 2007).

Few studies of ducks have assessed preferential use (i.e., selection; Johnson 1980) of foods by comparing food use and availability (Miller 1987). Studies that adequately describe food selection of dabbling ducks by concurrently estimating food use and availability are not available in most regions and habitats used by nonbreeding waterfowl in North America (Baldassarre and Bolen 2006). Most studies conducted during fall and winter collected data from hunter-harvested ducks, analyzed foods in gizzards, or did not measure food availability, thus precluding inferences of preferential food use and selection (Swanson and Bartonek 1970, Havera 1999, Baldassarre and Bolen 2006). Basic information on food use and selection by wintering dabbling ducks is necessary before conservation planners can use estimates of potential food availability to accurately calculate carrying capacity and habitat requirements. Kross et al. (2008) presented moist-soil seed abundance estimates for the MAV, but included some seeds and tubers that may not be used by waterfowl. Inclusion of seeds not used by waterfowl in estimates of food availability may result in overestimates of carrying capacity in moist-soil wetlands.

If unbiased food use and selection studies are not available, estimates of potential food availability and taxon-specific decomposition rates can be used to determine if

dabbling ducks potentially use seed and tuber taxa during winter. By measuring seed abundance and decomposition concurrently in moist-soil wetlands, seed reduction by decomposition can be estimated and compared with actual seed and tuber abundances. Seed and tuber taxa that decline more rapidly than predicted by decomposition alone are likely being removed by predators (e.g., ducks). Therefore, information on potential seed and tuber use by dabbling ducks can be inferred without actual collection and necropsy of actively feeding waterfowl (Swanson and Bartonek 1970).

I sampled moist-soil wetlands in the MAV during winters 2006–2009 to quantify differential decline in seeds and tubers of selected moist-soil plants to estimate decomposition and possible exploitation by waterfowl. My objectives were to 1) evaluate the assumption that moist-soil seed decomposition rates are constant, 2) estimate seed decomposition rates for moist-soil seeds, 3) identify taxa likely consumed by waterfowl by comparing observed and predicted declines in seed and tuber abundances, and 4) determine effect of removing taxa likely not used as food on estimates of seed mass available to waterfowl during winter in the MAV.

Study Area

The MAV is a 10 million-ha alluvial plain of the Mississippi River stretching from southern Missouri to the gulf coast of Louisiana and is important to migrating and wintering waterfowl (Reinecke et al. 1988, 1989; Fredrickson 2005). Historically, the MAV regularly flooded from overflow of the Mississippi River and its tributaries and was composed of mature bottomland hardwood forests (King et al. 2005). Presently, approximately 70% of the MAV has been cleared for row-crop agriculture and other

human uses, and flood control along major rivers and streams has partially replaced seasonal and temporary wetlands with small permanent basins or networks of ditches that remove water rapidly (Reinecke et al. 1988, 1989; Havera 1999; Fredrickson 2005; King et al. 2005; Manley et al. 2009).

I sampled 26 managed moist-soil wetlands within federal, state, and private waterfowl management complexes in Arkansas, Mississippi, and Tennessee. Most sites were located in the MAV; however, I selected 3 wetlands in eastern Mississippi within the Tombigbee River Basin and 2 wetlands in western Tennessee in the Lower Hatchie River Watershed of the Lower Mississippi River Basin because of close proximity and similar plant communities to the MAV (Boulton 2005, Keck and Etnier 2005). I selected managed moist-soil wetlands using the following criteria: 1) visual presence of continuous, robust stands of moist-soil vegetation; 2) adequate area for placement of a 2.5-ha treatment block; 3) surrounding landscape provided access to wetlands and isolation from human disturbance; and 4) availability from cooperators. I selected wetlands containing continuous stands of grasses (e.g., wild millets [*Echinochloa* spp.], panicgrass [*Panicum* spp.]), sedges (*Carex* spp., *Cyperus* spp.), and forbs (e.g., smartweeds [*Polygonum* spp.], teaweed [*Sida spinosa*]) that produce seeds and tubers consumed by waterfowl. However, wetlands also contained other plants that provided little or unknown nutritional value for waterfowl but contributed to robustness of vegetation (e.g., coffeeweed [*Sesbania herbacea*], cocklebur [*Xanthium strumarium*]; Chapter II).

Methods

Experimental Design

During falls and winters 2006–2009, I repeatedly sampled seeds and tubers in mowed, disked, and unmanipulated (control) plots in 26 moist-soil wetlands (i.e., sites; Appendix B; Chapter I, Fig. 1.1). Land managers mowed (~8–15 cm high), lightly disked (i.e., a single pass at a shallow depth), and did not manipulate vegetation (control) in 0.8-ha treatment plots within 2.5-ha blocks prior to flooding each site. Treatments were applied randomly to plots and separated by 10-m buffers of standing vegetation, and blocks were located within sanctuaries in National Wildlife Refuges, Wildlife Management Areas, and private lands. Land managers mowed and disked treatment plots in late October or early November and then flooded (3–45 cm) areas by approximately late November.

Seed and Tuber Abundances

I collected 10 soil core samples (10 cm in diameter and depth) from each treatment plot immediately after flooding but before waterfowl used wetlands, and monthly thereafter through late February (Stafford et al. 2006, Kross et al. 2008, Havens et al. 2009). To obtain core samples, I placed randomly a transect within each treatment plot and selected a random distance (0–25 m) to the first sample location. I then located each subsequent sample location at a fixed interval predetermined to span the treatment plot (Greer et al. 2007). I stored cores at -15°C until processed.

Decomposition in Experimental Plots

I estimated seed decomposition by placing 10 porous, fiberglass envelopes (30 x 30 cm; 1.3 mm aperture) containing 100 g (dry mass) of Japanese millet (*Echinochloa frumentacea*; hereafter, millet) in each treatment plot at each site immediately after flooding (Neely 1956). I was unable to obtain a mixture of harvested moist-soil seeds to estimate decomposition rates of individual taxa and used millet as a surrogate. Japanese millet is similar to naturally occurring millets and is planted commonly in wetlands managed for waterfowl (Michael 1983, Yabuno 1983, Nelms 2007, Strickland et al. 2009, Schummer et al. 2011). I placed envelopes along a transect located in the center of each treatment plot and selected randomly a distance (0–25 m) to the first sample location. After selecting the first location, I placed envelopes at fixed intervals predetermined to span each plot. I spread evenly seed across the envelopes before each was submerged and placed atop substrate and beneath vegetation. I covered envelopes with 10-mm aperture wire mesh and staked in place. I collected all envelopes in late February and stored at -15°C until processed.

Decomposition at 2-week Intervals

I also selected 7 moist-soil wetlands within the same management complexes as experimental wetlands to estimate rate of decomposition at 2-week intervals during winter 2008–2009 and determine if mean decomposition rates were constant (Greer et al. 2009, Chapter III). Selected wetlands had not been manipulated mechanically, but plots had received herbicide applications during the previous growing season (Chapter III). I placed 3 cylindrical wire exclosures (0.3-m tall x 0.5-m diameter) each containing 5 100-

g (dry mass) envelopes of millet in each of 3 transects in each wetland ($n = 9$ exclosures per wetland). I placed exclosures systematically to span the width of wetlands and spaced each transect 50–75 m apart. I removed one randomly selected envelope from each exclosure bi-weekly from mid- December 2008 to late February 2009 and stored at -15°C until processed.

Sample Processing

I processed core samples and millet envelopes in a random sequence by site and time period to account for possible bias associated with the duration samples were frozen. I thawed core samples in warm water; added a solution of 3% hydrogen peroxide (H_2O_2 ; Bohm 1979), baking soda, and water for 1–3 hours to disperse soil; and washed cores through 3 sieves (i.e., mesh sizes #50 [0.03 mm], #10[1.65 mm], and #4[4.75 mm]; Kross et al. 2008). I recovered and air dried seeds and other material from each sieve separately for 24–48 hrs. I homogenized materials retained by the small sieve (#50) and randomly selected a one-quarter subsample by mass (hereafter, small portion). Using forceps, I removed seeds and tubers from the small portion and from materials retained by the 2 large sieves (#s 4 and 10; hereafter, large portion; Kross et al. 2008). I enumerated and weighed seeds and tubers by genus or species (Seed Images 2008, Bryson and DeFelice 2009, Schummer et al. 2011). I multiplied data from the small portion by 4 and combined it with the large portions to estimate total mass per core sample (Reinecke and Hartke 2005, Kross et al. 2008).

To estimate decomposition of millet seeds, I thawed envelopes in warm water, washed seeds into a #50 sieve and rinsed thoroughly to remove inorganic and organic

matter, dried seeds at 80°C for 24–48 hrs to constant mass, and weighed seed to the nearest 0.1 mg.

Statistical Analyses

Decomposition

I evaluated the assumption that bi-weekly seed decomposition rates were constant during winter in moist-soil wetlands in the MAV. I used regression to model residual mass (dry) of millet by time period (2-week intervals) using exponential, linear, logarithmic, polynomial, and power functions in Microsoft Excel. I compared linear and curvilinear models using coefficients of determination (R^2 ; Nelms and Twedt 1996). Additionally, I modeled the decline in seed mass as a function of time period using repeated measures analysis of variance (ANOVA; PROC MIXED; SAS Institute, Inc. 2008). I designated biweekly sampling period, site, and transect as fixed effects and used sampling period as the repeated measure. I examined histograms and residual plots to ensure assumptions of analyses were met (Moser 2001, Littell et al. 2002, SAS Institute, Inc. 2008).

Comparison of Predicted and Observed Seed Abundances

I used published estimates of moist-soil seed decomposition rates (% dry mass loss / day; Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996) and observed mass estimates from core samples obtained in late November to predict mass of moist-soil seeds in December, January, and February. To account for variation between published and observed decomposition rates, I generated correction factors for each treatment plot

as a ratio of decomposition rates of millet in experimental wetlands and published values (observed % millet decline / published % millet decline; Neely 1956, Shearer et al. 1969). Nelms and Twedt (1996) did not measure millet decomposition; thus, I used rates from a congener (*E. colonum*) and assumed it decomposed similarly (Michael 1983, Yabuno 1983). Next, I multiplied correction factors by the published mean daily decomposition rates of each taxon to generate an adjusted mean daily decomposition rate. When taxon-specific mean daily decomposition rates were not available, I used rates from morphologically similar congeners. If decomposition rates from congeners were not available, I used a mean decomposition rate calculated for natural seeds ($\bar{x} = 0.189$; Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996). I multiplied the adjusted mean daily decomposition rate for each taxon by the initial seed mass to predict daily loss of mass and multiplied that product by the number of exposure days since initial sampling in November. I subtracted the latter product from the initial measure of seed mass to predict mass resulting from decomposition alone.

Next, I compared the predicted seed masses derived as described above to observed seed mass estimates from December, January, and February by converting values to percentages of the mass estimates obtained from November core samples. I removed sites that contained fewer than 4 seeds/core sample of each taxon during the first sampling period and did not analyze data from taxa that occurred at fewer than 3 sites. I also excluded *Cyperus* spp. tubers from analyses because of infrequent occurrence.

I analyzed the relative percentage of mass remaining in each seed taxon at a given sampling period using linear mixed models (PROC MIXED) with class (i.e., observed or predicted seed mass) as a fixed effect and treatment (i.e., mow, disk, or control), site, and

year as random effects. I used month (December, January, or February) as the repeated measure. I did not test for treatment effects because I adjusted predicted seed mass estimates using observed decomposition rates from each treatment plot. I examined plots of data frequency, means, variances, and residuals for each taxon. If residuals were not distributed normally, I used $\log(x+1)$, $\ln(x+1)$, or \sqrt{x} to normalize data (Littell et al. 2002, Greer et al. 2009, Zar 2009). If variances of observed and predicted mass estimates appeared heterogeneous, I specified the Kenward-Roger approximation to the degrees of freedom and used data transformations or permitted the variances to differ among expected and observed groups in the repeated statement (Moser 2001, Littell et al. 2002, SAS Institute, Inc. 2008). I modeled the response variable using the appropriate covariance structures and chose one with least AIC_c score and used restricted maximum likelihood estimation to generate parameters (Littell et al. 2002). Because the response variable (% mass remaining) incorporated measurement error, I chose an $\alpha = 0.05$. I calculated means and standard errors from untransformed data.

Occasionally, seed masses observed in December, January, or February exceeded 100% (e.g., clustervine). Because changes in seed masses were relative to November samples, abundances >100% represented measurement error from estimating seed mass from core samples (H. M. Hagy, Mississippi State University, unpublished data). As ANOVA is sensitive to increases as well as decreases in seed mass, I inferred evidence of seed removal only when significant decreases occurred ($P < 0.05$).

Effect of Non-food Taxa on Abundance Estimates

I assessed the difference between estimating seed abundances (kg/ha) using all seeds present in core samples and only taxa reported to be consumed by waterfowl. I identified seed taxa as potentially consumed by ducks based on results of previous analyses and food-use studies. I conducted a literature search to identify food-use studies of dabbling ducks collected from freshwater wetlands in the MAV or nearby locations in the Coastal Plain (Vigil et al. 2000). I adjusted seed masses using seed size-class correction factors to account for negative bias associated with core sample processing (H. M. Hagy, Mississippi State University, unpublished data) and calculated means and variances of percentage decline in seed abundance (kg[dry]/ha) using all seeds that occurred in experimental moist-soil wetlands and only those identified as waterfowl foods.

Results

Decomposition

Decomposition of millet was 8.9% (SE = 1.4, $n = 5$) per 2-week sample period and was similar among sample periods ($F_{4, 4.1} = 4.44$, $P = 0.086$) and transects ($F_{2, 37.6} = 0.04$, $P = 0.959$), but differed among sites ($F_{5, 16.8} = 8.40$, $P < 0.001$). A linear model ($R^2 = 0.99$) accounted for variation in millet decomposition as well or better than curvilinear models (Table 2.1).

Comparison of Predicted and Observed Seed Abundances

I identified 42 seed taxa in core samples, but only 21 taxa occurred with sufficient frequency to compare predicted and observed seed mass estimates. I did not analyze cocklebur (*Xanthium strumarium*) and floating primrose (*Ludwigia peploides*) as seeds often are retained within capsules during winter and are not likely consumed by waterfowl (Strader and Stinson 2005). Additionally, cocklebur and floating primrose seed capsules float and therefore may disperse among treatment plots unpredictably (H. M. Hagy, Mississippi State University, personal observation). I included coffeeweed seeds (*Sesbania herbacea*) from mowed and disked plots in analyses, but not those from control plots because coffeeweed plants often remained standing and dehisced seeds throughout winter.

Seed mass of 15 taxa declined faster than predicted by decomposition rates ($P < 0.01$; Table 2.2). For example, predicted mass of arrowhead (*Sagittaria latifolia*) seeds consistently exceeded observed mass from December – February suggesting that predators removed seeds from wetlands (Table 2.2). Dabbling ducks used experimental plots more than other waterfowl species and were observed commonly foraging in all sites and plots (Chapter I). However, morning-glory (*Ipomoea* spp.), clustervine (*Jacquemontia tamnifolia*) and coffeeweed seed mass did not decline during winter and flatsedge (*Cyperus odoratus*), spikerush (*Eleocharis* spp.), and pigweed (*Amaranthus* spp.) seed masses did not decline faster than predicted by decomposition.

Effect of Non-food Taxa on Abundance Estimates

Only 25 of 42 seed taxa in my core samples were identified previously as foods consumed by dabbling ducks in the MAV (Table 2.3). I removed 17 seed taxa that either were reported as duck foods in the literature or did not decline in my experimental wetlands more than could be explained by decomposition from analyses. Removal of these taxa decreased mass estimates by 30.9% (SE = 1.3%, $n = 264$). When I included 3 additional taxa previously reported to occur in dabbling duck diets but which did not decline faster than expected from decomposition (i.e., flatsedge, pigweed, and spikerush), seed mass was reduced by 26.8% (SE = 1.3%, $n = 264$). Most (91.9%, $n = 264$) seed mass removed from core samples was coffeeweed (47.4%), cocklebur (21.1%), floating primrose (11.9%), morning-glory (6.9%), and clustervine (4.6%).

Discussion

Data from envelopes containing millet supported the assumption of Greer et al. (2009) and findings of Nelms and Twedt (1996) that seed decomposes at a constant rate during winter in moist-soil wetlands in the MAV. Therefore, use of constant decomposition rates to predict values for winter decomposition of moist-soil seeds was justified.

I assumed that seed populations in experimental moist-soil wetlands were finite and could be estimated with adequate precision. However, several possible sources of emigration and immigration existed for seeds in winter: 1) seeds may float and disperse by water, 2) seeds may have been deposited by wind, or 3) seeds may be transported among wetlands by waterfowl (Figuerola and Green 2002, Neff and Baldwin 2005).

Most of my experimental wetlands were flooded using water pumped from underground wells and were hydrologically isolated from other above-ground water sources.

Furthermore, moist-soil seeds sink after becoming saturated with water (Chapter III) and are unlikely to refloat even if wetlands became hydrologically connected above ground during flooding events. Therefore, it is unlikely that seeds immigrated into wetlands by floating. Similarly, wind-facilitated dispersal of one of the analyzed taxa (i.e., *Cyperus odoratus*) has been shown to be limited relative to other pathways (Neff and Baldwin 2005). Several studies have demonstrated the potential for seed dispersal via digestive systems (Mueller and van der Valk 2002, Wongsriphuek et al. 2008) or on external surfaces of waterfowl (Vivian-Smith and Stiles 1994); however, number of seeds passing intact through waterfowl guts is limited (Neff and Baldwin 2005) and not likely to be a significant source of biomass relative to seed abundances in winter (Chapter I).

Furthermore, seeds deposited in wetlands because of low digestibility (e.g., *Cyperus* spp., *Ludwigia* spp.; Neff and Baldwin 2005) would not represent energy sources for waterfowl and deposition and consumption would be in equilibrium.

An additional source of variation in analyses is that estimates of seed mass from core samples often vary considerably as moist-soil seeds and tubers occur in patchy distributions (Lovvorn and Gillingham 1996, van Eerden and Munsterman 1997, Kross et al. 2008). Furthermore, subsampling during core sample processing can result in overestimation of seed abundances. For example, seed abundance estimates in December, January, and February were sometimes >100% of values observed in the late November. These disparities probably reflect measurement error resulting from subsampling and estimating seed abundances from limited numbers of core samples.

However, by excluding sites when initial seed abundances of certain taxa were low, I reduced the chance of generating abundance estimates with extreme variability. Furthermore, I allowed seed abundances to exceed 100% of the initial value to incorporate measurement error in analyses. Consequently, increases in abundance between sampling months (e.g., clustervine) provided evidence of measurement error or immigration.

During winter, 15 taxa of seeds declined faster than predicted by decomposition, suggesting that seeds were removed from wetlands by dabbling ducks. I observed numerous dabbling ducks feeding diurnally in study wetlands throughout winter, but few diving ducks (Aythini), geese, or other seed-eating waterbirds (Chapter I). As dabbling ducks frequently consume moist-soil seeds in winter (Bellrose 1980, Delnicki and Reinecke 1986; Table 2.3), I infer the disparity in observed and predicted seed decline was due to feeding ducks. I assume the 6 taxa that did not decline or declined at a rate consistent with decomposition (i.e., clustervine, coffeeweed, flatsedge, morning-glory, pigweed, spikerush) were not ingested by waterfowl in my experimental wetlands or were deposited at the same rate as removal.

Studies of winter food habits of dabbling ducks in the MAV have reported commonly consumption of spikerush and pigweed but not clustervine or coffeeweed (Table 2.3). Flatsedge seeds were reported as a “less attractive” food consumed by northern pintail (*Anas acuta*) and mallard (*A. platyrhynchos*) in coastal freshwater marshes (Dillon 1957) and occurred as a minor component of diets in other studies (e.g., Chamberlain 1959, Delnicke and Reinecke 1986). Similarly, Dillon (1959) reported morning-glory as an “unimportant” food of mallards in freshwater marshes in Louisiana,

and no other studies identified it in dabbling duck diets. No studies have reported consumption of coffeeweed seed in the MAV, and Neely (1956) indicated “little use” of this seed by ducks compared to its abundance in South Carolina wetlands. I identified no studies that reported consumption of cocklebur or floating water primrose. Strader and Stinson (2005) reported cocklebur had no food value and Fleming (2010) reported *Ludwigia* spp. had low forage quality for ducks.

When I removed seeds not reported as waterfowl foods, moist-soil seed abundance estimates from core samples were reduced by ~30%. Seeds that are not consumed by waterfowl and are included in carrying capacity estimates may bias moist-soil habitat requirements because the mass from these seeds is falsely assumed to contribute metabolizable energy of waterfowl. Reduced seed abundances in carrying capacity estimates would result in an increased need for foraging habitats to meet nutrient requirements of wintering waterfowl populations targeted by the Lower Mississippi Valley Joint Venture (LMVJV; Loesch et al. 1994). Although my experimental wetlands were not selected randomly from all seasonal herbaceous wetlands in the MAV, I sampled managed moist-soil wetlands on state, federal, and private lands in three states in the MAV. Therefore my results are likely representative of managed moist-soil wetlands in the MAV and indicate that the estimated mass of moist-soil seeds usable by waterfowl is less than the value reported by Kross et al. (2008) and presently used by the LMVJV (i.e., 556 kg/ha).

Seed consumption by waterfowl likely depends on the interaction of seed composition in wetlands and other factors such as accessibility, risk, body condition, opportunity costs of foraging, and other factors (Lovvorn and Gillingham 1996, Fritz et

al. 2001, Klaassen et al. 2007). Therefore, taxa that did not decline faster than predicted by decomposition may be only incidentally consumed by dabbling ducks and may not represent a significant source of food in managed wetlands in the MAV. I recommend comprehensive diet and food selection studies be implemented in the MAV so conservation planners can verify these results and predict more accurately waterfowl food use and habitat requirements. Failure to accurately estimate and provide sufficient foraging habitats for wintering waterfowl may influence negatively population demographics (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Dubovsky and Kaminski 1994, Loesch et al. 1994, Krapu et al. 2004).

Management Implications

I produced evidence that seed masses of clustervine, coffeeweed, flatsedge, morning-glory, pigweed, and spikerush should be removed from carrying capacity estimates. Furthermore, I determined that many seeds present in moist-soil wetlands have not been widely reported to occur in waterfowl diets and also should be removed from carrying capacity models (e.g., cocklebur, floating primrose). Assuming that my experimental wetlands were representative of moist-soil wetlands in the MAV, seed abundance estimates from Kross et al. (2008) would be reduced by 31% from 556 kg/ha to 384 kg/ha. I recommend the LMVJV remove from their models of carrying capacity the seed masses of any taxa that have not been reported to occur commonly in diets of waterfowl.

LITERATURE CITED

- Anderson, H. G. 1959. Food habits of migratory ducks in Illinois. *Illinois Natural History Survey Bulletin* 27:289–344.
- Baldassarre, G. A., and E. G. Bolen. 2006. *Waterfowl ecology and management*. Second edition. Krieger, Malabar, Florida, USA.
- Ballard, B. M., J. E. Thompson, M. J. Petrie, 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.
- Bellrose, F. C. 1980. *Ducks, geese, and swans of North America*. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bohm, W. 1979. *Methods of studying root systems*. Springer-Verlag, Berlin, Germany.
- Boulton, M. A. D. 2005. *Spatio-temporal patterns of geomorphic adjustment in channelized tributary streams of the Lower Hatchie River Basin, West Tennessee*. Dissertation, University of Tennessee, Knoxville, USA.
- Bryson, C. T., and M. S. DeFelice. 2009. *Weeds of the south*. University of Georgia Press, Athens, USA.
- Canadian Wildlife Service and U.S. Fish and Wildlife Service. 1986. *North American waterfowl management plan*. Canadian Wildlife Service and U.S. Fish and Wildlife Service. Washington, D.C., USA.
- Chamberlain, J. L. 1959. Gulf coast marsh vegetation as food of wintering waterfowl. *Journal of Wildlife Management* 23:97–10.
- 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.
- Combs, D. L., and L. H. Fredrickson. 1996. Foods used by mallards wintering in southeastern Missouri. *Journal of Wildlife Management* 60:603–610.

- Dabbert, C. B., and T. E. Martin. 2000. Diet of mallards wintering in greentree reservoirs in southeastern Arkansas. *Journal of Field Ornithology* 71:423–428.
- Delnicki, D., and K. J. Reinecke. 1986. Mid-winter food use and body weights of mallards and wood ducks in Mississippi. *Journal of Wildlife Management* 50:43–51.
- Dillon, O. W. 1957. Food habits of wild ducks in the rice-marsh transition area of Louisiana. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 12:114–119.
- Dillon, O. W. 1959. Food habits of wild mallard ducks in three Louisiana parishes. *Transactions of the North American Wildlife and Natural Resources Conference* 24:374–382.
- Dubovsky, J. A., and R. M. Kaminski. 1994. Potential reproductive consequences of winter-diet restriction in mallards. *Journal of Wildlife Management* 58:780–786.
- Dugger, B. D., M. L. Moore, R. S. Finger, and M. J. Petrie. 2007. True metabolizable energy for seeds of common moist-soil plant species. *Journal of Wildlife Management* 71:1964–1967.
- Fleming, K. S. 2010. Effects of management and hydrology on vegetation, winter waterbird use, and water quality on Wetlands Reserve Program lands, Mississippi. Thesis, Mississippi State University, Mississippi State, USA.
- Figuerola, J., and A. J. Green. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology* 47:483–494.
- Forsyth, B. 1965. December food habits of the mallard (*Anas platyrhynchos* Linn.) in the Grand Prairie of Arkansas. *Proceedings of the Arkansas Academy of Science* 19:74–78.
- Fredrickson, L. H. 2005. Contemporary bottomland hardwood systems: structure, function and hydrologic condition resulting from two centuries of anthropogenic activities. Pages 19–35 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Fredrickson, L. H., and F. A. Reid. 1988. Waterfowl use of wetland complexes. Leaflet 13.2.1 *in* D. H. Cross, editor. *Waterfowl Management Handbook*. U.S. Fish and Wildlife Service. Washington, D.C., USA.

- Fritz, H., D. Durant, and M. Guillemain. 2001. Shape and sources of variations of the functional response of wildfowl: an experiment with mallards. *Oikos* 93:488–496.
- Glasgow, L. L., and H. A. Junca. 1962. Mallard foods in southwest Louisiana. *Proceedings of the Louisiana Academy of Science* 25:63–74.
- 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* 71:1561–66.
- Greer, D. M., B. D. Dugger, K. J. Reinecke, and M. J. Petrie. 2009. Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 73:1125–1133.
- Gruenhagen, N. M., and L. H. Fredrickson. 1990. Food use by migratory female mallards in northwest Missouri. *Journal of Wildlife Management* 54:622–626.
- Gurd, D. B. 2006. Filter-feeding dabbling ducks (*Anas* spp.) can actively select particles by size. *Zoology* 109:120–126.
- Havens, J. H., R. M. Kaminski, J. B. Davis, and S. K. Riffell. 2009. Winter abundance of waterfowl and waste rice in managed Arkansas rice fields. *Proceedings of the Annual Southeastern Association of Fish and Wildlife Agencies Conference* 63:41–46.
- Havera, S. P. 1999. Waterfowl of Illinois: status and management. *Illinois Natural History Survey Special Publication* 21.
- Heitmeyer, M. E. 2006. The importance of winter floods to mallards in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:101–110.
- Heitmeyer, M. E., and L. H. Fredrickson. 1981. Do wetland conditions in the Mississippi delta hardwoods influence mallard recruitment? *Transactions of the North American Wildlife and Natural Resources Conference* 46:44–57.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- 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.
- Kaminski, R. M., and E. A. Gluesing. 1987. Density and habitat-related recruitment in mallards. *Journal of Wildlife Management* 51:141–148.

- Keck, B. P., and D. A. Etnier. 2005. Distributional changes of the fishes of the Hatchie River system in western Tennessee and northern Mississippi. *Southeastern Naturalist* 4:597–626.
- King, S. L., J. P. Shepard, K. Ouchley, J. A. Neal, and K. Ouchley. 2005. Bottomland hardwood forests: past, present, and future. Pages 1–17 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Klaassen, R. H. G., B. A. Nolet, and C. H. A. van Leeuwen. 2007. Prior knowledge about spatial pattern affects patch assessment rather than movement between patches in tactile-feeding mallard. *Journal of Animal Ecology* 76:20–29.
- Krapu, G. L., D. A. Brandt, and R. R. Cox. 2004. Less waste corn, more land in soybeans, and the switch to genetically modified crops: trends with important implications for wildlife management. *Wildlife Society Bulletin* 32:127–136.
- Kross, J., R. M. Kaminski, K. J. Reinecke, E. J. Penny, and A. T. Pearse. 2008. Moist-soil seed abundance in managed wetlands in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:707–714.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. *SAS for mixed models*, Second edition. SAS Institute, Inc. Cary, North Carolina, USA.
- Loesch, C. R., K. J. Reinecke, and C. K. Baxter. 1994. Lower Mississippi Valley Joint Venture evaluation plan. North American waterfowl management plan, U. S. Fish and Wildlife Service, Vicksburg, Mississippi, USA.
- Lovvorn, J. A., and M. P. Gillingham. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77:435–451.
- Manley, S. W., R. M. Kaminski, P. B. Rodrigue, J. C. Dewey, S. H. Schoenholtz, P. D. Gerard, and K. J. Reinecke. 2009. Soil and nutrient retention in winter-flooded ricefields with implications for watershed management. *Journal of Soil and Water Conservation* 64:173–182.
- Martin, A. C., and F. M. Uhler. 1939. Food of game ducks in the United States and Canada. U.S. Department of Agricultural Bulletin 634, Washington, D. C., USA.

- Michael, P. W. 1983. Taxonomy and distribution of *Echinochloa* species with special reference to their occurrence as weeds of rice. Pages 291–306 in Proceedings of the conference on weed control in rice, International Rice Research Institute, Los Baños, Laguna, Philippines.
- Miller, M. R. 1987. Fall and winter foods of northern pintails in the Sacramento Valley, California. *Journal of Wildlife Management* 51:405–414.
- Miller, M. R., and J. M. 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. *The Condor* 108:166–177.
- Moser, E. B. 2001. Repeated measures modeling with PROC MIXED. Proceedings of the Twenty-ninth Annual SAS Users Group International Conference Cary, North Carolina, USA. <<http://www2.sas.com/proceedings/sugi29/188-29.pdf>>. Accessed 14 May 2010.
- Mueller, M. H., and A. G. van der Valk. 2002. The potential role of ducks in wetland seed dispersal. *Wetlands* 22:170–178.
- Neely, W. W. 1956. How long do duck foods last underwater? *Transactions of the North American Wildlife and Natural Resources Conference* 21:191–198.
- Neff, K. P., and A. H. Baldwin. 2005. Seed dispersal into wetlands: techniques and results for a restored tidal freshwater marsh. *Wetlands* 25:392–404.
- Nelms, K. D. 2007. Wetland management for waterfowl: a handbook. Mississippi River Trust, Stoneville, Mississippi, USA.
- Nelms, C. O., and D. J. Twedt. 1996. Seed deterioration in flooded agriculture fields during winter. *Wildlife Society Bulletin* 24:85–88.
- Pearse, A. T. 2007. Design, evaluation, and applications of an aerial survey to estimate abundance of wintering waterfowl in Mississippi. Dissertation, Mississippi State University, Mississippi State, USA.
- Prince, H. H. 1979. Bioenergetics of postbreeding dabbling ducks. Pages 103–117 in T. A. Bookhout, editor. *Waterfowl and wetlands: an integrated review*. Proceedings of the Thirty-ninth Midwest Fish and Wildlife Conference, Madison, Wisconsin, USA.
- Reinecke, K. J., R. C. Barkley, and C. K. Baxter. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. Pages 325–337 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, USA.

- Reinecke, K. J., and K. M. Hartke. 2005. Estimating moist-soil seeds available to waterfowl with double sampling for stratification. *Journal of Wildlife Management* 69:794–799.
- Reinecke, K. J., R. M. Kaminski, D. J. Moorhead, J. D. Hodges, and J. R. Nassar. 1989. Mississippi Alluvial Valley. Pages 203–247 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, USA.
- SAS Institute, Inc. 2008. SAS® 9.2 Enhanced Logging Facilities, SAS Institute, Inc., Cary, North Carolina, USA.
- Schoffman, R. J. 1947. Food of game ducks at Reelfoot Lake, Tennessee. *Journal of the Tennessee Academy of Science* 22:4–8.
- Schummer, M. L., H. M. Hagy, K. S. Fleming, J. C. Cheshier, and J. T. Callicutt. 2011. Moist-soil wetland plants of the Mississippi Alluvial Valley. University Press of Mississippi, Jackson, USA. In Press.
- Seed Images. 2008. Discover seeds. Colorado State University. Fort Collins, USA. <<http://www.seedimages.com>>. Accessed 24 Feb. 2009.
- Shearer, L. A., B. J. Jahn, and L. Lenz. 1969. Deterioration of duck foods when flooded. *Journal of Wildlife Management* 33:1012–1015.
- Stafford, J. D., R. M. Kaminski, K. J. Reinecke, and S. W. Manley. 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:61–69.
- Strader, R. W., and P. H. Stinson. 2005. Moist-soil management guidelines for the U.S. Fish and Wildlife Service Southeast Region. <<http://www.fws.gov/columbiawildlife/MoistSoilReport.pdf>>. Accessed 20 Sept. 2009.
- Strickland, B. K., R. M. Kaminski, K. Nelms, and A. Tullos, editors. 2009. *Waterfowl habitat management handbook*. Mississippi State University Extension Service Publication 1864, Mississippi State, USA.
- Sutherland, W. J., and C. W. Anderson. 1993. Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. *Journal of Theoretical Biology* 160:223–230.
- Swanson, G. A., and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of blue-winged teal. *Journal of Wildlife Management* 34:739–746.

- Tabatabai, F. R., J. A. Huggins, and R. A. Smith. 1983. Mallard food habits in western Tennessee. *Journal of the Tennessee Academy of Science* 38:24–26.
- Taylor, J. P., and L. M. Smith. 2005. Migratory bird use of belowground foods in moist-soil managed wetlands in the Middle Rio Grande Valley, New Mexico. *Wildlife Society Bulletin* 33:574–582.
- van Eerden, M. R., and M. J. Munsterman. 1997. Patch use upon touch: filter-feeding European Teal (*Anas crecca*) have environmentally and socially determined foraging goals. Pages 165–185 in M. R. van Eerden, editor. *Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands*, Rijksuniversiteit Groningen, The Netherlands.
- Vigil, J. F., R. J. Pike, and D. G. Howell. 2000. A tapestry of time and terrain: U.S. Geological Survey Geologic Investigations Series 2720. <<http://pubs.usgs.gov/imap/i2720/>>. Accessed 23 June 2010.
- Vivian-Smith, G., and E. W. Stiles. 1994. Dispersal of salt marsh seeds on the feet and feathers of waterfowl. *Wetlands* 14:316–319.
- Williams, B. K., M. D. Koneff, and D. A. Smith. 1999. Evaluation of waterfowl conservation under the North American Waterfowl Management Plan. *Journal of Wildlife Management* 63:417–440.
- Wills, D. 1971. Food habit study of mallards and pintails on Catahoula Lake, Louisiana, with notes of food habits of other species. *Proceedings of the Annual Conference of Southeast Association of Game and Fish Commissioners* 25:289–294.
- Wongsripuek, C., B. D. Dugger, and A. M. Bartuszevige. 2008. Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. *Wetlands* 28:290–299.
- Wright, T. W. 1959. Winter foods of mallards in Arkansas. *Proceedings of the Annual Conference of Southeast Association of Game and Fish Commissioners* 13:291–296.
- Yabuno, T. 1983. Biology of *Echinochloa* species. Pages 307–318 in *Proceedings of the conference on weed control in rice*, International Rice Research Institute, Los Baños, Laguna, Philippines.
- Zar, J. H. 2009. *Biostatistical analysis*. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Table 2.1. Models of millet (*Echinochloa frumentaceae*) decomposition as a function of 2-week time intervals with coefficients of determination (R^2) from 6 moist-soil wetlands^a during December 2008 – February 2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

Model	R^2
Linear	0.99
Polynomial - 2nd order	0.99
Polynomial - 3rd order	0.99
Polynomial - 4th order	0.99
Exponential	0.97
Logarithmic	0.89
Power	0.85

^bOne wetland was drained inadvertently during winter and was removed from analyses.

Table 2.2 Seeds recovered from core samples in the Mississippi Alluvial Valley during November 2006–2008 through February 2007–2009 and their mean adjusted percentage decomposition per day (\bar{x}), predicted (P) and observed (O) seed mass remaining as a percentage of November estimates, and statistics (n , P) from a repeated measures analysis of variance testing for differences in predicted and observed seed decline ($\alpha = 0.05$).

Taxon	\bar{x}	<u>December</u>		<u>January</u>		<u>February</u>		n	P
		P	O	P	O	P	O		
Alismataceae									
<i>Sagittaria latifolia</i>	0.189	94.5	39.2	91.7	14.7	88.7	53.1	9	0.001
Amaranthaceae									
<i>Amaranthus</i> spp.	0.189	92.4	181.9	86.7	72.9	81.5	119.5	33	0.383
Convolvulaceae									
<i>Ipomoea</i> spp.	0.448	86.3	65.7	75.7	102.0	65.4	96.2	33	0.514
<i>Jacquemontia tamnifolia</i>	0.457	81.2	73.9	65.5	121.8	55.0	128.5	17	0.052
Cyperaceae									
<i>Carex</i> spp.	0.189	93.7	5.1	88.3	37.7	83.6	10.2	11	0.001
<i>Cyperus odoratus</i>	0.189	93.9	96.2	88.8	93.2	83.2	66.5	67	0.680
<i>Eleocharis</i> spp.	0.189	94.2	128.0	89.3	90.5	84.5	56.7	27	0.885
<i>Rhynchospora corniculata</i>	0.019	99.2	88.7	98.7	39.2	98.2	42.0	24	0.001

Table 2.2. Continued.

Fabaceae										
<i>Sesbania herbacea</i>	0.257	91.6	99.9	84.3	104.7	76.0	108.2	43	0.582	
Malvaceae										
<i>Sida spinosa</i>	0.189	93.0	71.5	87.8	57.9	82.7	84.0	54	0.001	
Poaceae										
<i>Digitaria</i> spp.	0.189	94.5	76.3	90.4	73.8	86.4	23.9	22	0.001	
<i>Echinochloa</i> spp.	0.284	89.7	57.1	81.8	50.4	74.2	42.6	161	0.001	
<i>Panicum</i> spp.	0.393	87.2	53.3	76.9	37.4	65.9	37.9	119	0.001	
<i>Paspalum laeve</i>	0.076	97.3	56.4	95.2	31.3	92.9	36.8	24	0.003	
<i>Paspalum urvillei</i>	0.076	97.1	24.5	94.9	37.7	92.3	18.9	34	0.001	
<i>Setaria</i> spp.	0.229	91.5	39.8	84.9	44.2	78.1	50.0	51	0.001	
<i>Urochloa platyphylla</i>	0.426	84.0	24.2	72.4	28.4	61.1	25.3	23	0.001	
Polygonaceae										
<i>Polygonum hydropiperoides</i>	0.095	96.6	84.7	94.1	96.9	91.5	57.2	55	0.002	
<i>Polygonum lapathifolium</i>	0.162	94.2	56.7	89.6	44.1	84.8	47.5	130	0.001	
<i>Polygonum pennsylvanicum</i>	0.219	92.4	62.9	86.3	49.8	79.8	55.1	132	0.001	
Rubiaceae										
<i>Diodia virginiana</i>	0.189	93.9	71.5	89.2	31.3	84.4	24.9	26	0.001	

Table 2.3. Seed taxa consumed by dabbling ducks in the Mississippi Alluvial Valley and references.

Taxon	Reference ^a
<i>Althaea officinalis</i>	5
<i>Amaranthus</i> spp. ^b	6, 8, 12
<i>Bidens</i> spp.	2, 10, 11, 15
<i>Carex</i> spp.	6, 9, 10, 11
<i>Cyperus</i> spp. (seeds) ^b	1, 4, 5, 6, 7, 8, 10, 11, 14, 15
<i>Cyperus</i> spp. (tuber)	2, 14
<i>Digitaria</i> spp.	8, 9, 10
<i>Diodia virginiana</i>	8, 9, 14
<i>Echinochloa</i> spp.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 14, 15
<i>Eleocharis</i> spp. ^b	1, 5, 6, 8, 10, 11, 14, 15
<i>Heliotropium</i> spp.	1, 10, 11, 14
<i>Leersia oryzoides</i>	3, 4, 8, 10, 11
<i>Oryza sativa</i>	1, 3, 4, 5, 6, 7, 8, 11, 14, 15
<i>Panicum</i> spp.	1, 4, 5, 6, 7, 8, 9, 13, 14, 15
<i>Paspalum</i> spp.	1, 5, 6, 7, 8, 9, 11, 15
<i>Polygonum hydropiperoides</i>	3, 4, 5, 6, 7, 8, 9, 10, 13, 14, 15
<i>Polygonum lapathifolium</i>	3, 9, 10, 13, 15
<i>Polygonum pensylvanicum</i>	3, 7, 9, 10, 13, 15
<i>Rhynchospora</i> spp.	5, 6, 9, 15
<i>Sagittaria</i> spp.	9
<i>Scirpus</i> spp.	1, 8, 11
<i>Setaria</i> spp.	8, 9
<i>Sida spinosa</i>	9, 13
<i>Sorghum bicolor</i>	2, 7, 15
<i>Urochloa platyphylla</i>	4, 6, 8, 9, 15

^a1 - Chamberlain 1959, 2 - Combs and Fredrickson 1996, 3 - Dabbert and Martin 2000, 4 - Delnicki and Reinecke 1986, 5 - Dillon 1957, 6 - Dillon 1959, 7 - Forsythe 1965, 8 - Glasgow and Junca 1962, 9 - Table 2.2, 10 - Heitmeyer 2006, 11 - Martin and Uhler 1939, 12 - Schoffman 1947, 13 - Tabatabai et al. 1983, 14 - Wills 1971, 15 - Wright 1959

^bChapter II analyses indicated taxa likely was not consumed by waterfowl

CHAPTER III
WINTER WATERFOWL RESPONSE TO SEED DENSITY AND A FOOD
AVAILABILITY THRESHOLD IN MOIST-SOIL WETLANDS IN THE
MISSISSIPPI ALLUVIAL VALLEY

The North American Waterfowl Management Plan (NAWMP) established a framework for science-based conservation of North American waterfowl and wetlands and recommended forming regional partnerships (i.e., Joint Ventures) of federal, state, and non-governmental organizations to implement management programs (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986). The Lower Mississippi Valley Joint Venture (LMVJV) and other conservation planners in regions used by nonbreeding waterfowl set a primary goal of providing adequate foraging habitat on private and public land to support waterfowl during winter (Loesch et al. 1994, CVJV 2006). Estimates of abundance and metabolizable energy of foods, daily energy requirements of waterfowl, and food density thresholds below which foraging becomes energetically unprofitable are required for accurate estimation of carrying capacity (Reinecke et al. 1989).

Accurate estimates of carrying capacity help the LMVJV prioritize conservation of foraging habitats important to waterfowl in winter (Raveling and Heitmeyer 1989; Moon and Haukos 2006, 2009; Abraham et al. 2007; Moon et al. 2007). Wetland area is typically abundant during winter in the Mississippi Alluvial Valley (MAV; Uihlein 2000,

Abraham et al. 2007); however, recent studies have revealed that food in harvested crop fields seasonally managed as wetlands for waterfowl have decreased from historical values (Manley et al. 2004, Stafford et al. 2006, Greer et al. 2009, Foster et al. 2010). Reduced food availability in harvested crop fields could result in an overestimation of carrying capacity and possibly negative demographic consequences for waterfowl (Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Loesch et al. 1994, Abraham et al. 2007, Greer et al. 2009).

Seasonal wetlands managed for herbaceous vegetation and flooded during autumn and winter (i.e., moist soil) can offset reduced food abundance in harvested crop fields (Reinecke et al 1989, Stafford et al. 2006, Kross et al. 2008a, Foster et al. 2010). Recent studies indicate that managed moist-soil wetlands may contain more duck energy days (i.e., average energetic requirement of one dabbling duck per day; DED; Reinecke et al. 1989) than harvested crop fields during winter (Bowyer et al. 2005, Stafford et al. 2006, Kross et al. 2008b, Foster et al. 2010) and waterfowl intensively forage in these wetlands during fall and winter (Twedt and Nelms 1999, Stafford et al. 2007, O'Neil et al. 2008, Chapter I). Kross et al. (2008b) provided estimates of moist-soil seed abundance in the MAV, but included seeds that may not be consumed by waterfowl (Chapter II) and did not adjust estimates for a threshold of food density that limits profitable foraging.

Waterfowl often forage in patches containing food densities that exceed a critical threshold (i.e., energy expended searching for and processing foods exceeds energy gained; van Gils et al. 2004) rather than seek patches with greatest food densities (Tome 1988, van Eerden and Munsterman 1997, Klaassen et al. 2007). Waterfowl may exhibit this strategy because foods that are submerged or buried in sediments are cryptic and

individuals must assess patch quality while foraging (Klaassen et al. 2007), conspecifics and other environmental factors influence patch use (van Eerden and Munsterman 1997, Arzel et al. 2007), or waterfowl maximize fitness in foraging habitats rather than food intake rate (Morris 1989). Because waterfowl may not abandon or cease foraging when food densities become too low for profitable exploitation (Chapter I), waterfowl may reduce wetland foods to levels near critical density before abandonment (Goss-Custard et al. 2002, van Gils et al. 2004).

Optimally foraging animals must balance benefits of foraging in a patch with the physiological costs of obtaining and metabolizing foods, risk of predation, and missed opportunity costs of foraging elsewhere (Pyke et al. 1977, Brown 1988, Adams-Hunt and Jacobs 2007, Ydenberg et al. 2007). Although food abundance may be a component of patch selection, animals have been shown to forage in patches with greater fitness benefits (Caraco 1980). Brown (1988) used the phrase “giving-up” density (GUD) to describe a threshold of food abundance at which foraging costs exceeded benefits gained from continued foraging. Brown (1988) reported that granivorous desert rodents abandoned foraging patches at different seed densities depending on perceived risks within each patch. GUDs have been demonstrated to vary among foraging locations and depend on search time, predation risk, and opportunity costs (Gawlik 2002, Nolet et al. 2006, van Gils and Tijssen 2007, Richman and Lovvorn 2009). Variable GUDs among locations may complicate precise estimation of food availability and carrying capacity (Greer et al. 2009). Brown (1988) and others have indicated the need for field experiments involving manipulated food densities to test optimal foraging models and incorporate environmental variability into GUD estimates (Bernstein et al. 1988).

Several researchers have tested predictions of optimal foraging theory and extended Brown's (1988) work by investigating foraging strategies of wetland birds (Amano et al. 2004, Nolet et al. 2006, van Gils and Tijssen 2007, Nolet and Klaassen 2009). Waterbirds that feed on submerged foods in wetlands are difficult to study as successes of foraging bouts are usually not known (Klaassen et al. 2007). Therefore, researchers typically observe foraging birds and sample wetland food resources before and after waterbird use to infer food depletion and GUDs (Lovvorn and Gillingham 1996, Gawlik 2006, Nolet et al. 2006). There is evidence that waterfowl reach GUDs and abandon habitats when foraging profitability is reduced below a threshold value (Lovvorn and Gillingham 1996, Greer et al. 2009). For example, Canvasbacks (*A. valisineria*) and other diving ducks (*Aythya* spp.) foraged on *Vallisneria* spp. tubers until no further depletion occurred but did not deplete tubers to the same densities among years, habitats, and studies (Lovvorn 1994a,b; Sponberg and Lodge 2005). Similarly, other researchers have reported that foraging thresholds of tundra swans (*Cygnus columbianus*) consuming *Potamogeton* spp. tubers varied with water depth, sediment composition, and other factors (Beekman et al. 1991; Nolet et al. 2002, 2006).

Scientists have estimated a GUD for waterfowl in flooded rice fields in the MAV (Reinecke et al. 1989, Greer et al. 2009). Greer et al. (2009) observed waterfowl abandoning flooded rice fields when waste grain was reduced to 50 kg/ha and reported only slight variation (CV = 7.1%) in GUD among sites. Thus, Greer et al. (2009) suggested the LMVJV use 50 kg/ha as a lower threshold of food density available to waterfowl in rice fields. However, no previously published study has reported a GUD for seeds, tubers, and aquatic macroinvertebrates in moist-soil wetlands in the MAV or

conducted studies to determine if waterfowl abandon wetlands when a foraging threshold is reached. Estimates of a food density threshold in moist-soil wetlands would enable wildlife managers to determine waterfowl carrying capacity accurately and enhance cost-efficiency of habitat conservation (Goss-Custard et al. 2002).

I evaluated waterfowl use and food abundance in managed moist-soil wetlands in the MAV during winters 2006–2009 to estimate food density at which waterfowl abandoned wetlands, stopped foraging, or continued to forage without further reducing food abundance (Chapter I). I estimated that the combined abundance in late-winter of moist-soil seeds, tubers, and invertebrates in mowed, disked, and non-manipulated moist-soil wetlands was ~50% less than estimates in late fall, but remained ~5 times greater than the GUD estimate for harvested rice fields (Chapter I). Additionally, seeds, tubers, and invertebrates did not decline markedly from December–February of each year despite continued waterfowl foraging in wetlands. Furthermore, food abundances were similar among treatments, but differed among sites when food densities stabilized in mid winter. Therefore, I conducted experiments to test waterfowl responses to experimentally manipulated seed density in moist-soil wetlands during December 2008–February 2009. My objectives were to 1) quantify waterfowl use and foraging effort in experimental plots with differing initial seed densities, 2) determine if waterfowl abandoned patches at a similar density of seeds among treatments and sites, and 3) estimate food densities at which waterfowl abandoned patches, stopped foraging, or continued to feed without further reducing food abundance in experimental plots.

Study Area

The MAV is a 10 million-ha alluvial plain of the Mississippi River stretching from southern Missouri and Illinois to the gulf coast of Louisiana and is important for nonbreeding waterfowl (Reinecke et al. 1988, 1989; Fredrickson 2005, Baldassarre and Bolen 2006). Historically, the MAV regularly flooded from overflow of the Mississippi River and associated tributaries and was composed of mature bottomland hardwood forests and natural wetlands (King et al. 2005). Presently, approximately 70% of the MAV has been cleared for row-crop agriculture and other human uses and flood control along major rivers and streams has replaced seasonal and temporary wetlands with small permanent basins or networks of ditches to remove water rapidly (Reinecke et al. 1988, 1989; Havera 1999; Fredrickson 2005; King et al. 2005; Manley et al. 2009).

I selected and sampled managed moist-soil wetlands in federal, state, and private waterfowl management complexes in the MAV of Mississippi and Tennessee (Fig. 3.1, Appendix B). In spring 2008, I met with waterfowl habitat managers to determine availability of study wetlands within sanctuary areas of management complexes. I selected wetlands using the following criteria: 1) presence of continuous moist-soil vegetation that had not yet begun to develop seed clusters, 2) adequate size for placement of a 2-ha block of treatments, 3) surrounding landscape provided isolation from disturbance and access to wetlands to observe waterbirds, and 4) availability for summer herbicide application and winter access. I selected moist-soil wetlands dominated by annual grasses (e.g., *Echinochloa* spp., *Panicum* spp., *Paspalum* spp.) or smartweeds (i.e., *Polygonum* spp.), but few sedges (i.e., *Cyperus* spp.) so that tuber abundance would be likely be minimal.

Methods

Experimental Design

I conducted experiments to determine if waterfowl using moist-soil wetlands reduced seed and tuber abundances to similar densities among supplemental food plots and wetlands. I added biologically relevant densities of seeds, quantified waterfowl use and behavior, and estimated seed reduction through time in moist-soil wetlands in the MAV. I deposited Japanese millet (*Echinochloa frumentacea*; hereafter millet) in 3 adjacent, 0.5-ha plots separated by a 15-m buffer where no millet was added. I used millet as a surrogate moist-soil seed because it is similar to naturally occurring millets and is planted commonly in wetlands managed for waterfowl (Michael 1983, Yabuno 1983, Nelms 2007, Strickland et al. 2009, Schummer et al. 2011). I randomly selected a density (i.e., 50 [GUD in rice fields; Greer et al. 2009], 250 [seed and tuber threshold from Chapter I], and 550 kg/ha [moist-soil seed and tuber abundance in the MAV in late fall; Kross et al. 2008b]) and added millet to each plot. Before spreading millet, I measured water depths at 10 locations along 2 randomly placed transects in each treatment plot and installed a water depth gauge so mean depths for each treatment could be inferred from the gauge without disturbing waterfowl. I placed porous bags of millet in each wetland for 48 hours to saturate seed so it would sink and evenly spread by hand in each treatment plot. I used a sweep net to recover millet that did not sink, soaked recovered millet for an additional 48 hours, and redistributed it by hand.

Waterbird Abundance

I conducted 3 scan sample surveys of waterfowl and their behavior during each of 3 visits per week to determine if and when waterfowl abandoned, ceased foraging in, or reduced foraging rates until late February or early March when a large portion of waterfowl migrated from study areas (Kaminski and Prince 1981, Martin and Bateson 1998). I surveyed plots diurnally from approximately sunrise – 3 hrs after sunrise or 3 hrs before sunset – sunset and alternated timing of surveys among site visits (Arzel and Elmberg 2004, Amano et al. 2006, Greer et al. 2009). I recorded number of birds of each species and their instantaneous behavior (i.e., feeding, resting, swimming, or aggression) from elevated blinds without disturbing waterfowl (Kaminski and Prince 1981). I waited 5 minutes after entering the blind to begin counts and between scans. If waterfowl were slightly disturbed during a scan by a natural event, I censored that scan, waited 5 minutes, and scanned again. If a major disturbance caused departure or redistribution of most waterfowl occupying the wetland, I left the site and returned at another time. During inclement weather, I noticed birds feeding between 1000–1400 CST and conducted several mid-day surveys, but did so equally among study sites. After each survey, I recorded water depth and inferred depths in each treatment plot.

Seed and Tuber Abundances

I collected 10 core samples (10 cm in depth and diameter) from each treatment plot before addition of millet and during each sampling period (Greer et al. 2009, Havens et al. 2009). I collected samples along a randomly placed transect within each plot. I randomly selected the distance (0–25 m) to the first sample location and then located

each subsequent sample location at a fixed interval predetermined to span each plot (Greer et al. 2007). I stored core samples at -15°C until processed.

I processed core samples in a random sequence by site and time period to account for any bias associated with duration samples were frozen. I thawed samples in warm water; added a solution of 3% hydrogen peroxide (H₂O₂; Bohm 1979), baking soda, and water for 1–3 hrs to disperse soil; and washed cores through 3 sieves (i.e., mesh sizes #50 [0.03 mm], #10[1.65 mm], and #4[4.75 mm]; Kross et al. 2008*b*; Chapter I, II). I recovered and air dried seeds and other material from each sieve separately for 24–48 hrs. I homogenized fine materials retained by the small sieve (#50) and selected randomly a one-quarter subsample by mass (hereafter, small portion). I removed seeds and tubers from the small portion and from materials retained by 2 large sieves (#s 4 and 10; hereafter, large portion; Kross et al. 2008*b*). I enumerated and weighed seeds by genus or species (Martin and Barkley 1961, Seed Images 2008, Bryson and DeFelice 2009, Schummer et al. 2011). I multiplied data from the small portion by 4 and combined the product with data from the large portion to estimate seeds per core sample (Kross et al. 2008*b*).

Pilot Experiment

In February–March 2008, I conducted a pilot experiment to evaluate experimental methods and establish a preliminary foraging threshold for waterfowl in the MAV. In early February, immediately after closure of the waterfowl hunting season, I added millet to 2 moist-soil wetlands on private lands that had been used by waterfowl throughout winter 2007–2008 (Fig. 3.1). I collected core samples before addition of millet, and 2

more times at 2-week intervals until early March 2008 (Greer et al. 2009, Havens et al. 2009).

Principal Experiment

I conducted experiments to estimate a foraging threshold for dabbling ducks in winter at 7 wetlands in the MAV from mid-December 2008 through late-February 2009 (Appendix 2). In early summer, I selected study sites with continuous stands of moist-soil vegetation that had not begun to produce seeds, land managers indicated had been used extensively in previous years by ducks, and met logistical criteria as described previously. During summer and fall 2008, I applied a non-selective herbicide (Glyphosate) to deter seed production but preserve vegetative structure in experimental wetlands. Land managers flooded (6–45 cm) wetlands in late October or early November to encourage early migrating waterfowl to deplete seeds from previous growing seasons. I collected core samples in mid December before addition of millet, 2 weeks after addition, and then once monthly until late February 2009.

I estimated decomposition of millet in each treatment plot at 2-week intervals following initial millet deposition. I placed 3 cylindrical wire exclosures (0.3-m tall x 0.5-m diameter) each containing 5 100-g (dry mass) envelopes of millet in each treatment plot ($n = 9$ exclosures per wetland; Neely 1956). I placed exclosures systematically across treatment plots. I removed one randomly selected envelope from each exclosure biweekly from mid December to late February and stored envelopes at -15°C . To process samples, I thawed envelopes in warm water, washed seeds into a #50 sieve and rinsed

thoroughly to remove inorganic and organic matter, dried seed at 80°C for 24–48 hrs to constant mass, and weighed to the nearest 0.1 mg.

I assumed human activity did not influence waterfowl behavior differently among sites because plots were located in sanctuaries free from hunting or unrestricted activity. Brasher (2010) reported that nocturnal use of passively managed moist-soil wetlands by ducks was less than diurnal use, but many of these wetlands were unused by ducks in his study. Steckel (2003) found that ducks used moist-soil wetlands diurnally and nocturnally, and Moon and Haukos (2008) reported that female northern pintail (*Anas acuta*) used playa wetlands with differing proportions of emergent cover similarly diurnally and nocturnally. Therefore, I assumed waterfowl were able to feed diurnally without human disturbance and diurnal use was representative of cumulative wetland use.

Statistical Analyses

Pilot Experiment

I used repeated measures analysis of variance (ANOVA) to determine effects of millet supplementation (i.e., treatment), water depth, and interaction of depth and treatment on abundance of feeding dabbling ducks with survey period as the repeated measure (Proc MIXED; SAS Institute, Inc. 2008). I did not have a sufficient number of observations to include survey period as a fixed effect. I used abundances of feeding dabbling ducks rather than total abundance because dabbling duck abundance accounted for most waterbird use of plots and behaviors other than feeding (e.g., resting, swimming) only indicate use of site for refuge or loafing. I averaged duck abundances and behaviors among the 3 scan surveys per site visit.

I converted seed mass estimates to DEDs using published true metabolizable energy values (Table 3.1; Checkett et al. 2002, Kaminski et al. 2003, Straub 2008) and the following equation:

$$DED = \frac{\sum(F_{1...j} * TME_{1...j})}{DER}$$

where F is food density (g/ha) of each taxa_{1...j}, TME is true metabolizable energy of specific foods_{1...j}, and DER is the estimate used by the LMVJV for mean daily energy requirements of dabbling ducks that typically use moist-soil wetlands in the MAV (294.35 kcal/day; Reinecke and Uihlein 2006, Reinecke and Kaminski 2007, Murray et al. 2009). I used repeated measures ANOVA to test if DEDs differed among treatments with DED/ha as the dependent variable, treatment (50, 250, or 550 kg/ha) as a fixed effect, and sampling interval as a fixed effect and a repeated measure (PROC MIXED; Littell et al. 2006, SAS Institute, Inc. 2008). I did not test for interactions among fixed effects because of insufficient sample size.

Principal Experiment

Waterbird Abundance.— I standardized repeated measurements of duck abundance among sites by combining surveys within weeks (i.e., 7-day periods) because intervals between bird surveys differed slightly as a result of accidental disturbance, logistical constraints, or vagaries of weather. I compared Pearson correlation coefficients among potential response variables (i.e., all dabbling ducks [Anatini], mallards [*Anas platyrhynchos*], and dabbling ducks other than mallards) and selected density of all dabbling ducks observed feeding as the dependent variable because it was correlated with

feeding mallards ($r = 0.64$, $n = 114$) and dabbling ducks other than mallards observed feeding ($r = 0.93$, $n = 114$). I excluded diving ducks (Aythyini), waterbirds other than ducks, and geese (Anserini) from analyses as they represented a small portion of observed avifauna. I used repeated measures ANOVA to determine effects of millet supplementation (i.e., treatment) on abundance of dabbling ducks that were feeding and proportion of dabbling ducks feeding compared to all other activities combined (PROC MIXED; SAS Institute, Inc. 2008). In separate models, I modeled abundance and proportion of all dabbling ducks observed feeding using treatment, survey week, water depth, interaction of treatment and week, and interaction of treatment and depth as fixed effects; site as a random effect; and survey week as a repeated measure (PROC MIXED; SAS Institute, Inc. 2008). Additionally, I modeled abundance and proportion of all dabbling ducks observed feeding using the same explanatory variables and modeling procedure, but only data from only the first 2 weeks when most millet decline occurred (individual surveys 1–5 not averaged within the first 2 weeks [late December – early January]). I used the raw survey data in the previous 2 analyses because there were only 2 weeks of standardized observations between late December–early January when most seed removal occurred in wetlands and surveys 1–5 were approximately equally spaced in time.

Duck Energy Days.— I used repeated measures ANOVA to test if DEDs differed among treatments with DED/ha as the dependent variable, treatment as a fixed effect, sampling interval as a repeated measure, site as a random effect, and DED of the original or previous sampling period as a covariate (PROC MIXED; Littell et al. 2006, SAS

Institute, Inc. 2008). Additionally, I used ANOVA to model DEDs in early January as a function of the fixed effects of site and treatment to determine if seed abundances varied among sites and plots after the sampling period when no further decreases in food abundance occurred.

Seed and Tuber Abundances.— Although I used DEDs as the primary measure of seed and tuber abundance among treatments and sites, I conducted separate analyses to compare abundances (kg[dry]/ha) of experimentally added millet and all other seeds and tubers combined to identify possible influences of seed composition on food depletion. I modeled millet abundance from early January–February 2009 using repeated measures ANOVA with treatment, site, survey period, interaction of site and treatment, and interaction of treatment and survey period as fixed effects and survey period as a repeated measure. I modeled natural seed and tuber abundance from mid-December–February 2009 using repeated measures ANOVA with treatment, site, survey period, interaction of site and treatment, and interaction of treatment and survey period as fixed effects and survey period as a repeated measure.

Decomposition.— I modeled millet decomposition (biweekly mass remaining) using repeated measures ANOVA. I designated site, treatment, and week as fixed effects and week as the repeated measure.

Existence Energy and Energy Removal.— To determine if dabbling duck abundance was related to energy removed from experimental plots, I estimated the energy required to sustain the estimated numbers of dabbling ducks that used my

experimental plots during each month (i.e., existence energy [EE]) and compared to energy apparently removed from plots (ER; Richardson and Kaminski 1992, Barras et al. 1996). I calculated mean duck abundance per day and multiplied it by number of days in each survey interval to estimate cumulative duck abundance. I assumed diurnal observations of duck abundance were representative of daily abundance. I multiplied cumulative duck abundance by 294.35 kcal/day to estimate EE of dabbling ducks using plots (Reinecke and Uihlein 2006, Reinecke and Kaminski 2007, Murray et al. 2009). I calculated ER using the following equation,

$$ER = \frac{\sum(F_{1,i} - F_{j+1,i}) * TME_i}{DER}$$

where F is food density (g/ha) of taxa_{*i*} at each sample period_{*j*}, TME is metabolizable energy (kcal/g) of taxa_{*i*}, and DER is the daily energetic requirement of dabbling ducks in the MAV (294.35 kcal/day). I compared EE with ER using repeated measure ANOVA (Chapter I). The dependent variable was ER; EE, treatment, sampling period, the interaction of sampling period and EE, and the interaction of treatment and EE were fixed effects; site was a random effect; and sampling period was the repeated measure.

Prior to all analyses, I examined data histograms, variances of independent variables, and plots of residuals to ensure data met assumptions of analyses and used recommended data transformations as needed (Littell et al. 2006, Zar 2009). When using repeated measures, I used Akaike's Information Criterion to select an appropriate covariance structure and specified restricted maximum likelihood estimation of fixed effects. I determined $\alpha = 0.05$, a priori. Additionally, I performed Tukey's pair-wise

multiple comparisons tests of means among treatments when $P \leq 0.05$. I calculated means and standard errors from untransformed data.

Results

Pilot Experiment

Dabbling ducks used only one of 2 wetlands in the pilot experiment, hence these results include only the wetland apparently used by ducks. Dabbling ducks accounted for 99% ($n = 48$ surveys) of the waterbirds observed in plots and most (98%) were American green-winged teal (43%; *A. crecca*), northern pintail (32%; *A. acuta*), mallard (11%), gadwall (6%; *A. strepera*), and northern shoveler (6%; *A. clypeata*). Abundance of feeding dabbling ducks was related inversely to water depth ($F_{1, 42} = 7.6$, $P = 0.008$), but did not differ by treatment ($F_{2, 42} = 1.9$, $P = 0.165$) or the interaction of depth and treatment ($F_{2, 42} = 1.8$, $P = 0.175$). Ninety percent of feeding dabbling ducks used plots with a mean depth ≤ 13 cm ($\bar{x} = 10.3$ cm, $SE = 0.2$, range = 9–13 cm, $n = 48$ surveys).

During the first 2 weeks of the pilot experiment from early- to mid-February 2008, experimentally placed millet and naturally occurring seeds and tubers combined were reduced by 17, 54, and 74% in the 50, 250, and 550 kg/ha treatments, respectively. After 4 weeks, all seeds and tubers had decreased by 36% in the 50 kg/ha treatment, while reduction in the 250 and 550 kg/ha treatments remained similar to previous levels (59% and 79%, respectively). There was no difference in DEDs among treatments ($F_{2, 2} = 5.3$, $P = 0.158$) or survey periods ($F_{1, 2} = 1.4$, $P = 0.365$) from mid February to early March 2008. Waterfowl abandoned the wetland in late February at which time 1467

DEDs (SE = 28.1) and 194 kg/ha (SE = 20.6) of seeds and tubers remained among treatments.

Principal Experiment

Waterbird Abundance

I analyzed data from 4 of 7 experimental wetlands supplemented with millet in December 2008. One wetland was drained inadvertently and 2 others were not used by dabbling ducks. Most waterbirds observed from December 2008–February 2009 were dabbling ducks (97%, $n = 114$ surveys), including mallard (48%), gadwall (29%), northern shoveler (11%), American green-winged teal (6%), northern pintail (4%), and others (<2%; Anatini). Diving ducks accounted for 2% of all waterbirds observed and were mostly (89%) lesser scaup (*Aythya affinis*). I observed few other waterbirds (<1% of all birds) using experimental wetlands.

From mid-December 2008–February 2009, abundance of feeding dabbling ducks varied inversely by week ($F_{9, 66.9} = 4.94$, $P < 0.001$; Fig. 3.2), but not by treatment ($F_{2, 67.8} = 0.52$, $P = 0.597$), water depth ($F_{1, 58.1} = 0.92$, $P = 0.343$), interaction of treatment and week ($F_{18, 66.2} = 0.36$, $P = 0.991$), or interaction of treatment and water depth ($F_{2, 67.9} = 0.21$, $P = 0.811$; Table 3.2). In early winter (i.e., mid-December–early January) when most seed reduction occurred, abundance of feeding dabbling ducks varied inversely with survey period ($F_{4, 10.8} = 5.53$, $P = 0.011$), but not with treatment ($F_{2, 9.2} = 0.40$, $P = 0.679$), water depth ($F_{1, 5.7} = 1.87$, $P = 0.222$), interaction of depth and treatment ($F_{2, 5.74} = 0.56$, $P = 0.601$), or interaction of treatment and survey period ($F_{8, 11.9} = 1.98$, $P = 0.139$; Table 3.2).

From mid-December 2008 to February 2009, proportion of dabbling ducks observed feeding was related positively to week ($F_{9, 51.6} = 2.45$, $P = 0.021$; Fig. 3.2) and inversely to water depth ($F_{1, 46.5} = 6.14$, $P = 0.017$), but not to treatment ($F_{2, 46.4} = 0.70$, $P = 0.502$), interaction of treatment and week ($F_{18, 50.9} = 1.08$, $P = 0.397$), or interaction of treatment and water depth ($F_{2, 46} = 0.58$, $P = 0.563$). From mid-December 2008 to early January 2009, proportion of dabbling ducks observed feeding varied inversely with water depth ($F_{1, 23} = 7.36$, $P = 0.012$), but not with effects of treatment ($F_{2, 23} = 0.35$, $P = 0.706$), survey period ($F_{4, 23} = 1.68$, $P = 0.189$), interaction of depth and treatment ($F_{2, 23} = 0.17$, $P = 0.844$), or interaction of treatment and survey period ($F_{8, 23} = 0.77$, $P = 0.629$).

Seed and Tuber Abundances

Before deposition of millet, plots contained 6.2 kg/ha (SE = 2.4, $n = 12$ plots) of wild millets (*Echinochloa* spp.) naturally present in the seed bank. Given low abundances of wild millets, I did not differentiate between supplemented Japanese millet and wild millet in core samples. From mid-December 2008 to February 2009, mass of natural seeds and tubers combined declined 14% (SE = 8.1, $n = 12$), whereas millet declined 96% (SE = 1.4; Table 3.3). Mass of millet did not decline further from early January to late February ($F_{2, 18} = 0.21$, $P = 0.815$) and was not related to interaction of treatment and sampling period ($F_{4, 18} = 0.75$, $P = 0.571$), but differed by site ($F_{3, 18} = 7.26$, $P = 0.002$), treatment ($F_{2, 18} = 6.14$, $P = 0.009$), and interaction of site and treatment ($F_{6, 18} = 3.42$, $P = 0.019$; Table 3.4). Millet abundance was approximately 3 times greater in the 250 than the 50 kg/ha treatment ($t_{18} = 3.39$, $P = 0.008$), but did not differ between the 250 and 550 ($t_{18} = 2.02$, $P = 0.135$) or the 50 and 550 kg/ha treatments ($t_{18} = 1.36$, $P = 0.341$).

Natural seed and tuber abundance varied by site ($F_{3, 18} = 18.03$, $P < 0.001$), but was not related to sampling period ($F_{2, 18} = 0.33$, $P = 0.725$), treatment ($F_{2, 18} = 0.31$, $P = 0.735$), interaction of site and treatment ($F_{6, 18} = 1.76$, $P = 0.165$), or interaction of treatment and sampling period ($F_{4, 18} = 0.17$, $P = 0.951$). Among plots, natural seed and tuber abundance combined was 170.1 kg/ha (SE = 29.1, CV = 0.17; Range = 23.7–386.8 kg/ha) and millet was 10.2 kg/ha (SE = 2.6, CV = 0.25; Range = 1.8–30.4 kg/ha) after waterfowl stopped foraging or ceased statistically significant depletion of seeds.

Duck Energy Days

From early January–late February after millet supplementation, potential DEDs did not vary by treatment ($F_{2, 29} = 0.04$, $P = 0.957$; Fig. 3.2) and were independent of the DED estimate in the previous sample period ($F_{1, 29.3} = 0.05$, $P = 0.833$). In early January, after significant reduction of all seeds and tubers ceased, DEDs varied by study site ($F_{3, 6} = 17.43$, $P = 0.002$), but not by treatment ($F_{2, 6} = 0.19$, $P = 0.835$). In early January among study sites and plots, dabbling ducks reduced all seeds and tubers in wetlands to 1,078 DED/ha (SE = 184.1; $n = 12$; range 130–2238 DED/ha).

Existence Energy and Energy Removal

Energy reduction in plots from December – February was not related existence energy ($F_{1, 26} = 1.90$, $P = 0.180$; Fig. 1.3), treatment ($F_{2, 26} = 1.56$, $P = 0.229$), survey period ($F_{2, 26} = 3.13$, $P = 0.060$), or the interactions of EE and survey period ($F_{2, 26} = 1.13$, $P = 0.338$) or EE and treatment ($F_{2, 26} = 0.13$, $P = 0.876$). From late December–early January, ER from wetlands was greater than EE in 9 of 12 treatment plots. However, EE exceeded ER from mid January–February in all but one treatment plot (Fig. 3.3).

Decomposition

Decomposition of millet in experimental wetlands was 34% (SE = 4.3, $n = 4$) from mid-December – late February; however, millet decomposed 6.8% (SE = 1.0) between mid-December and early January, when most seed removal occurred. Decomposition of millet was 8.9% (SE = 1.4, $n = 5$) per 2-week sample period and differed by site ($F_{5, 16.8} = 8.41$, $P < 0.001$), but not by period ($F_{4, 41.3} = 4.44$, $P = 0.086$) or treatment ($F_{2, 37.6} = 0.04$, $P = 0.959$).

Discussion

Waterbird Abundance

Dabbling ducks were the most common guild of waterbirds observed using experimental wetlands, and most ducks were mallard and gadwall. As these species commonly consume seeds in winter (Bellrose 1980, Baldassarre and Bolen 2006), I assumed seed reduction was largely due to consumption by dabbling ducks and decomposition. Because most seeds were removed from experimental wetlands within 2 weeks after millet supplementation, I inferred that most removal was due to dabbling ducks and not decomposition which was approximately 7% during the same time period. Throughout the remainder of winter (e.g., early January–February), dabbling ducks continued to use and forage in experimental wetlands, but did not reduce seed densities more than explained by decomposition. Natural seeds and tubers did not decline markedly (~14%) during winter and may not have been consumed by dabbling ducks in experimental wetlands. Because I analyzed only seeds reportedly consumed by

waterfowl (Chapter II), natural seeds may have been distributed too sparsely to be energetically profitable for waterfowl in experimental wetlands.

Seed and Tuber Abundances

After declining 70% during the first 2 weeks of exposure, combined seeds and DEDs did not differ among treatments, but were markedly different among wetland study sites. From early January–February, millet abundance differed among treatments and sites, but had been reduced to low densities and did not change during this period (Table 3.4). Furthermore, residual levels were not indicative of the treatment levels in mid-December. Greer et al. (2009) determined that waterfowl abandoned rice fields in the MAV when ~50 kg/ha of rice grains remained. As their findings were consistent among rice fields, Greer et al. (2009) suggested the LMVJV use 50 kg/ha as a lower food availability threshold and suggested similar food thresholds be estimated for other major foraging habitats (e.g., flooded hardwood forests and seasonal herbaceous wetlands). Unlike Greer et al. (2009), I was unable to estimate a lower food threshold that was similar among moist-soil wetlands. Furthermore, dabbling ducks did not abandon wetlands when seed abundances no longer decreased, but rather increased foraging rates throughout winter. However, dabbling ducks reduced seeds in experimental wetlands to similar abundances among treatments suggesting that other factors such as predation, risk, and opportunity costs may have been similar among treatment plots within sites, but different among wetlands (Brown 1988, Guillemain et al. 2001, Fritz et al. 2001, Amano et al. 2004, van Gils et al. 2004). Thus, dabbling ducks may have reached a food profitability threshold unique to each experimental wetland.

In late December–early January, ER from wetlands was greater than EE in 9 of 12 treatment plots. However, EE exceeded ER from January–February in all except one plot (Fig. 3.3). Therefore, ducks using experimental wetlands may have fed in alternate habitats to meet energy needs from January–February. Because ducks continued to forage in experimental wetlands but were unlikely to meet their energetic requirements from foods present, densities of seeds and tubers from January–February may have been insufficient for waterfowl to exploit profitably. My observations indicated that dabbling ducks did not stop foraging or abandoned plots as expected if food abundance reached a GUD (Brown 1988), but continued to feed in sites where mean seed densities probably were below levels necessary for profitable foraging.

Nonbreeding birds congregate to avoid predation and improve acquisition of foods (Sutherland 1983, Arengo and Baldassarre 1995); however, increasing predator density may increase interference or exploitative competition for finite foods (Pöysä et al. 1998). If habitat use follows ideal free distribution, foraging birds disperse among patches at densities that reflect variation in food densities among patches (Fretwell and Lucas 1970). The ideal free model predicts that as predator density increases within a patch, foraging profitability decreases and some individuals settle in patches of lower food density (i.e., quality) to equalize energy intake rates and, presumably, fitness (Fretwell and Lucas 1970, Sutherland 1983, Arengo and Baldassarre 1995). In late December when food densities differed among plots, I did not find strong evidence that dabbling ducks were foraging in experimental wetlands consistent with models of ideal free distribution. However, dabbling duck density tended to be slightly greater in plots with greater initial millet abundance (Table 3.2). As neither dabbling duck abundance

nor feeding effort was related to seed and tuber density among treatment plots, other factors may have influenced distribution of ducks in experimental wetlands. Martin (1995) reported that birds were more influenced by direct survival threats (i.e., predation risk) than food quantity in foraging sites; thus, dabbling ducks in my experimental wetlands may have responded to aspects of habitat quality other than food abundance (e.g., survival probability [*sensu* Fretwell and Lucas 1970]).

Morris and Mukherjee (2007) advocated use of foraging behaviors to index habitat quality and carrying capacity. Although other studies have used foraging behavior of birds to infer habitat quality (Lyons 2005, Dobbs et al. 2007, Castillo-Guerrero et al. 2009), my results indicate dabbling ducks may not use foraging patches or vary behavior relative to food resources in winter in the MAV. Similarly, Percival et al. (1998) found that waterfowl abundance did not always correlate with food availability, and Fleming (2010) reported that waterfowl abundance was not always associated with an index of habitat quality in winter. Complexities of habitat selection and decision-making processes may contribute to these contradictory results (Johnson 2007). Furthermore, state-dependent influences such as nutrient requirements, predation risk, social status, and variable metabolic requirements likely result in different fitness-maximizing strategies among individuals which makes discontinuities in foraging strategies difficult to detect (Percival et al. 1998, Nolet et al. 2001, van Gils et al. 2004, Morris and Mukherjee 2007, Castillo-Guerrero et al. 2009). Furthermore, waterbirds may use conspecifics or other proximate cues as habitat selection criteria which may not reflect food availability (Pöysä et al 1998, Chapter I). As I did not observe a change in waterfowl foraging rates or use of plots before and after seed depletion (i.e., a cessation

in further food reduction greater than decomposition rates), I caution researchers that assessing patch quality using behavior of nonbreeding dabbling ducks may require different metrics or methods than used in my experiments (van Gils et al. 2004).

Variation in foraging profitability among wetlands also may have been influenced by opportunity costs associated with alternate food sources or difference in predation risk among wetlands. I assumed that most influences on foraging profitability (e.g., water depth, soils, thermoregulation costs, and human disturbances) were similar among plots within sites. Water depth varied slightly temporally and spatially, but remained within ranges reported desirable to dabbling ducks and did not vary by treatments (Fredrickson and Taylor 1982, Euliss and Harris 1987, Chapter I). However, slight variations in water depth have been reported to affect GUD of other waterbirds and may have influenced foraging profitability among my study sites (Gawlik 2002). Soil characteristics likely did not influence foraging profitability of millet because it was spread on top of substrate and litter (Nolet et al. 2006, Nolet and Klaasen 2009). However, other taxa of moist-soil seeds that were buried in the substrate may have caused food acquisition costs to vary among sites. Furthermore, I selected sites in waterfowl sanctuaries and observers did not disturb waterfowl when conducting observations. Thus, human disturbance is not a likely explanation for differences in food exploitation among sites (Brown 1988, Madsen and Fox 1995, Percival et al. 1998). Finally, it is not likely that differences in seed abundance were related to environmental effects on thermoregulation or metabolism because all wetlands were located in the central – northern portion of the MAV and there was no consistent trend between seed depletion and latitude (Lovvorn 1989, Guillemain et al. 2002).

A likely source of variation in foraging profitability among wetlands may have been differences in foraging or processing costs associated with many different seed taxa in moist-soil wetlands. Natural seeds vary in size, metabolizable energy, digestibility, chemical composition, and morphology, all of which influence energy gain (Barras et al. 1996, van Eerden and Munsterman 1997, Kaminski et al. 2003). My experimental plots contained 28.1 (SE = 1.1, $n = 4$) taxa of moist-soil seeds, even though seed production was limited in the previous growing season. Waterfowl are able to differentiate among natural seeds when submerged or buried in substrate and may select taxa by size or nutritional content (Lovvorn and Gillingham 1996, van Eerden and Munsterman 1997, Figuerola et al. 2005, Gurd 2006, Richman and Lovvorn 2009). Furthermore, because natural seeds are submerged in wetlands and often buried in substrate, evaluation of foraging profitability is likely not possible without active sampling by waterfowl. Seeds buried deep in sediments may not have biased estimates of availability because seeds in the top 5 cm of core samples have been shown to account for approximately 80% of all seeds in core samples of 10 cm in depth (Olmstead 2010, G. Evans-Peters, Oregon State University, unpublished data). Therefore, foraging profitability may be linked to seed and tuber composition in wetlands and waterfowl are likely unable to assess profitability without foraging (Klaassen et al. 2007).

Brasher (2010) acknowledged the possibility that moist-soil seeds may float and be redistributed by wind and water after wetland flooding. Floating seeds could aggregate along shorelines and edges of vegetation leading to irregular seed distribution and difficulties in deriving unbiased estimates of seed abundance. However, I sampled plots after wetlands had been flooded for at least 7 days and did not observe floating

seeds or waterfowl foraging wetland edges where seeds may have aggregated if such redistribution had occurred. In a post-hoc laboratory experiment, I determined that 94.4% (SE = 0.7%, $n = 8$) of millet sank immediately after soaking in water for 48 hrs per my experimental protocol. Furthermore, only an additional 5.6% (SE = 0.7%, $n = 8$) of millet seeds that initially sank refloated during the subsequent 2-week period. Moreover, because I recovered seeds that did not immediately sink with sweep nets, significant bias from seed redistribution is unlikely, and waterfowl consumption was the most likely cause of rapid millet decline in experimental wetlands.

I did not find evidence that diurnal dabbling duck abundance was related to food availability in experimental wetlands. Instead, ducks may have responded to other factors associated with the specific site or surrounding habitats (van Gils and Tijssen 2007, Brasher 2010). The functional response of ducks enable them to benefit from increasing food abundances by increasing their intake rate (Arzel et al. 2007), but they lack omniscient knowledge of the spatial variation of submerged foods and must learn by active sampling (Lovvorn and Gillingham 1996). Other studies have shown that birds behave as fitness maximizers rather than energy maximizers and feed in patches above a critical food density rather than in patches with greatest density (Creswell 1994, Lovvorn and Gillingham 1996, Nolet et al. 2006). My data from late December and early January revealed that ducks fed in all available foraging patches equally, but reduced seeds disproportionately among treatments. Therefore, seed densities and intake rates may have been related positively. If this was the case, then dabbling ducks may not have had omniscient knowledge of food availability among treatments and used patches because

food density exceeded the critical density rather than foraged in the most profitable patches (Tome 1988, van Eerden and Munsterman 1997, Klaassen et al. 2007).

Because my experimental wetlands were located in sanctuaries, ducks may have used these sites primarily for risk aversion rather than foraging. However, I did not find that dabbling ducks reduced their foraging effort after a food density threshold was reached, but rather observed an increase in the proportion of ducks foraging throughout winter. Arengo and Baldassarre (1995) observed a similar pattern in American flamingos (*Phoenicopterus ruber ruber*) that foraged longer when food was less abundant. Perhaps ducks consumed invertebrates or grit in experimental wetlands; however, aquatic invertebrates may be less abundant in moist-soil wetlands than other wetland types in the MAV (Chapter I, Wehrle et al. 1995, Batema et al. 2005) and dabbling duck species abundant in my study wetlands primarily consume seeds during winter (Bellrose 1980, Combs and Fredrickson 1996, Ballard et al. 2004). Furthermore, dabbling ducks would likely not need to forage intensively for grit in wetlands as small stones and other inorganic matter were abundant in core samples (H. Hagy, Mississippi State University, unpublished data).

Mean millet density among plots and sites in early January (~10 kg/ha) was only a fifth of the GUD estimate for harvested rice (50 kg/ha) and similar to residual corn abundance after waterfowl ceased feeding in dry fields (15 kg/ha; Baldassarre and Bolen 1984, Reinecke et al. 1989, Greer et al. 2009). However, abundance of residual millet and natural seeds and tubers combined was 3–4 times the GUD in rice fields (i.e., ~180 kg/ha; Principal Experiment). Naylor (2002) determined that moist-soil wetlands in California contained 30 and 163 kg/ha of natural seeds and tubers at the end of winters

1999–2000 and 2000–2001, respectively, but did not present data on individual taxa. He speculated yearly differences in residual food abundances were due to greater seed abundance in other foraging habitats, and differences from 50 kg/ha (Reinecke et al. 1989) were due to the increased heterogeneous structure of moist-soil wetlands compared to rice fields. Greer et al. (2007) indicated that moist-soil seeds declined by 70 and 87% to approximately 459 and 235 kg/ha, respectively, during winters 2000–2001 and 2000–2002 in northern Missouri wetlands. In both years, decline of barnyardgrass (*Echinochloa* spp.) exceeded that of other seeds (Greer et al. 2007). Sponberg and Lodge (2005) and Lovvorn (1994a) also showed that canvasbacks (*Aythya valisineria*) reduced tubers to densities that varied among wetlands and years and tuber selection depended on size (Lovvorn and Gillingham 1996). Thus, other studies have shown similar variability in residual seed and tuber densities after waterfowl abandon wetlands.

Greer et al. (2009) indicated that food availability thresholds probably vary among locations, but demonstrated variability was slight in flooded rice fields after harvest and would not substantially bias carrying capacity models. Furthermore, they questioned the feasibility of building complex models to account for variable food thresholds based on ecological variables. I agree that complex carrying capacity models would be difficult to parameterize, but observed variable food availability thresholds in moist-soil wetlands in the MAV. Because millet declined rapidly and to much lesser densities than natural seeds, a fixed density threshold for all seeds and tubers combined may not accurately reflect responses of waterbirds in a stochastic environment (Table 3.3). Therefore, seed composition of wetlands may contribute significantly to variation in a food density threshold.

Whereas GUD was defined as a threshold that explains animal movement to another patch based on opportunity costs, I define a food availability threshold (FAT) as a density of foods at which animals no longer reduce food resources within a patch because various environmental factors limit availability. The FAT for waterfowl in moist-soil wetlands in winter is likely less than initial GUDs at which food resources are abundant on the landscape and movements among foraging patches may be motivated by food abundance in other patches (Charnov 1976, Brown 1988, van Gils et al. 2004). My experiment identified FATs that likely approximated the critical food density and were unique to each moist-soil wetland (i.e., food density where daily energy acquisition equals energy expended searching for and processing foods [threshold of energy balance, Nolet et al. 2006]; Nolet et al. 2002, van Gils et al. 2004, Richman and Lovvorn 2009). Differences in residual densities of taxa after waterfowl no longer removed seeds suggest that FATs may depend on taxonomic composition of foraging patches and a single aggregate seed density may not accurately predict FAT.

My research produced seminal data on foraging ecology for dabbling ducks and a range of FATs which illustrate the complexities predicting food availability in moist-soil wetlands in winter. I advocate a combination of concurrent estimation of food availability and diet analysis of experimentally-collected dabbling ducks to determine strategies of waterfowl in wetlands where food resources are near FAT in the MAV. Future researchers may desire to examine the relative influence of predation risk, seed composition, human disturbance, other wetland characteristics, and endogenous factors on FAT for dabbling ducks in moist-soil wetlands. Determination of the relative

influences of environmental and endogenous factors on FAT might allow accurate prediction of food availability without complex models (Greer et al. 2009).

Management Implications

Currently, NAWMP Joint Ventures use daily ration models to predict duck use and determine energetic carrying capacity of habitats. Potential variability among estimates of FAT indicates that daily ration models assuming a fixed foraging efficiency threshold may not predict accurately duck use of wetland foods, and other factors that influence fitness prospects may contribute to waterfowl habitat use and food availability. I estimated that experimentally manipulated densities of millet plus moist-soil seeds and tubers present in the seed bank were reduced to approximately 180 kg/ha in study sites in my principal experiment. However, residual seed densities varied among taxa and sites indicating that a fixed FAT may not measure accurately food availability. Assuming 180 kg/ha approximates FAT for managed moist-soil wetlands in the MAV because, on average, ducks did not reduce aggregate seed masses below this value, estimates of seed availability provided by Kross et al. (2008b) would be reduced by approximately 32% (i.e., 180 kg/ha divided by 556 kg/ha). However, estimates of reduction in seed and tuber availability would range from 5–71% when I applied the maximum and minimum estimates of seed reduction among the 12 experimental plots in early December. Reduced food availability in moist-soil wetlands might indicate the need for active management to increase seed and tuber production or increased moist-soil habitat in the MAV. Scientists and conservation planners should consider evaluating relative influences of other factors (e.g., disturbance, predation risk, location, soil substrate, water

depth, etc.) on the FAT to determine if more complex models are needed to estimate food availability for waterfowl in moist-soil wetlands in the MAV.

LITERATURE CITED

- Abraham, K., M. Anderson, R. Clark, L. Colpitts, E. Reed, R. Bishop, J. Eadie, M. Petrie, F. Rohwer, M. Tome, and A. Rojo. 2007. North American waterfowl management plan continental progress assessment final report. <<http://www.fws.gov/birdhabitat/NAWMP/files/FinalAssessmentReport.pdf>>. Accessed 1 July 2010.
- Adams-Hunt, M. M., and L. F. Jacobs. 2007. Cognition of foraging. Pages 105–138 in D. W. Stephens, J. S. Brown, and R. C. Ydenberg, editors. Foraging behavior and ecology. University of Chicago Press, Chicago, Illinois, USA.
- Amano, T., K. Ushiyama, G. Fujita, and H. Higuchi. 2004. Alleviating grazing damage by white-fronted geese: an optimal foraging approach. *Journal of Applied Ecology* 41:675–688.
- Amano, T., K. Ushiyama, G. Fujita, and H. Higuchi. 2006. Foraging patch selection and departure by non-omniscient foragers: a field example in white-fronted geese. *Ethology* 112:544–553.
- Arengo, F. A., and G. A. Baldassarre. 1995. Effects of food density on the behavior and distribution of nonbreeding American flamingos in Yucatan, Mexico. *Condor* 97:325–334.
- Arzel, C., and J. Elmberg. 2004. Time use, foraging behavior and microhabitat use in a temporary guild of spring-staging dabbling ducks (*Anas* spp.). *Ornis Fennica* 81:157–168.
- Arzel, C., M. Guillemain, D. B. Gurd, J. Elmberg, H. Fritz, A. Arnaud, C. Pin, and F. Bosca. 2007. Experimental functional response and inter-individual variation in foraging rate of teal (*Anas crecca*). *Behavioural Processes* 75:66–71.
- Baldassarre, G. A., and E. G. Bolen. 2006. Waterfowl ecology and management. Second edition. Krieger, 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.

- Barras, S. C., R. M. Kaminski, and L. A. Brennan. 1996. Acorn selection by female wood ducks. *Journal of Wildlife Management* 60:592–602.
- Batema, D. L., R. M. Kaminski, and P. A. Magee. 2005. Wetland invertebrate communities and management of hardwood bottomlands in the Mississippi Alluvial Valley. Pages 173–199 in L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Beekman, J. H., M. R. van Eerden, and S. Dirksen. 1991. Bewick's swans (*Cygnus columbianus bewickii*) utilizing the changing resource of *Potamogeton pectinatus* during autumn in the Netherlands. Pages 238–248 in J. Sears and P. J. Bacon, editors. *Proceedings of the Third International Swan Symposium*, December 1989, Oxford, United Kingdom.
- Bellrose, F. C. 1980. *Ducks, geese, and swans of North America*. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bernstein, C., A. Kacelnik, and J. R. Krebs. 1988. Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology* 57:1007–1026.
- Bohm, W. 1979. *Methods of studying root systems*. Springer-Verlag, Berlin, Germany.
- Bowyer, M. W., J. D. Stafford, A. P. Yetter, C. S. Hine, M. M. Horath, and S. P. Havera. 2005. Moist-soil plant seed production for waterfowl at Chautauqua National Wildlife Refuge, Illinois. *American Midland Naturalist* 154:331–341.
- Brasher, M. G. 2010. *Duck use and energetic carrying capacity of actively and passively managed wetlands in Ohio during autumn and spring migration*. Dissertation, The Ohio State University, Columbus, USA.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral and Ecological Sociobiology* 22:37–47.
- Bryson, C. T., and M. S. DeFelice. 2009. *Weeds of the south*. University of Georgia Press, Athens, USA.
- Canadian Wildlife Service and U.S. Fish and Wildlife Service. 1986. *North American waterfowl management plan*. Canadian Wildlife Service and U.S. Fish and Wildlife Service. Washington, D.C., USA.
- Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology* 61:119–128.

- Castillo-Guerrero, J. A., G. Fernandez, G. Arellano, and E. Mellink. 2009. Diurnal abundance, foraging behavior, and habitat use by non-breeding marbled godwits and willets at Guerrero Negro, Baja California Sur, Mexico. *Waterbirds* 32:400–407.
- Central Valley Joint Venture Implementation Plan [CVJV]. 2006. U. S. Fish and Wildlife Service, Sacramento, California, USA.
- 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.
- Combs, D. L., and L. H. Fredrickson. 1996. Foods used by mallards wintering in southeastern Missouri. *Journal of Wildlife Management* 60:603–610.
- Creswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* 63:589–600.
- Dobbs, R. C., T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes. 2007. Population density affects foraging behavior of male black-throated blue warblers during the breeding season. *Journal of Field Ornithology* 78:133–139.
- Dugger, B. D., M. L. Moore, R. S. Finger, and M. J. Petrie. 2007. True metabolizable energy for seeds of common moist-soil plant species. *Journal of Wildlife Management* 71:1964–67.
- Euliss, N. H., and S. W. Harris. 1987. Feeding ecology of northern pintails and green-winged teal wintering in California. *Journal of Wildlife Management* 51:724–732.
- Figuerola, J., R. Mateo, A. J. Green, J. Mondain-Monval, H. Lefranc, and G. Mentaberre. 2005. Grit selection in waterfowl and how it determines exposure to ingested lead shot in Mediterranean wetlands. *Environmental Conservation* 32:226–236.
- Fleming, K. S. 2010. Effects of management and hydrology on vegetation, winter waterbird use, and water quality on Wetlands Reserve Program lands, Mississippi. Thesis, Mississippi State University, Mississippi State, USA.
- Foster, M. A., M. J. Gray, and R. M. Kaminski. 2010. Agricultural seed biomass for migrating and wintering waterfowl in the southeastern United States. *Journal of Wildlife Management* 74:489–495.

- Fredrickson, L. H. 2005. Contemporary bottomland hardwood systems: structure, function and hydrologic condition resulting from two centuries of anthropogenic activities. Pages 19–35 in L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally-flooded impoundments for wildlife. U. S. Fish and Wildlife Service Resource Publication 148, Washington, D.C., USA.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Fritz, H., D. Durant, and M. Guillemain. 2001. Shape and sources of variations of the functional response of wildfowl: an experiment with mallards. *Oikos* 93:488–496.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72:329–346.
- Goss-Custard, J. D., R. A. Stillman, A. D. West, R. W. G. Caldow, and S. McGorty. 2002. Carrying capacity in overwintering migratory birds. *Biological Conservation* 105:27–41.
- 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.
- Greer, D. M., B. D. Dugger, K. J. Reinecke, and M. J. Petrie. 2009. Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 73:1125–1133.
- Guillemain, M., P. Duncan, and H. Fritz. 2001. Switching to a feeding method that obstructs vision increases head-up vigilance in dabbling ducks. *Journal of Avian Biology* 32:345–350.
- Guillemain, M., H. Fritz, and P. Duncan. 2002. Foraging strategies of granivorous dabbling ducks wintering in protected areas of the French Atlantic coast. *Biodiversity and Conservation* 11:1721–1732.
- Gurd, D. B. 2006. Filter-feeding dabbling ducks (*Anas* spp.) can actively select particles by size. *Zoology* 109:120–126.

- Havens, J. H., R. M. Kaminski, J. B. Davis, and S. K. Riffell. 2009. Winter abundance of waterfowl and waste rice in managed Arkansas rice fields. *Proceedings of the Annual Southeastern Association of Fish and Wildlife Agencies Conference* 63:41–46.
- Havera, S. P. 1999. Waterfowl of Illinois: status and management. *Illinois Natural History Survey Special Publication* 21.
- Hoffman, R. D., and T. A. Bookout. 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.
- Johnson, M. D. 2007. Measuring habitat quality: a review. *The Condor* 109:489–504.
- 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.
- Kaminski, R. M., and E. A. Gluesing. 1987. Density- and habitat-related recruitment in mallards. *Journal of Wildlife Management* 51:141–148.
- Kaminski, R. M., and H. H. Prince. 1981. Dabbling duck activity and foraging responses to aquatic macroinvertebrates. *Auk* 98:115–126.
- King, S. L., J. P. Shepard, K. Ouchley, J. A. Neal, and K. Ouchley. 2005. Bottomland hardwood forests: past, present, and future. Pages 1–17 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Klaassen, R. H. G., B. A. Nolet, and C. H. A. Van Leeuwen. 2007. Prior knowledge about spatial pattern affects patch assessment rather than movement between patches in tactile-feeding mallard. *Journal of Animal Ecology* 76:20–29.
- Kross, J., R. M. Kaminski, K. J. Reinecke, and A. T. Pearse. 2008*a*. Conserving waste rice for wintering waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:1383–1387.
- Kross, J., R. M. Kaminski, K. J. Reinecke, E. J. Penny, and A. T. Pearse. 2008*b*. Moist-soil seed abundance in managed wetlands in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:707–714.

- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models, Second edition. SAS Institute, Inc. Cary, North Carolina, USA.
- Loesch, C. R., K. J. Reinecke, and C. K. Baxter. 1994. Lower Mississippi Valley Joint Venture evaluation plan. North American waterfowl management plan, U. S. Fish and Wildlife Service, Vicksburg, Mississippi, USA.
- Lovvorn, J. R. 1989. Distributional responses of canvasback ducks to weather and habitat change. *Journal of Applied Ecology* 26:113–130.
- Lovvorn, J. R. 1994a. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. *Hydrobiologia* 280:223–233.
- Lovvorn, J. R. 1994b. Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering Canvasbacks. *Journal of Animal Ecology* 63:11–23.
- Lovvorn, J. R., and M. P. Gillingham. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77:435–451.
- Lyons, J. E. 2005. Habitat-specific foraging of prothonotary warblers: deducing habitat quality. *The Condor* 107:41–49.
- Madsen, J., and A. D. Fox. 1995. Impacts of hunting disturbance on waterbirds – a review. *Wildlife Biology* 1:193–207.
- 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.
- Manley, S. W., R. M. Kaminski, P. B. Rodrigue, J. C. Dewey, S. H. Schoenholtz, P. D. Gerard, and K. J. Reinecke. 2009. Soil and nutrient retention in winter-flooded ricefields with implications for watershed management. *Journal of Soil and Water Conservation* 64:173–182.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- Martin, A. C., and W. D. Barkley. 1961. Seed identification manual. University of California Press, Berkeley, USA.
- Martin, P., and P. Bateson. 1998. Measuring behavior: an introductory guide. Second edition. Cambridge University Press, United Kingdom.

- Michael, P. W. 1983. Taxonomy and distribution of *Echinochloa* species with special reference to their occurrence as weeds of rice. Pages 291–306 in Proceedings of the conference on weed control in rice, International Rice Research Institute, Los Baños, Laguna, Philippines.
- Moon, J. A., and D. A. Haukos. 2006. Survival of female northern pintails wintering in the Playa Lakes Region. *Journal of Wildlife Management* 70:777–783.
- Moon, J. A., and D. A. Haukos. 2008. Habitat use of female northern pintails in the playa lakes region of Texas. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 62:82–87.
- Moon, J. A., and D. A. Haukos. 2009. Factors affecting body condition of northern pintails wintering in the Playa Lakes Region. *Waterbirds* 32:87–95.
- Moon, J. A., D. A. Haukos, and L. M. Smith. 2007. Declining body condition of northern pintails wintering in the Playa Lakes Region. *Journal of Wildlife Management* 71:218–221.
- Morris, D. W. 1989. Density-dependent habitat selection: testing the theory with fitness data. *Evolutionary Ecology* 3:80–94.
- Morris, D. W., and S. Mukherjee. 2007. Can we measure carrying capacity with foraging behavior? *Ecology* 88:597–604.
- Murray, B. C., W. A. Jenkins, R. A. Kramer, and S. P. Faulkner. 2009. Valuing ecosystem services from wetlands restoration in the Mississippi Alluvial Valley. Report No. 09-02, Nicholas Institute for Environmental Policy Solutions, Duke University. <<http://www.nicholas.duke.edu/institute/msvalley.pdf>>. Accessed 14 Aug. 2010.
- 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, USA.
- Neely, W. W. 1956. How long do duck foods last underwater? *Transactions of the North American Wildlife and Natural Resources Conference* 21:191–198.
- Nelms, K. D. 2007. Wetland management for waterfowl: a handbook. Mississippi River Trust, Stoneville, Mississippi, USA.
- Nolet, B. A., R. M. Bevan, M. Klaasen, O. Langevoord, and Y. G. J. T. Van der Heijden. 2002. Habitat switching by Bewick's swans: maximization of average long-term energy gain? *Journal of Animal Ecology* 71:979–993.

- Nolet, B. A., V. N. Fuld, and M. E. C. van Rijswijk. 2006. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos* 112:353–362.
- Nolet, B. A., and M. Klaasen. 2009. Retrodicting patch use by foraging swans in a heterogeneous environment using a set of functional responses. *Oikos* 118:431–439.
- Nolet, B. A., O. Langevoord, and R. M. Bevan. 2001. Spatial variation in tuber depletion by swans explained by differences in net intake rates. *Ecology* 82:1655–1667.
- 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.
- Olmstead, V. G. 2010. Evaluation of management strategies on moist-soil seed availability and depletion on Wetland Reserve Program sites in the Mississippi Alluvial Valley. Thesis, Arkansas Tech University, Russellville, USA.
- Percival, S. M., W. J. Sutherland, and P. R. Evans. 1998. Intertidal habitat loss and wildfowl numbers: applications of a spatial depletion model. *Journal of Applied Ecology* 35:57–63.
- Pöysä, H., J. Elmberg, K. Sjöberg, and P. Nummi. 1998. Habitat selection rules in breeding mallards (*Anas platyrhynchos*): a test of two competing hypotheses. *Oecologia* 114:283–287.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52:137–154.
- Raveling, D. G., and M. E. Heitmeyer. 1989. Relationships of population size and recruitment of pintails to habitat conditions and harvest. *Journal of Wildlife Management* 53:1088–1103.
- Reinecke, K. J., R. C. Barkley, and C. K. Baxter. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. Pages 325–337 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, USA.
- Reinecke, K. J., and R. M. Kaminski. 2007. Lower Mississippi Valley Joint Venture, waterfowl working group memorandum. U.S. Fish and Wildlife Service, Vicksburg, Mississippi, 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, USA.
- Reinecke, R. M., and W. B. Uihlein. 2006. Lower Mississippi Valley Joint Venture, waterfowl working group memorandum. U.S. Fish and Wildlife Service, Vicksburg, Mississippi, USA.
- Richardson, D. M., and R. M. Kaminski. 1992. Diet restriction, diet quality, and prebasic molt in female mallards. *Journal of Wildlife Management* 56:531–539.
- Richman, S. E., and J. R. Lovvorn. 2009. Predator size, prey size and threshold food densities of diving ducks: does a common prey base support fewer large animals? *Journal of Animal Ecology* 78:1033–1042.
- SAS Institute, Inc. 2008. SAS[®] 9.2, Enhanced Logging Facilities, Cary, North Carolina, USA.
- Schummer, M. L., H. M. Hagy, K. S. Fleming, J. C. Cheshier, and J. T. Callicutt. 2011. Moist-soil wetland plants of the Mississippi Alluvial Valley. University Press of Mississippi, Jackson, USA. In Press.
- Seed Images. 2008. Discover seeds. Colorado State University. Fort Collins, USA. <<http://www.seedimages.com>>. Accessed 24 Feb. 2009.
- Sherfy, M. H. 1999. Nutritional value and management of waterfowl and shorebird foods in the Atlantic Coastal moist-soil impoundments. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, USA.
- Sherfy, M. H., R. L. Kilpatrick, and K. E. Webb, Jr. 2001. Nutritional consequences of gastrolith ingestions in blue-winged teal: a test of the hard-seed for grit hypothesis. *Journal of Wildlife Management* 65:406–414.
- Sponberg, A. F., and D. M. Lodge. 2005. Seasonal belowground herbivory and a density refuge from waterfowl herbivory for *Vallisneria americana*. *Ecology* 86:2127–2134.
- Stafford, J. D., 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 Valleys. *Waterbirds* 30:394–402.
- Stafford, J. D., R. M. Kaminski, K. J. Reinecke, and S. W. Manley. 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:61–69.

- Steckel, J. D. 2003. Food availability and waterfowl use in mid-migration habitats in central and northern Ohio. Thesis, The Ohio State University, Columbus, USA.
- Straub, J. N. 2008. Energetic carrying capacity of habitats used by spring migrating waterfowl in the Upper Mississippi and Great Lakes Region during spring migration. Thesis, The Ohio State University, Columbus, USA.
- Strickland, B. K., R. M. Kaminski, K. D. Nelms, and A. Tullos, editors. 2009. Waterfowl habitat management handbook. Mississippi State University Extension Service Publication 1864, Mississippi State, USA.
- Sutherland, W. J. 1983. Aggregation and the 'ideal free' distribution. *Journal of Animal Ecology* 52:821–828.
- Tome, M. W. 1988. Optimal foraging: food patch depletion by ruddy ducks. *Oecologia* 76:27–36.
- Twedt, D. J., and C. O. Nelms. 1999. Waterfowl density on agricultural fields managed to retain water in winter. *Wildlife Society Bulletin* 27:924–930.
- Uihlein, W. B. 2000. Extent and distribution of waterfowl habitat managed on private lands in the Mississippi Alluvial Valley. Dissertation, Mississippi State University, Mississippi State, USA.
- van Eerden, M. R., and M. J. Munsterman. 1997. Patch use upon touch: filter-feeding European teal (*Anas crecca*) have environmentally and socially determined foraging goals. Pages 165–185 in M. R. Van Eerden, editor. *Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands*, Rijksuniversiteit Groningen, The Netherlands.
- van Gils, J. A., P. Edelaar, G. Escudero, and T. Piersma. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104:197–204.
- van Gils, J. A., and W. Tijssen. 2007. Short-term foraging costs and long-term fueling rates in central-place foraging swans revealed by giving-up exploitation times. *American Naturalist* 169:609–620.
- Wehrle, B. W., R. M. Kaminski, B. D. Leopold, and W. P. Smith. 1995. Aquatic invertebrate resources in Mississippi forested wetlands during winter. *Wildlife Society Bulletin* 23:774–783.
- Yabuno, T. 1983. Biology of *Echinochloa* species. Pages 307–318 in *Proceedings of the conference on weed control in rice*, International Rice Research Institute, Los Baños, Laguna, Philippines.

Ydenberg, R. C., J. S. Brown, and D. W. Stephens. 2007. Foraging: an overview. Pages 1–28 *in* D. W. Stephens, J. S. Brown, and R. C. Ydenberg, editors. Foraging behavior and ecology. University of Chicago Press, Chicago, Illinois, USA.

Zar, J. H. 2009. Biostatistical analysis. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Table 3.1. Seeds and tubers recovered from moist-soil core samples and commonly consumed by waterfowl (Chapter II), their true metabolizable energy values (TME; kcal/g), and reference.

Taxa	TME	Reference
Alismataceae		
<i>Sagittaria</i> spp.	3.06	Hoffman and Bookout 1985
Amaranthaceae		
<i>Amaranthus</i> spp.	2.97	Checkett et al. 2002
Asteraceae		
<i>Bidens</i> spp.	0.55	Sherfy 1999
<i>Iva annua</i>	2.39	Kaminski et al. 2003
Boraginaceae		
<i>Heliotropium indicum</i>	2.39	Kaminski et al. 2003
Cyperaceae		
<i>Carex</i> spp.	1.36	Straub 2008
<i>Cyperus</i> spp. (seeds)	1.41 1.96 1.69	Ballard et al. 2004 Sherfy 1999 \bar{x}
<i>Cyperus</i> spp. (tubers)	2.50	Straub 2008
<i>Eleocharis</i> spp.	0.50 -0.18 0.16	Dugger et al. 2007 Sherfy 1999 \bar{x}
<i>Scirpus</i> spp.	1.92 0.65 ^a 0.64 0.50	Ballard et al. 2004 Dugger et al. 2007 Sherfy 1999 Sherfy 1999

Table 3.1. Continued.

	0.93	\bar{x}
Malvaceae		
<i>Althaea officinalis</i>	2.19	Straub 2008
<i>Sida spinosa</i>	2.19	Straub 2008
Poaceae		
<i>Digitaria</i> spp.	3.10	Checkett et al. 2002
	3.09	Checkett et al. 2002
	3.10	\bar{x}
<i>Echinochloa</i> spp.	2.61	Checkett et al. 2002
	2.54	Reinecke et al. 1989
	2.65	Sherfy 1999
	2.67	Sherfy et al. 2001
	2.62	\bar{x}
<i>Eragrostis</i> spp.	2.39	Kaminski et al. 2003
<i>Leersia oryzoides</i>	3.00	Hoffman and Bookout 1985
	2.82	Hoffman and Bookout 1985
	2.91	\bar{x}
<i>Oryza sativa</i>	3.34	Reinecke et al. 1989
<i>Panicum</i> spp.	2.75	Checkett et al. 2002
	2.05	Sherfy 1999
	2.54	Sherfy 1999
	2.45	\bar{x}
<i>Paspalum dilatatum</i>	1.57	Checkett et al. 2002
<i>Paspalum urvillei</i>	1.57	Checkett et al. 2002
<i>Setaria</i> spp.	2.88	Checkett et al. 2002

Table 3.1. Continued.

<i>Sorghum bicolor</i>	3.36	Sherfy 1999
	3.49	Sherfy et al. 2001
	3.43	\bar{x}
<i>Urochloa platyphylla</i>	2.73	Straub 2008
Polygonaceae		
<i>Polygonum hydropiperoides</i>	1.59	Ballard et al. 2004
<i>Polygonum lapathifolium</i>	1.52	Checkett et al. 2002
<i>Polygonum pensylvanicum</i>	1.08	Hoffman and Bookout 1985
	1.25	Hoffman and Bookout 1985
	1.30	Sherfy et al. 2001
	1.21	\bar{x}
<i>Rhynchospora</i> spp.	1.86	Checkett et al. 2002
Rubiaceae		
<i>Diodia virginiana</i>	2.39	Kaminski et al. 2003

^a*Scirpus maritimus* also known as *Schoenoplectus maritimus*

Table 3.2. Density of all dabbling ducks (Anatini; ducks/ha/site/survey; \bar{x} , SE; $n = 4$) and those feeding in 0.5-ha plots supplemented in mid-December 2008 with 50, 250, or 550 kg/ha of Japanese millet (*Echinochloa frumentacea*) observed from mid-December 2008 to late February 2009 and mid-December 2008 to early January 2009 (Late December) in 4 experimental wetlands in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.

Group	Period	Millet density (kg/ha)					
		50		250		550	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Dabbling ducks	December–February	44.4	14.6	46.1	6.7	63.1	17.6
	Late December	49.1	22.5	66.7	18.3	124.0	68.7
Feeding dabbling ducks	December–February	18.3	7.0	21.2	4.9	27.1	9.2
	Late December	20.9	14.6	24.6	9.0	50.6	29.5

Table 3.3. Density of Japanese millet (*Echinochloa frumentacea*; kg[dry]/ha; \bar{x} , SE; $n = 4$) plus other *Echinochloa* species and other seeds and tubers present in 4 experimental wetlands from mid-December 2008 to late-February 2009 in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.

Taxon	Mid December		Early January		Late January		Late February	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
<i>Echinochloa</i> spp.	286.7	63.6	10.2	2.6	11.9	3.3	10.9	3.8
<i>Polygonum pensylvanicum</i>	63.9	14.5	58.7	12.3	70.8	19.6	55.1	12.4
<i>Sida spinosa</i>	50.7	18.0	47.4	16.7	40.5	14.9	53.9	24.3
<i>Polygonum hydropiperoides</i>	32.7	16.8	26.8	15.6	22.7	12.6	20.3	12.4
<i>Rhynchospora</i> spp.	17.3	8.6	21.8	10.9	25.9	12.4	17.7	8.9
<i>Digitaria</i> spp.	4.4	2.5	2.0	1.7	2.1	0.7	3.4	2.7
<i>Panicum</i> spp.	3.1	1.1	1.9	1.3	1.1	0.7	1.4	0.7
Others	2.7	0.9	3.1	1.8	2.5	0.7	2.0	0.9

Table 3.3 Continued.

<i>Polygonum lapathifolium</i>	1.7	0.7	6.1	2.8	6.3	3.8	1.9	1.2
<i>Urochloa platyphylla</i>	1.7	0.7	1.1	0.4	1.3	0.3	0.4	0.2
<i>Setaria spp.</i>	1.2	0.7	1.2	0.4	1.5	0.8	1.4	0.5

Table 3.4 Combined density of Japanese millet (*Echinochloa frumentacea*; kg[dry]/ha; \bar{x} , SE; $n = 4$) and naturally occurring *Echinochloa* species in 0.5-ha plots supplemented in mid-December 2008 with 50, 250, or 550 kg/ha of Japanese millet before deposition of millet (Pre-treatment), in early and late January 2009, and in late February 2009 in 4 experimental, moist-soil wetlands in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.

Density	Pre-treatment		Early January		Late January		Late February	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
50	3.8	1.7	5.5	1.8	4.7	1.9	7.5	5.6
250	6.0	4.7	13.4	5.8	18.9	7.1	18.3	9.1
550	8.9	6.0	11.7	5.3	12.2	5.4	7.0	3.8

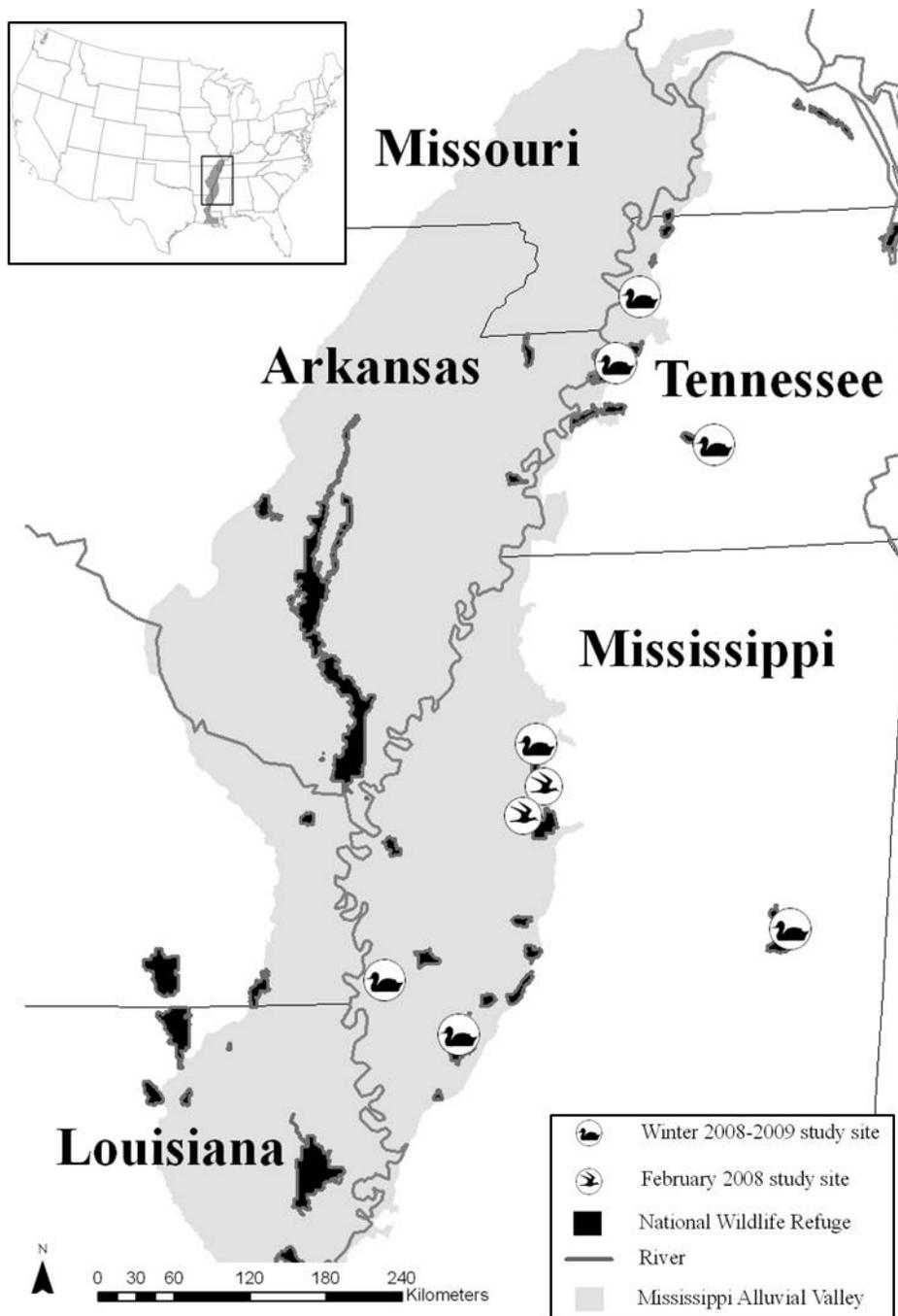


Figure 3.1. Locations of 2 study sites sampled during February 2008 and 7 study sites sampled from mid-December 2008 to late February 2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

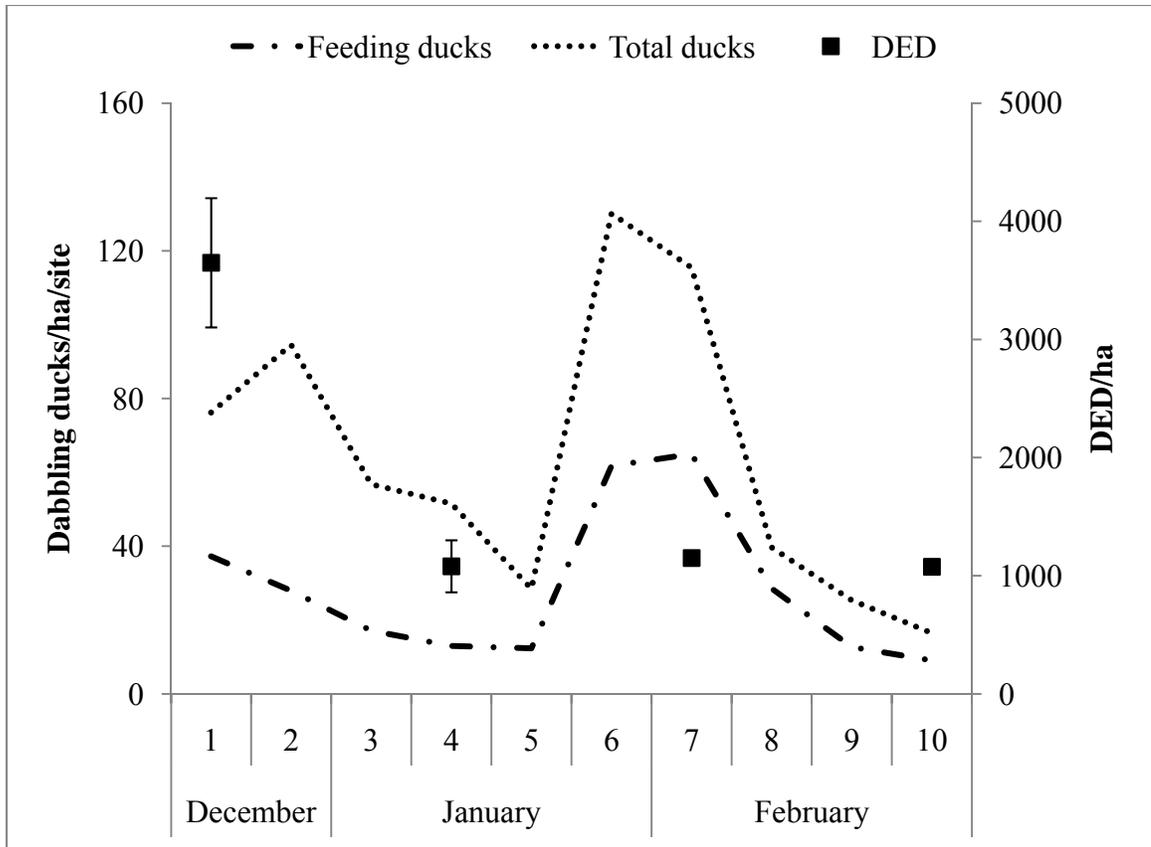


Figure 3.2. Density of total and feeding dabbling ducks (Anatini; ducks/ha/site) and estimated duck energy days (DED/ha \pm SE; Reinecke and Kaminski 2007) in 0.5-ha plots supplemented in mid-December with 50, 250, or 550 kg/ha of Japanese millet (*Echinochloa frumentacea*) in 4 experimental wetlands sampled during mid-December 2008 to late February 2009 in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.

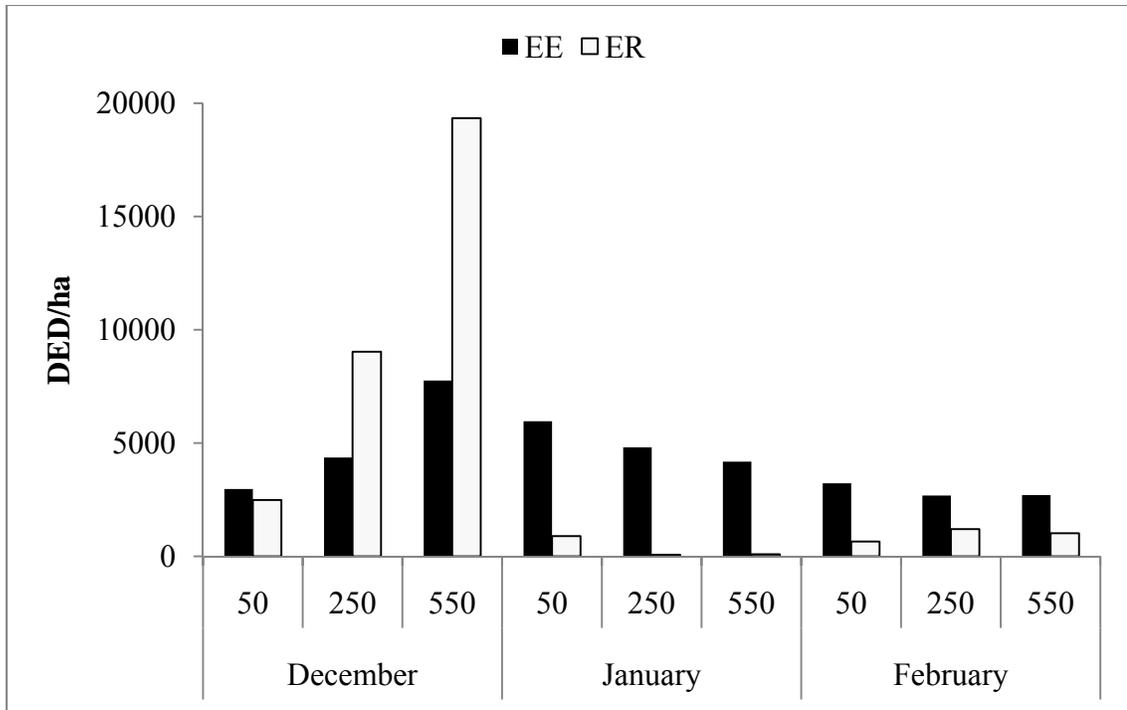


Figure 3.3. Existence energy (EE) and energy removed (ER) expressed as of dabbling duck energy days (DED/ha; Anatini; Reinecke and Kaminski 2007) in 0.5-ha plots supplemented in mid-December with 50, 250, or 550 kg/ha of Japanese millet (*Echinochloa frumentacea*) in 4 experimental wetlands sampled from mid-December 2008 to late February 2009 in western Mississippi and Tennessee portions of the Mississippi Alluvial Valley.

CHAPTER IV

SYNTHESIS

The North American Waterfowl Management Plan (NAWMP) encouraged scientists and managers to estimate carrying capacity and enhance habitats of nonbreeding waterfowl in North America (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986, Yaich et al. 2000). Conservation partnerships implementing NAWMP (i.e., Joint Ventures) in regions used by nonbreeding waterfowl set habitat objectives based on an assumption that food may be a limiting resource for migrating and wintering waterfowl (Reinecke et al. 1989, Loesch et al. 1994, Abraham et al. 2007). Consequently, since the 1990s, scientists have estimated food resources in and evaluated management strategies for waterfowl foraging habitats in these regions (Miller 1987; Stafford et al. 2006; Brasher et al. 2007; Kross et al. 2008*a,b*; Straub 2010).

Seasonal wetlands are a principal component of habitats for nonbreeding dabbling ducks (Abraham et al. 2007) and provide diverse ecological services for people (Heitmeyer and Vohs 1984, Ewel 1997, Mitsch and Gosselink 2000, Tockner and Stanford 2002, Vymazal 2007). In the Mississippi Alluvial Valley (MAV), wetland drainage for agriculture and flood control along major rivers and streams has replaced many seasonal and temporary wetlands with small permanent basins or networks of ditches to remove water rapidly from the landscape (Reinecke et al. 1988, Fredrickson

2005). Large reservoirs, levees, ditches, and flood control channels have reduced extent, frequency, and duration of flooding from the Mississippi River and its tributaries, thus also reducing shallow wetlands valuable to wildlife (Reinecke et al. 1988, Havera 1999, Manley et al. 2009).

In addition to wetland loss, modern farming practices result in fewer waste agricultural grains and natural seeds in harvested crop fields that are flooded in fall and winter for waterfowl than historically present (Krapu et al. 2004, Manley et al. 2004, Stafford et al. 2006, Foster et al. 2010, Hagy et al. 2010). Management and autumn and winter flooding of natural, annual vegetation (e.g., moist-soil plants) have been recommended to mitigate decreased waterbird food abundance in harvested crop fields (Stafford et al. 2006, Kross et al. 2008a). Moist-soil wetlands provide more food in early winter than harvested rice fields, the most abundant seasonally managed wetland type in the MAV (Uihlein 2000, Stafford et al. 2006, Kross et al. 2008b). However, no previous study has quantified winter waterfowl use in response to seed and tuber abundance in or estimated a foraging threshold for moist-soil seeds in the MAV.

Recent studies have demonstrated benefits of managing moist-soil wetlands for waterfowl (Brasher et al. 2007, Greer et al. 2007, Fleming 2010). However, vegetation can grow tall and dense in moist-soil wetlands and may deter waterfowl use until plants topple and form openings (R. M. Kaminski, Mississippi State University, personal communication). Autumn manipulation of robust moist-soil vegetation after seeds have matured can create food-rich openings and “hemi-marsh” conditions (i.e., approximate equal coverage of emergent vegetation and open water after flooding) attractive to

waterfowl on breeding and wintering ranges (Kaminski and Prince 1981, Smith et al. 2004). I manipulated robust moist-soil vegetation in autumn to create plots of open water and emergent vegetation after flooding to test if experimentally treated areas were used differently by waterfowl and if relative abundance of seed, tubers, and aquatic invertebrates differed among treatments in sanctuaries in the MAV during winters 2006–2009.

In Chapter I, I estimated decline in seed and tuber abundances, waterfowl use, and seed decomposition during winter in response to autumn mowing, light disking, and no manipulation (control) of robust moist-soil vegetation. Dabbling ducks (Anatini) were more abundant than other waterbird guilds (e.g., diving ducks [Aythyini], geese [Anserini], wading birds) in experimental wetlands and used mowed plots most, followed by disked and control plots. I did not detect a relationship between potential daily energy requirements and seed and tuber depletion by ducks within plots (Richardson and Kaminski 1992, Barras et al. 1996, Chapter I). Furthermore, disking resulted in a 30% reduction of seeds and tubers available to waterfowl, but diurnal use of and feeding by dabbling ducks in disked plots did not differ from mowed plots. Control plots had the greatest seed and tuber abundance in late autumn and invertebrate density throughout winter, but the least waterfowl use. Therefore, dabbling duck abundance was related to factors other than food density (e.g., vegetation structure) in experimental wetlands.

I also reported in Chapter I that seeds and tubers declined most during the first month of winter. Despite different abundances of dabbling ducks among treatment plots, seed and tuber abundances did not differ among plots but varied among wetland study

sites from late December – February of each winter. I believe dabbling ducks reduced seeds and tubers to densities where continued foraging was not energetically profitable or other fitness costs exceeded the benefits gained (Brown 1988, Brown and Kotler 2007, Greer et al. 2009). Ecologists refer to residual abundances of seeds and tubers after animals stop foraging and abandon food patches as giving-up density (GUD; Brown 1988). However, in my experiment, dabbling ducks did not “give-up” foraging or abandon plots, but instead they continued foraging throughout winter despite little evidence of continued removal of seeds, tubers, or aquatic invertebrates. Therefore, I hypothesized that dabbling ducks reached a food availability threshold (FAT) where food abundance within wetlands was below energetically profitable acquisition densities, but ducks did not abandon or cease foraging in wetlands because of the cryptic nature of submerged foods or other factors (Fretwell and Lucas 1970, Brown and Kotler 2007).

In Chapter II, I predicted rate of decline of individual taxa of moist-soil seeds using published and measured decomposition rates and compared with the actual seed decline. I detected 15 seed taxa that declined faster than explained by decomposition alone, suggesting seeds were likely removed from wetlands by waterfowl. I identified 8 other taxa that have been identified as common foods of waterfowl in the MAV and assessed effects of removing taxa possibly not used by ducks from estimates of food availability. Removing non-food taxa from seed and tuber estimates reduced carrying capacity estimates in managed moist-soil wetlands in my study by ~30%. I suggest results of this study be evaluated by collecting actively foraging waterfowl to determine their food use while concurrently measuring food availability.

In Chapter III, I conducted a pilot experiment in February 2008 in which I manipulated food densities in 2 wetlands that had been previously used by ducks throughout winter. I selected Japanese millet as a surrogate moist-soil seed and added it to each wetland at densities of 50, 250, and 550 kg/ha. Ducks reduced supplemental food among densities to similar pre-treatment levels within 2 weeks and diurnal duck abundance did not indicate dabbling ducks foraged differently in treatment plots. Following the pilot experiment, I used herbicide during summer and early autumn 2008 to suppress annual seed production and deposited the aforementioned densities of Japanese millet in 7 wetlands in the MAV in mid-December 2008. Similar to results from Chapter I and the pilot experiment, I determined that dabbling duck use of experimental plots was not related to initial seed density and residual abundances of seeds and tubers varied among taxa and wetlands, but not treatment plots. Therefore, a FAT for dabbling ducks in winter may be influenced by factors other than food abundance (e.g., predation risk, opportunity costs, seed composition), which may vary among foraging locations (Brown and Kotler 2007).

In Chapters I and III, I was unable to estimate a precise FAT for seeds and tubers among moist-soil wetlands in contrast to Greer et al. (2009), who did so for flooded rice fields in the MAV. Residual densities of individual seed taxa varied among wetlands and, thus, seed composition may have influenced FAT (Appendix C). Variation in true metabolizable energy among moist-soil seeds and tubers, selective feeding by waterfowl, and different morphologies of plant propagules may influence waterfowl to feed selectively (Barras et al. 1996, van Eerden and Munsterman 1997, Kaminski et al. 2003,

Figuerola et al. 2005, Gurd 2006). Variable residual seed abundances among wetlands after waterfowl stopped reducing seeds and tubers suggests a constant FAT value could bias estimates of food availability and carrying capacity of moist-soil wetlands.

Currently, conservation planners use fixed FATs in carrying capacity estimates for waterfowl in the MAV (Loesch et al. 1994, J. Tirpak, U.S. Fish and Wildlife Service, personal communication). Variable FATs among moist-soil wetlands could reduce accuracy of these models. Spatial depletion models can be parameterized to include factors affecting FAT in moist-soil wetlands; however, these parameters have not been estimated and some may be difficult to measure (e.g., seed composition of individual wetlands). Greer et al. (2009) questioned the feasibility of measuring relevant ecological variables for enough sites to build reliable predictive models. I agree that spatial depletion models would be difficult to parameterize and might not substantially improve accuracy of carrying capacity estimates given that moist-soil habitats compose a small-portion of available foraging habitats in comparison to agricultural fields, flooded bottomlands, permanent wetlands, and other habitats in the MAV (Uihlien 2000). However, I suggest scientists estimate the relative effects of risk, disturbance, seed composition, and other factors on FAT on small scales or using captive ducks. Identifying one or several factors that most influence FAT may allow conservation planners to improve models of carrying capacity for waterfowl in the MAV without using complex modeling procedures.

In preceding chapters, I evaluated management practices for waterfowl in moist-soil wetlands and identified potential sources of bias in models of energetic carrying

capacity for waterfowl in the MAV. Although FAT was variable among sites, residual seed densities were 2–10 times greater in moist-soil wetlands than flooded rice fields in the MAV. If conservation planners use a median value of 220 kg/ha for FAT in moist-soil wetlands in the MAV (~180 [Chapter II] and ~260 [Chapter III]), moist-soil seed and tuber estimates would be reduced by approximately 40% from the current estimate of 556 kg/ha (Kross et al. 2008). Furthermore, removal of seed taxa that may not be consumed by waterfowl would result in an additional ~30% decrease in seed and tuber abundance. Together, these reductions result in a ~70% decrease in seed availability estimates for waterfowl in moist-soil wetlands. The Lower Mississippi Valley Joint Venture (LMVJV) currently estimates seed and tuber abundance in MAV moist-soil wetlands at 556 kg/ha and other foods at 44 kg/ha (i.e., aquatic invertebrates; Reinecke and Kaminski 2007). A 70% reduction in available seeds and tubers for waterfowl equates to 210 kg/ha or ~1770 DEDs/ha compared to the LMVJs current estimate of 4,615 DEDs/ha for moist-soil wetlands and 340 DEDs/ha for harvested rice fields in the MAV (Reinecke and Kaminski 2007). Decreased food availability in moist-soil wetlands could justify additional habitat needs or emphasis on active management of moist-soil habitats to increase seed and tuber yields (Fredrickson and Taylor 1982, Fleming 2010).

LITERATURE CITED

- Abraham, K., M. Anderson, R. Clark, L. Colpitts, E. Reed, R. Bishop, J. Eadie, M. Petrie, F. Rohwer, M. Tome, and A. Rojo. 2007. North American waterfowl management plan continental progress assessment final report. <<http://www.fws.gov/birdhabitat/NAWMP/files/FinalAssessmentReport.pdf>>. Accessed 1 July 2010.
- Barras, S. C., R. M. Kaminski, L. A. Brennan. 1996. Acorn selection by female wood ducks. *Journal of Wildlife Management* 60:592–602.
- Brasher, M. G., 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.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral and Ecological Sociobiology* 22:37–47.
- Brown, J. S., and B. P. Kotler. 2007. Foraging and the ecology of fear. Pages 437–480 *in* D. W. Stephens, J. S. Brown, and R. C. Ydenberg, editors. *Foraging behavior and ecology*. University of Chicago Press, Chicago, Illinois, USA.
- Canadian Wildlife Service and U.S. Fish and Wildlife Service. 1986. North American waterfowl management plan. Canadian Wildlife Service and U.S. Fish and Wildlife Service. Washington, D.C., USA.
- Ewel, K. C. 1997. Water quality improvement by wetlands. Pages 329–344 *in* G. C. Daily, editor. *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington D.C., USA.
- Figuerola, J., R. Mateo, A. J. Green, J. Mondain-Monval, H. Lefranc, and G. Mentaberre. 2005. Grit selection in waterfowl and how it determines exposure to ingested lead shot in Mediterranean wetlands. *Environmental Conservation* 32:226–236.
- Fleming, K. S. 2010. Effects of management and hydrology on vegetation, winter waterbird use, and water quality on Wetlands Reserve Program lands, Mississippi. Thesis, Mississippi State University, Mississippi State, USA.

- Foster, M. A., M. J. Gray, and R. M. Kaminski. 2010. Agricultural seed biomass for migrating and wintering waterfowl in the southeastern United States. *Journal of Wildlife Management* 74:489–495.
- Fredrickson, L. H. 2005. Contemporary bottomland hardwood systems: structure, function and hydrologic condition resulting from two centuries of anthropogenic activities. Pages 19–35 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. *Ecology and management of bottomland hardwood systems: the state of our understanding*. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, Missouri, USA.
- Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally-flooded impoundments for wildlife. U. S. Fish and Wildlife Service Resource Publication 148, Washington, D.C., USA.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- 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.
- Greer, D. M., B. D. Dugger, K. J. Reinecke, and M. J. Petrie. 2009. Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 73:1125–1133.
- Gurd, D. B. 2006. Filter-feeding dabbling ducks (*Anas* spp.) can actively select particles by size. *Zoology* 109:120–126.
- Hagy, H. M., G. M. Linz, and W. J. Bleier. 2010. Wildlife conservation sunflower plots as habitat for migratory birds. *American Midland Naturalist* 164:119–135.
- Havera, S. P. 1999. Waterfowl of Illinois: status and management. Illinois Natural History Survey Special Publication 21.
- Heitmeyer, M. E., and P. A. Vohs, Jr. 1984. Characteristics of wetlands used by migrant dabbling ducks in Oklahoma, USA. *Wildfowl* 35:61–70.
- 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.

- Kaminski, R. M., and H. H. Prince. 1981. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. *Journal of Wildlife Management* 45:1–15.
- Krapu, G. L., D. A. Brandt, and R. R. Cox. 2004. Less waste corn, more land in soybeans, and the switch to genetically modified crops: trends with important implications for wildlife management. *Wildlife Society Bulletin* 32:127–136.
- Kross, J., R. M. Kaminski, K. J. Reinecke, and A. T. Pearse. 2008a. Conserving waste rice for wintering waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:1383–1387.
- Kross, J., R. M. Kaminski, K. J. Reinecke, E. J. Penny, and A. T. Pearse. 2008b. Moist-soil seed abundance in managed wetlands in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 72:707–714.
- Loesch, C. R., K. J. Reinecke, and C. K. Baxter. 1994. Lower Mississippi Valley joint venture evaluation plan. North American waterfowl management plan, U. S. Fish and Wildlife Service, Vicksburg, Mississippi, 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.
- Manley, S. W., R. M. Kaminski, P. B. Rodrigue, J. C. Dewey, S. H. Schoenholtz, P. D. Gerard, and K. J. Reinecke. 2009. Soil and nutrient retention in winter-flooded rice fields with implications for watershed management. *Journal of Soil and Water Conservation* 64:173–182.
- Miller, M. R. 1987. Fall and winter foods of northern pintails in the Sacramento Valley, California. *Journal of Wildlife Management* 51:405–414.
- Mitsch, W. J., and J. G. Gosselink. 2000. *Wetlands*. Third edition. John Wiley and Sons, New York, USA.
- Reinecke, K. J., R. C. Barkley, and C. K. Baxter. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. Pages 325–337 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, USA.
- Reinecke, K. J., and R. M. Kaminski. 2007. Lower Mississippi Valley Joint Venture, waterfowl working group memorandum. U.S. Fish and Wildlife Service, Vicksburg, Mississippi, 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, USA.
- Richardson, D. M., and R. M. Kaminski. 1992. Diet restriction, diet quality, and prebasic molt in female mallards. *Journal of Wildlife Management* 56:531–539.
- Smith, L. M., D. A. Haukos, and R. M. Prather. 2004. Avian responses to vegetative pattern in playa wetlands during winter. *Wildlife Society Bulletin* 32:474–480.
- Stafford, J. D., R. M. Kaminski, K. J. Reinecke, and S. W. Manley. 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management* 70:61–69.
- Straub, J. N. 2008. Energetic carrying capacity of habitats used by spring migrating waterfowl in the Upper Mississippi and Great Lakes Region during spring migration. Thesis, The Ohio State University, Columbus, USA.
- Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29:308–330.
- Uihlein, W. B. 2000. Extent and distribution of waterfowl habitat managed on private lands in the Mississippi Alluvial Valley. Dissertation, Mississippi State University, Mississippi State, USA.
- van Eerden, M. R., and M. J. Munsterman. 1997. Patch use upon touch: filter-feeding European teal *Anas crecca* have environmentally and socially determined foraging goals. Pages 165–185 in M. R. van Eerden, editor, Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands, Rijksuniversiteit Groningen, The Netherlands.
- Vymazal, J. 2007. Removal of nutrients in various types of constructed wetlands. *Science of the Total Environment* 380:48–65.
- Yaich, S. C., J. Andrew, K. Babcock, V. Bevill, S. Brown, J. Kushlan, T. Melchior, G. Myers, D. Pashley, D. Smith, and M. Steinkamp. 2000. The North American bird conservation initiative in the United States: a vision of American bird conservation. U.S. Fish and Wildlife Service, Arlington, Virginia. <<http://www.nabci-us.org/aboutnabci/NABCIifndtn.pdf>>. Accessed 27 Aug. 2010.

APPENDIX A
COMMON AND SCIENTIFIC NAMES OF PLANT TAXA

Table A.1. Scientific and common names of plant taxa.

Scientific Name	Common Name
<i>Althaea officinalis</i>	Marsh mallow
<i>Amaranthus</i> spp.	Pigweed
<i>Bidens</i> spp.	Beggarticks
<i>Carex</i> spp.	Sedge
<i>Cyperus</i> spp.	Sedge
<i>Digitaria</i> spp.	Crabgrass
<i>Diodia virginiana</i>	Virginia buttonweed
<i>Echinochloa</i> spp.	Millet, barnyardgrass
<i>Eleocharis</i> spp.	Spikerush
<i>Eragrostis</i> spp.	Teal grass
<i>Heliotropium indicum</i>	Indian heliotrope
<i>Ipomoea</i> spp.	Morning glory
<i>Iva annua</i>	Sumpweed
<i>Jacquemontia tamnifolia</i>	Small-flower morning glory
<i>Leersia oryzoides</i>	Rice cutgrass
<i>Oryza sativa</i>	Cultivated rice
<i>Panicum</i> spp.	Panicgrass
<i>Paspalum dilatatum</i>	Dallisgrass

Table A.1. Continued.

<i>Paspalum laeve</i>	Field paspalum
<i>Paspalum urvillei</i>	Vasey's grass
<i>Polygonum hydropiperoides</i>	Swamp smartweed
<i>Polygonum lapathifolium</i>	Curltop smartweed
<i>Polygonum pennsylvanicum</i>	Pennsylvania smartweed
<i>Rhynchospora</i> spp.	Beaksedge
<i>Sagittaria latifolia</i>	Arrowhead
<i>Scirpus</i> spp.	Bulrush
<i>Setaria</i> spp.	Foxtail
<i>Sesbania herbacea</i>	Coffeeweed
<i>Sida spinosa</i>	Teaweed
<i>Sorghum bicolor</i>	Grain sorghum
<i>Urochloa platyphylla</i>	Signalgrass
<i>Xanthium strumarium</i>	Cocklebur

APPENDIX B

LOCATIONS OF STUDY SITES IN EASTERN MISSISSIPPI, WESTERN
TENNESSEE, AND THE MISSISSIPPI ALLUVIAL VALLEY

Table B.1. Locations of study sites in U.S. Fish and Wildlife Service National Wildlife Refuges (NWR); Mississippi Department of Wildlife, Fisheries, and Parks Wildlife Management Areas (MWMA); Tennessee Wildlife Resources Agency Wildlife Management Areas (TWMA); and private lands in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley during November 2006–2008 through February 2007–2009.

Site	Longitude/latitude ^e	Nearest City
Chickasaw NWR ^d	89° 37' 51" W, 35° 47' 48" N	Ripley, Tennessee
Coldwater NWR ^{a,b,d}	90° 8' 18" W, 34° 5' 20" N	Crowder, Mississippi
Wild Wings ^c	90° 4' 31" W, 33° 51' 33" N	Cascilla, Mississippi
Hatchie NWR ^d	89° 11' 50" W, 35° 29' 45" N	Brownsville, Tennessee
Lower Hatchie NWR ^d	89° 52' 41" W, 35° 35' 42" N	Gilt Edge, Tennessee
Mahannah MWMA ^a	90° 53' 18" W, 32° 32' 39" N	Redwood, Mississippi
Morgan Brake NWR ^b	90° 13' 13" W, 33° 14' 8" N	Tchula, Mississippi
Noxubee NWR ^{a,b,d}	88° 48' 40" W, 33° 16' 58" N	Brooksville, Mississippi

Table B.1. Continued.

Overflow NWR ^b	91° 38' 39" W, 33° 5'	Parkdale, Mississippi
Panther Swamp NWR ^{a,b,d}	90° 35' 12" W, 32° 50' 25" N	Yazoo City, Mississippi
St. Catherine's Creek NWR ^b	91° 27' 36" W, 31° 27' 56" N	Church Hill, Mississippi
Tuscumbia MWMA ^d	88° 38' 23" W, 34° 58' 34" N	Corinth, Mississippi
White Lake TWMA ^d	89° 30' 16" W, 36° 7' 21" N	Caruthersville, Missouri
Yazoo NWR ^{a,b,d}	90° 59' 30" W, 33° 5' 52" N	Hollandale, Mississippi
York Woods ^{a,c}	90° 9' 52" W, 34° 2' 59" N	Charleston, Mississippi

^aStudy site in winter 2006–2007

^bStudy site in winter 2007–2008

^cStudy site in February–March 2008

^dStudy site in winter 2008–2009

^eDegrees (°), minutes ('), seconds (")

APPENDIX C
DENSITIES OF SEEDS AND TUBERS IN CONTROL, LIGHTLY DISKED,
AND MOWED PLOTS FROM NOVEMBER–FEBRUARY

Table C.1. Density of seeds and tubers (kg[dry]/ha; \bar{x} , SE) naturally occurring in unmanipulated (control), lightly disked, and mowed plots (n) of robust vegetation in managed moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

Taxon	Month	Control			Disk			Mow		
		\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	n
Alismataceae										
<i>Sagittaria</i> spp.	November	6.0	-	1	3.7	-	1	13.8	-	1
	December	2.9	-	1	1.7	-	1	3.1	-	1
	January	0.2	-	1	1.5	-	1	0.0	-	1
	February	5.1	-	1	2.4	-	1	1.3	-	1
Amaranthaceae										
<i>Amaranthus</i> spp.	November	17.1	4.9	3	25.4	11.8	3	27.4	9.6	4
	December	20.9	7.8	3	30.0	15.5	3	18.7	7.2	4
	January	13.7	5.0	3	18.4	4.5	3	9.0	2.3	4
	February	18.4	7.8	3	15.3	4.1	3	19.3	7.4	4
Cyperaceae										
<i>Carex</i> spp.	November	70.3	-	1	2.6	-	1	26.4	-	1
	December	3.7	-	1	2.7	-	1	3.6	-	1
	January	18.4	-	1	15.5	-	1	13.4	-	1
	February	11.8	-	1	0.5	-	1	6.4	-	1

Table C.1. Continued.

<i>Cyperus odoratus</i>	November	17.3	7.0	10	21.8	8.0	9	30.1	10.0	8
	December	18.6	8.9	8	19.5	6.7	10	32.3	15.1	7
	January	18.3	8.2	8	28.7	11.8	8	25.8	9.5	8
	February	16.7	4.6	9	26.4	7.6	9	13.3	5.8	8
<i>Cyperus</i> spp. (tubers)	November	272.7	190.6	7	139.7	45.1	7	119.6	70.4	7
	December	198.8	86.3	7	165.2	51.7	7	177.4	91.7	7
	January	117.2	58.6	7	119.2	40.6	7	139.5	39.8	7
	February	75.3	37.2	7	53.1	21.9	7	76.8	52.7	7
<i>Eleocharis</i> spp.	November	48.0	29.6	5	23.6	21.9	4	13.3	3.7	4
	December	25.5	13.0	5	39.2	24.8	4	15.1	4.2	4
	January	45.4	34.5	5	21.1	8.5	4	12.5	6.3	4
	February	22.9	11.6	5	19.5	13.0	4	13.6	9.1	4
<i>Rhynchospora</i> spp.	November	25.8	8.2	8	18.6	6.0	6	36.4	21.7	6
	December	33.7	10.8	7	35.1	19.5	6	25.2	15.8	6
	January	14.5	5.3	8	18.8	7.4	6	9.1	3.6	6
	February	11.6	2.9	8	17.8	8.4	6	14.2	9.5	6

Table C.1. Continued.

Malvaceae

<i>Sida spinosa</i>	November	89.1	32.9	9	62.4	25.8	9	45.5	18.9	8
	December	97.5	37.4	8	86.5	44.7	8	34.5	12.2	7
	January	66.7	29.6	9	82.1	34.5	9	33.2	12.5	8
	February	96.5	35.7	9	73.8	39.2	8	36.2	15.7	8

Poaceae

<i>Digitaria</i> spp.	November	171.8	94.4	3	62.0	44.0	4	51.8	47.3	2
	December	32.9	20.8	3	66.6	34.5	4	65.6	63.8	2
	January	19.5	12.4	3	72.0	57.3	4	14.7	12.5	2
	February	6.6	3.3	3	21.3	13.9	4	18.8	10.4	2

<i>Echinochloa</i> spp.	November	182.8	58.3	17	121.4	38.4	13	230.6	88.6	16
	December	28.8	6.4	16	71.1	23.0	13	57.4	18.3	16
	January	43.9	10.2	16	37.8	12.7	12	29.6	8.6	17
	February	20.8	5.3	17	44.0	10.4	13	27.6	7.6	17

<i>Panicum dichotomiflorum</i>	November	135.3	45.3	12	108.3	41.7	13	78.3	24.2	11
	December	22.5	6.3	11	58.4	23.5	13	23.4	6.6	10
	January	26.9	15.1	11	29.2	8.1	12	16.6	4.4	11
	February	17.6	4.0	12	37.2	10.5	13	21.2	6.8	11

Table C.1. Continued.

<i>Paspalum laeve</i>	November	83.8	51.1	3	45.8	32.7	3	116.4	39.1	4
	December	39.3	19.6	3	68.3	41.2	3	26.3	13.9	3
	January	24.0	20.4	2	-	-	-	22.6	10.4	4
	February	15.4	6.7	3	68.0	40.5	3	34.3	14.4	4
<i>Paspalum urvillei</i>	November	54.0	33.4	3	6.8	2.3	5	18.1	11.3	3
	December	10.4	3.7	2	8.2	3.1	5	24.3	20.3	3
	January	11.1	2.6	3	7.0	3.2	5	3.7	1.6	3
	February	15.8	13.5	3	6.4	5.3	5	4.0	2.8	3
<i>Setaria</i> spp.	November	99.1	64.2	5	188.5	58.6	4	120.4	53.3	3
	December	12.5	7.2	4	33.0	17.4	4	49.7	30.4	3
	January	12.8	6.9	5	35.1	16.1	4	40.7	17.8	3
	February	11.2	4.2	5	55.3	30.7	4	75.4	33.5	3
<i>Urochloa platyphylla</i>	November	65.8	36.4	5	173.3	63.2	3	65.3	33.6	3
	December	22.8	16.0	5	21.9	13.2	3	27.5	23.9	3
	January	9.1	5.3	5	49.5	31.9	3	17.5	10.0	3
	February	12.9	5.3	5	35.3	22.4	3	22.5	15.6	3

Table C.1. Continued.

Polygonaceae

<i>Polygonum lapathifolium</i>	November	175.6	68.0	13	161.7	65.2	13	236.4	130.1	13
	December	80.2	40.2	11	98.8	46.7	12	141.5	65.7	12
	January	50.7	21.6	13	91.2	41.0	13	70.0	32.9	13
	February	48.9	17.3	13	66.9	25.5	12	73.2	26.1	13

<i>Polygonum hydropiperoides</i>	November	16.2	5.0	7	20.3	4.1	6	14.8	6.3	7
	December	16.2	6.2	7	18.8	6.1	6	11.7	5.1	6
	January	17.2	11.8	6	15.5	5.9	5	17.9	8.0	7
	February	13.6	4.5	7	8.1	2.9	6	11.6	5.9	7

<i>Polygonum pennsylvanicum</i>	November	292.0	64.6	14	139.0	18.6	13	283.6	65.0	13
	December	122.6	31.7	13	103.0	15.5	13	106.3	24.6	13
	January	116.5	34.1	14	101.2	16.9	13	75.7	16.0	14
	February	124.4	39.8	14	109.2	16.1	13	85.3	15.7	14

Rubiaceae

<i>Diodia virginiana</i>	November	34.7	7.2	4	30.0	13.1	3	31.2	19.1	3
	December	23.3	16.0	4	39.7	25.4	3	24.5	20.1	2
	January	9.5	5.5	3	16.5	9.1	2	25.7	15.9	3
	February	10.6	6.0	4	7.5	2.9	3	29.7	22.1	3

APPENDIX D
WATERBIRDS OBSERVED IN MANAGED MOIST-SOIL WETLANDS DURING
NOVEMBER 2006–2008 THROUGH FEBRUARY 2007–2009

Table D.1. Waterbirds observed in managed moist-soil wetlands during November 2006–2008 through February 2007–2009 in eastern Mississippi, western Tennessee, and the Mississippi Alluvial Valley.

Common Name	Scientific Name	Detections
Dabbling ducks		
Mallard	<i>Anas platyrhynchos</i>	43,671
Gadwall	<i>Anas strepera</i>	10,567
Northern pintail	<i>Anas acuta</i>	8,603
Northern shoveler	<i>Anas clypeata</i>	8,367
American green-winged teal	<i>Anas crecca</i>	7,559
American wigeon	<i>Anas americana</i>	585
Unknown dabbling duck		392
Wood duck	<i>Aix sponsa</i>	49
American black duck	<i>Anas rubripes</i>	32
Blue-winged teal	<i>Anas discors</i>	17
Diving ducks		
Ring-necked duck	<i>Aythya collaris</i>	926
Hooded merganser	<i>Lophodytes cucullatus</i>	466
Lesser scaup	<i>Aythya affinis</i>	409
Canvasback	<i>Aythya valisineria</i>	6
Redhead	<i>Aythya americana</i>	4
Common goldeneye	<i>Bucephala clangula</i>	3
Ruddy duck	<i>Oxyura jamaicensis</i>	2
Bufflehead	<i>Bucephala albeola</i>	1
Geese		
Greater white-fronted goose	<i>Anser albifrons</i>	142
Canada goose	<i>Branta canadensis</i>	120
Snow goose	<i>Chen caerulescens</i>	11

Table D.1. Continued.

Other waterbirds		
American coot	<i>Fulica americana</i>	2,903
Pied-billed grebe	<i>Podilymbus podiceps</i>	51
White ibis	<i>Eudocimus albus</i>	24
Great blue heron	<i>Ardea herodias</i>	9
Sora	<i>Porzana carolina</i>	6
Killdeer	<i>Charadrius vociferus</i>	5
American bittern	<i>Botaurus lentiginosus</i>	3
Common snipe	<i>Gallinago gallinago</i>	2
