Articles

Aquatic Invertebrate Abundance and Biomass in Arkansas, Mississippi, and Missouri Bottomland Hardwood Forests During Winter

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Abstract

The Mississippi Alluvial Valley once had extensive bottomland hardwood forests, but less than 25% of the original area remains. Impounded bottomland hardwood forests, or greentree reservoirs, and naturally flooded forests are important sources of invertebrate or other prey for waterfowl, but no previous studies of invertebrate abundance and biomass have been at the scale of the Mississippi Alluvial Valley. Additionally, the Lower Mississippi Valley Joint Venture of the North American Waterfowl Management Plan requires precise, contemporary estimates of invertebrate biomass in hardwood bottomlands to determine potential foraging carrying capacity of these habitats for wintering ducks. We used sweep nets to collect aquatic invertebrates from four physiographically disjunct hardwood bottomlands in the Mississippi Alluvial Valley and Mississippi's Interior Flatwoods region during winters 2008–2010. Invertebrate abundance varied inversely with water depth in both early and late winter, with greatest abundances in depths ranging from 10 to 20 cm. The estimate of invertebrate biomass in naturally flooded forests of the Mississippi Alluvial Valley for both years combined was 18.39 kg(dry)/ha (coefficient of variation [CV] = 15%). When we combined data across regions, sites, greentree reservoirs and naturally flooded forests, and years, the estimate of mean invertebrate biomass decreased to 6.6 kg/ha but precision increased to CV = 9%. We recommend the Lower Mississippi Valley Joint Venture adopt 18.39 kg(dry)/ha as a revised estimate for invertebrate biomass for naturally flooded forests, because this estimate is reasonably precise and less than 2% of remaining hardwood bottomland is impounded greentree reservoirs in the Mississippi Alluvial Valley. Additionally, we recommend managing to invoke dynamic flooding regimes in greentree reservoirs to mimic natural flood events and provide maximal coverage of depths less than 30 cm to facilitate foraging ducks' access to nektonic and benthic invertebrates, acorns, and other natural seeds.

Keywords: forested wetland; greentree reservoir; invertebrate; waterfowl

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Introduction

Bottomland hardwood forests and associated floodplain wetlands historically covered more than10 million hectares in the Lower Mississippi Alluvial Valley (MAV; Reinecke et al. 1989; Fredrickson 2005; King et al. 2005). Wetland drainage, deforestation, and conversion of forests to agricultural and urban lands dramatically changed the MAV landscape and ecosystem during the 20th century (Sternitzke 1976; Schoenholtz et al. 2005). Today, less than 25% of the estimated bottomland hardwood forested area remains (Twedt and Loesch 1999; Ervin et al. 2006), but conservation initiatives are increasing the area of palustrine and riverine forested wetland systems (Cowardin et al. 1979 [Supplemental Material Reference S2]; Fredrickson et al. 2005).

Bottomland hardwood forests in the MAV have significant ecological, environmental, and economic values, because they are among the most productive forest communities on Earth and provide habitat for a great diversity of wildlife, including waterfowl (Fredrickson 2005; Heitmeyer et al. 2005; Mitsch and Gosselink 2007). At least eight species of ducks use bottomland hardwood forests seasonally, and these forests are particularly important to mallards *Anas platyrhynchos* and wood ducks *Aix sponsa* (Reinecke et al. 1989; Heitmeyer et al. 2005; Davis et al. 2007). Additionally, bottomland hardwood forests provide seasonal or year-round habitat for a great diversity of vertebrates and aquatic invertebrates (Wehrle et al. 1995; Batema et al. 2005; Heitmeyer et al. 2005).

Wintering mallards and wood ducks in the MAV forage on natural and agricultural seeds that provide carbohydrates and other nutrients (Delnicki and Reinecke 1986), but also ingest aquatic invertebrates primarily for protein (Dabbert and Martin 2000; Batema et al. 2005; Heitmeyer et al. 2005). Invertebrates nutritionally diversify carbohydrate-dominated diets and help build body mass, enable egg development, supply calcium for subsequent eggshell deposition, and are important for development of basic plumage by prebreeding females (Heitmeyer and Fredrickson 1990; Richardson and Kaminski 1992; Barras et al. 1996). Additionally, invertebrate biomass estimates in flooded bottomland hardwood and other forested wetlands are necessary to quantify completely the energetic carrying capacity (i.e., based on energy from plant and animal foods) of these habitats for migrating and wintering waterfowl by the Lower Mississippi Valley Joint Venture (LMVJV; a collaborative, regional partnership of government agencies, nonprofit organizations, corporations, tribes, and individuals that conserve habitat for priority bird species, other wildlife, and people) partners of the North American Waterfowl Management Plan (Reinecke et al. 1989; Loesch et al. 2000).

Concomitant studies of invertebrate abundance and community composition in greentree reservoirs (GTRs; a forested tract surrounded partially or fully by a levee) and naturally flooded forests (NFF; an unimpounded bottomland hardwood forest) are available at a local but not a regional scale, such as the MAV (Reinecke et al. 1989; Wehrle et al. 1995; Batema et al. 2005; Fredrickson 2005). Therefore, our objectives were to 1) model spatiotemporal variation in invertebrate abundance during winter relative to selected explanatory variables (see Methods), (2) generate contemporary, precise (coefficient of variation [CV] $\leq$ 15%; Stafford et al. 2006, Kross et al. 2008, Straub 2012) estimates of invertebrate biomass in NFFs and GTRs at a landscape scale across parts of Arkansas, Mississippi, and Missouri in the MAV that would be useful for conservation planning and implementation by the LMVJV, and 3) provide management implications consistent with our results and others previously published.

Study Areas

Mingo National Wildlife Refuge and Duck Creek Conservation Area, Missouri

Mingo National Wildlife Refuge (NWR) and Duck Creek Conservation Area are contiguous, and the U.S. Fish and Wildlife Service and Missouri Department of Conservation manages them, respectively (hereafter Mingo/Duck Creek). Mingo/Duck Creek covers 10,400 ha and is located in the northern MAV near Puxico, Missouri (36°N, 90°W). The site contains 7,000 ha of bottomland hardwood forests, the only remaining large tract of bottomland hardwood forests in the Missouri MAV (Heitmeyer et al. 1989; Supplemental Material S3). The GTRs at Mingo/Duck Creek underwent development during the 1940s (Fredrickson 2005) and currently contain approximately 60% red oaks *Quercus palustris*, *Q. phellos*, and *Q. pagoda* of similar age (70–80 y; Straub 2012).

White River National Wildlife Refuge, Arkansas

White River NWR is located in west-central MAV near St. Charles, Arkansas (34°N, 91°W). White River NWR encompasses a 145-km stretch of the lower 160 km of the White River near its confluence with the Mississippi River. White River NWR contains about 62,300 ha of bottomland hardwood forests and other wetlands (Oli et al. 1997). Average stand age for trees within our study plots was 70–80 y old, and stands contained 30%–40% red oaks (e.g., mostly *Q. texana*; Straub 2012). No GTRs existed in White River NWR; hence, we confined our study to NFFs.

Delta National Forest, Mississippi

Delta National Forest is managed by the U.S. Department of Agriculture (USDA) Forest Service in east-central MAV and located 23 km southeast of Rolling Fork, Mississippi (32°N, 90°W). Delta National Forest contains over 24,000 ha of bottomland hardwood forests interspersed with palustrine wetlands and is the only national forest comprised exclusively of bottomland hardwoods in the United States (Lowney and Hill 1989). There are approximately 2,000 ha of bottomland hardwood forests managed as GTRs, which generally are flooded annually from mid-November to early February (Wehrle et al. 1995). The bottomland hardwood forest in the Sunflower GTR is estimated to be 75–80 y old and contains approximately 42% red oaks (*Q. texana*, *Q. phellos*; Straub 2012).

Sam D. Hamilton Noxubee National Wildlife Refuge, Mississippi

We also sampled GTRs and NFFs at the Sam D. Hamilton Noxubee NWR (Noxubee NWR), located outside the MAV in the Interior Flatwoods (IF) Region in east-central Mississippi, 25 km south of Starkville, Mississippi (33°N, 88°W; Pettry 1977). We sampled this site because of previous aquatic invertebrate research at this study site (Duffy and LaBar 1994; Wehrle et al. 1995). Major hydrological features of Noxubee NWR include the Noxubee River, its tributaries, and Bluff and Loakfoma Lakes. Noxubee NWR is approximately 19,400 ha and comprises approximately 18,000 ha of bottomland hardwood forest and upland forest with four GTRs, one from which we collected samples to compare results with those of Wehrle et al. (1995; GTR1). The GTRs date from the 1960s and generally flood annually from late November to mid-February. The forest in GTR1 is an estimated 65–75 y old and contains approximately 35% red oaks *Q. pagoda*, *Q. phellos*, *Q. texana*, and *Q. nigra* (Straub 2012).

Methods

Study design

We used the *grts* design option of the SPSURVEY package (Kincaid and Olsen 2011) in Program R 2.11.1 (R Development Core Team 2008) to select random plot centers within each GTR and NFF. We established ten 0.2-ha circular sampling plots within each GTR (when one existed) and within an associated NFF at each study area (Foth 2011; Straub 2012). Our a priori goal was to obtain four random samples within all plots per GTR and NFF per month (*n* = 40/GTR and NFF/month; Table S1, Supplemental Material). Occasionally, some plots in NFFs were not inundated or incompletely inundated; consequently, we took one to three samples from flooded plots within NFFs to obtain greater than 20 NFF samples per month. We attempted to collect samples monthly at all study areas during November–February 2008–2010. However, lack of inundation, ice, or deep flooding precluded sampling some areas and months (*n* = 19; Foth 2011).

Invertebrate sampling and processing

We used a rectangular sweep net (23 cm × 45 cm, 500-μm mesh) to collect invertebrates from the substrate and water column (Cheal et al. 1993; Murkin et al. 1994; Wehrle et al. 1995; Gray et al. 1999). At each sample location, we also measured water depth in centimeters with a meter stick to relate depth to invertebrate abundance. We placed samples on ice at each site soon after collection and prior to transporting them to Mississippi State University. We stored all samples in a freezer at −10°C (Murkin et al. 1994; Stenroth and Nyström 2003). We used tap water for processing all samples, because other flotation media did not increase recovery of invertebrates from samples (Foth et al. 2012). We removed invertebrates by hand and identified them to Family (Pennak 1989; Merritt and Cummins 2008). We placed processed samples in an oven at 60°C for 18–24 h until they were dried to a constant mass and then weighed each Family (in micrograms) of invertebrates to extrapolate and estimate kilograms per hectare (Murkin et al. 1994; Foth 2011; Hagy and Kaminski 2012).

Statistical analyses

We used the *glmmADMB* package (Fournier et al. 2012) in R version 2.15 (R Development Core Team 2009) to model relationships between the mean number of invertebrates from two to four sweep net samples per plot or the number from a single sweep net sample when only one sample was obtained (hereafter, invertebrate abundance) and measured explanatory variables. We analyzed data at plot level, because we detected minor, yet significant, correlation among samples within plots (i.e., intraclass correlation coefficient within plots = 0.314, $P < 0.001$) likely as a consequence of large sample size of sweep net samples across areas and years (*n* = 791). We modeled invertebrate abundance rather than biomass (or transformation of mass data), because discrete counts of all invertebrates recovered from samples allowed more appropriate modeling techniques given strongly right skewed distribution of our data (Zuur et al. 2009). As explanatory variables, we selected sampling period (early winter [November–December] and late winter [January–February]), average water depth per plot (centimeters), percentage of red oak leaves among all intact identifiable leaves in sweep net samples (% RO), and species richness of trees in plots (Tree Richness).

Because our dataset had right skewed distributions with overdispersion, we fit abundance data with a generalized linear mixed model using the negative binomial distribution and log link function. The link function uses the natural logarithm of all raw data to linearize the relationship with measured covariates. However, we back-transformed (i.e., antilog) all parameter estimates because this allowed us to express our invertebrate data on the original scale of aggregate total invertebrates (Zuur et al. 2009). A priori, we formulated 12 ecologically important candidate models (Table 1) for possible explanation of variation in invertebrate abundance and ranked models according to Akaike's Second Order Information Criteria (AIC_C) to identify the best explanatory models or models (Akaike 1974; Burnham and Anderson 2002). We considered models competitive if AIC_C was within two delta AIC units of our top model (Burnham and Anderson 2002). We included YEAR as a categorical random effect to account for among year variation. We present parameter estimates (β), unconditional standard errors (SE), and 95% confidence intervals from the best model because only one model met our a priori AIC criterion.

For arithmetic mean estimates of invertebrate biomass at sites with GTRs and NFFs, we pooled data across GTRs and NFFs. However, we only used data from NFFs to generate the MAV-wide estimate, because GTRs comprise less than 2% of total area of bottomland hardwood forests in the MAV (Fredrickson 2005).

Table 1. A priori candidate models that we evaluated to explain variation in aquatic invertebrate abundance in bottomland hardwood systems in the Mississippi Alluvial Valley and Interior Flatwoods, Mississippi during winters 2008–2010. Models were ranked by Akaike's Information Criterion (AIC_C) and includes number of estimable parameters (K), model weight (ω_i), and deviance explained (%).

Model	K	AIC_C	ΔAIC	ω_i
Time period × water depth	6	2,558.9	0.0	1.0000
Water depth + time period + % RO	6	2,584.6	25.7	0.0000
Tree richness + water depth + time period + % RO	7	2,585.9	26.9	0.0000
Water depth + time period	4	2,595.2	36.3	0.0000
Time period × % RO	6	2,603.6	44.7	0.0000
% RO	4	2,609.4	50.4	0.0000
Water depth	4	2,611.7	52.8	0.0000
Tree richness + water depth	5	2,613.3	54.3	0.0000
Time period	4	2,618.5	59.5	0.0000
Time period × tree richness	6	2,621.8	62.8	0.0000
Null	3	2,623.9	64.9	0.0000
Tree richness	4	2,625.9	66.9	0.0000

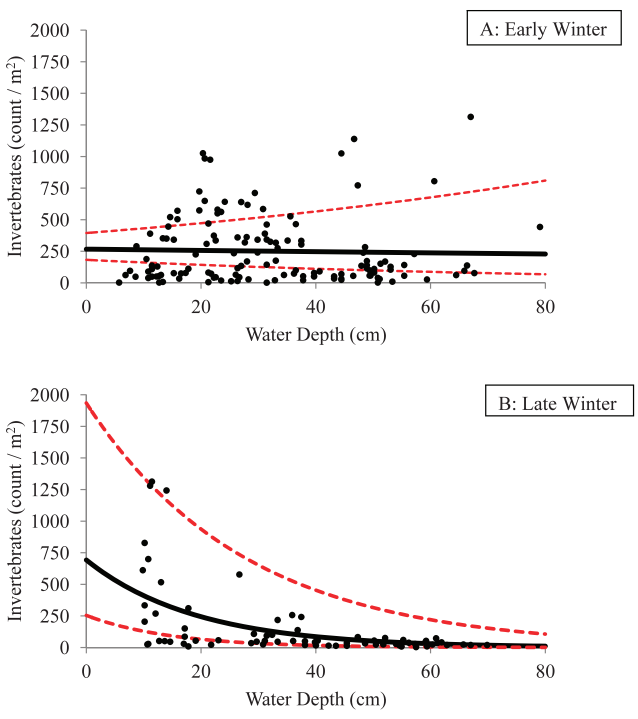

Figure 1. Relationship between aquatic invertebrate abundance (total organisms per square meter) and water depth (centimeter) during early winter (A; November–December) and late winter (B; January–February) in bottomland hardwood forests (greentree reservoirs [GTRs] and naturally flooded forests [NFFs]) in the Mississippi Alluvial Valley and Interior Flatwoods, Mississippi, winters 2008–2010. Circles denote invertebrate abundances from random plots in GTRs and NFFs (see Methods for details), solid lines are mean values for early and late winter, and dashed lines are 95% confidence intervals. All parameters are estimates from the most robust of 12 biologically relevant models that we considered (Table 2).

Results

Invertebrate abundance in GTRs and NFFs

The best model explaining variation in invertebrate abundance included the interaction of time period within winter and water depth (Table 1). We did not consider other models competitive because they were greater than 25 AIC_C units from our best model. Our top model indicated that invertebrate abundance responded differently to water depth based on the time period; however, there consistently was a negative relationship (Figure 1). In early winter invertebrate abundance slightly decreased with increasing water depth ($\beta = -0.0019$, SE = 0.005, 95% CI: -0.0126, 0.0087); in late winter this decrease was greater ($\beta = -0.0522$, SE = 0.008, 95% CI: -0.0682, -0.0362). During both early and late winter periods, invertebrate abundance was greatest in depths ranging from approximately 10–20 cm of surface water (Figure 1).

Site-specific and Mississippi Alluvial Valley–wide invertebrate biomass

In NFFs, Delta National Forest contained the greatest overall invertebrate biomass across both winters, whereas biomass was least at Noxubee NWR in both winters. White River NWR had the greatest invertebrate biomass in winter 2009–2010, but only 28 samples were obtained there because deep flooding limited our accessibility for sampling. The MAV-wide estimate of invertebrate biomass in NFFs for both years combined was 18.39 kg/ha and equaled our a priori goal for precision (CV = 15%; Table 2). When we combined data across regions, sites, GTRs and NFFs, and years, the estimate of mean invertebrate biomass decreased to 6.6 kg/ha and precision increased (CV = 9%; Table 2).

Discussion

Our study was the first we are aware of to quantify invertebrate resources in bottomland hardwood forests at a regional scale during winter despite previous

Table 2. Mean ($\bar{x}$) dry mass (kg/ha) of aquatic invertebrates (all taxa combined), standard errors (SE), and coefficient of variations (CV) estimated from sweep net samples (*n*) taken in bottomland hardwood forests (greentree reservoirs, naturally flooded forests [NFF], or both combined [C]) in the Mississippi Alluvial Valley (MAV) and Interior Flatwoods Region in Mississippi, (November–February 2008–2010).

Winter	Study area	*n*	$\bar{x}$	SE	CV (%)[a]
2008–2009	Delta National Forest, Mississippi (C)	116	6.41	1.41	22
	Sam D. Hamilton Noxubee National Wildlife Refuge (NWR), Mississippi (C)	119	1.34	0.46	34
2009–2010	Mingo/Duck Creek, Missouri (C)	136	6.20	0.97	16
	White River NWR, Arkansas (NFF)	28	18.00	3.74	21
	Delta National Forest, Mississippi (C)	252	10.22	1.60	16
	Sam D. Hamilton Noxubee NWR, Mississippi (C)	140	2.81	0.48	17
2008–2010	Delta National Forest, Mississippi (C)	368	9.02	1.18	13
	Noxubee NWR, Mississippi (C)	259	2.13	0.34	16
	MAV (NFF)	145	18.39	2.81	15
2008–2010	Overall (C)	791	6.60	0.61	9

[a] CV = (SE/$\bar{x}$) × 100.

localized studies within the MAV and IF (papers cited in Batema et al. 2005). We found that invertebrate abundance decreased with increasing water depth during winter, with greatest abundances in early and late winter occurring in depths ranging from 10 to 20 cm and generally less than 30 cm. The trend lines associated with Figure 1, during late winter, also suggest that depths less than 10 cm might provide even greater invertebrate abundances, but this trend may be more associated with concentrated invertebrates as floodwaters recede and GTRs are drawn down post waterfowl season. The steeper decline in abundance during late winter also was reflected in invertebrate biomass (Foth 2011). More deeply flooded forests, such as GTRs, may promote anoxic conditions as winter progresses due to decaying plant matter, leaching of metals (e.g., iron) and tannic acid, and stagnation of impounded water, unlike NFFs with temporally dynamic flooding from hydrologic flows and allochthonous inputs of leaf litter and nutrients from overbank flooding (Batema et al. 2005). Additionally, increased invertebrate abundance and biomass in shallower waters during winter may be related to warming ambient water temperatures, increasing day length, nutrient release from decomposition of organic matter, or a combination of these and other factors (White 1985; Duffy and LaBar 1994; Manley et al. 2004; Hagy and Kaminski 2012).

An additional explanation regarding increased invertebrate abundance and biomass in more shallowly flooded forests may be related to our unit of measurement. We scaled invertebrate abundance data two dimensionally (i.e., invertebrates per square meter) to be consistent with previous literature and so estimates could be scaled up for conservation uses (i.e., abundance or biomass per hectare). Because we sampled and collected invertebrates only from the water column and not benthos, abundances may have been conservative but also greater in shallow water because organisms were concentrated more so than in deeper wetlands. However, a post hoc analysis revealed a similar negative relationship between volumetric scaling of invertebrate abundance (invertebrates per cubic meter). Therefore, we are confident our results are robust regardless of measurement units.

In the northern MAV, Mingo/Duck Creek's NFFs had greater invertebrate biomass than the GTR at that site (Foth 2011). This pattern may be related to an earlier seasonal transition into autumn at Mingo/Duck Creek, where managers flood impoundments earlier for fall waterfowl hunting seasons, thereby possibly creating anoxic conditions in impounded waters earlier in winter (Batema et al. 2005). The NFF plots at Mingo/Duck Creek had dried by midwinter and were not accessible by wintering waterfowl that could exploit and reduce standing crops of invertebrates. However, water remained in the Mingo/Duck Creek GTR during fall–winter and provided wintering ducks with access to invertebrates, perhaps also contributing to reduced invertebrate biomass in the GTR.

Similarly, in the southern MAV, the NFF at Delta National Forest contained greater biomass than its associated GTR. The GTR there was flooded in early November and drained in mid-February. Invertebrates likely colonized newly available wetlands in the GTR allowing their numbers to increase and plateau by late January. Conversely, water levels and frequency of flooding in the NFFs at Delta National Forest were temporally and spatially dynamic. Flood pulses were brief (e.g., 1–10 d), occurred three to four times per winter, and created localized ponding after recession of floodwaters. These dynamic conditions may have enhanced aerobic conditions and nutrient release from decomposing leaf litter and allochthonous inputs of organic matter and nutrients conducive to increasing invertebrate standing crops (Batema et al. 2005).

Unlike the MAV, the GTR at Noxubee NWR had greater invertebrate biomass than its adjacent NFF, which may have been a function of hydrology and water quality of the Noxubee River watershed and Bluff Lake, contiguous with this GTR. Noxubee NWR is in the upper reaches of the Noxubee River, and the surrounding hardwood bottomlands contribute significant allochthonous detritus (Vannote et al. 1980). During overflows, flood water disperses leaf litter and possibly invertebrates from the floodplain. During significant floods, riverine water enters the GTR from overbank flooding of the Noxubee River and terrestrial runoff, likely transporting leaf litter and nutrients to the GTR from the watershed. Thus, the impounded GTR may receive increased amounts of allochthonous detritus that serves as substrates and food for invertebrates, and when it combines with fresh, oxygenated water invertebrate abundance and mass may increase. Moreover, flowing water from Bluff Lake initially floods the GTR at Noxubee NWR each fall (Wehrle et al. 1995). This diversion of fresh water and associated nutrients and invertebrates may influence the increased standing crop of invertebrates in GTR1. However, none of these hypotheses have undergone testing, thus justifying future research.

Differences in flooding regimes and landscape agricultural practices between the MAV and IF probably influenced invertebrate population and community dynamics and biomass. Soil and water fertility is greater in the MAV compared to the IF (Wehrle et al. 1995). The MAV primarily contains fertile alluvial clays, whereas the Noxubee NWR flood plain has fine sandy loams (Pettry 1977). Also, MAV bottomlands are surrounded by agricultural lands, which typically contain greater nitrogen and phosphorus levels, sediments, and pollutants than IF sites (Stanturf et al. 2000). Inputs of nitrogen and phosphorus may influence algal and microbial growth and increase primary and secondary production. The IF region surrounding Noxubee NWR has had little row crop agriculture since the late 1980s and now primarily is range and forest lands, likely reducing nutrient inputs into the Noxubee River and Noxubee NWR lands (Kaminski et al. 2005; USDA 2007).

Seasonally dynamic invertebrate populations provide wildlife with abundant and renewed food during important annual life cycle events, such as prebasic molt of female mallards and wood ducks in late winter (Richardson and Kaminski 1992; Barras et al. 2001; Heitmeyer 2006). Although GTRs only contribute less than 2% to the overall area of bottomland forests in the MAV, these habitats provide food and other resources for waterfowl, especially in drought years, and waterfowl hunting opportunities (Fredrickson 2005). Moreover, sound red oak acorns persist through most winters if not depredated, and some species reach peak abundance in January (e.g., Nuttall oak *Quercus texanii*); thus, flooded GTRs and NFFs may provide important foraging habitats for ducks in mid to late winter when other wetlands may be depleted of foods (e.g., Leach et al. 2012; Straub 2012).

Management and Research Implications

Previously, the LMVJV conservation planners had geographically limited data on invertebrate abundance and biomass and taxonomic composition from bottomland hardwood forests (Batema et al. 1985; Wehrle et al. 1995). Energetic and abundance estimates of waterfowl foods exist for the MAV (Kaminski et al. 2003; Stafford et al. 2006; Reinecke and Kaminski 2007 (S6 Supplemental Material); Kross et al. 2008; Straub 2012), but the current accepted value of 11.4 kg/ha for invertebrate biomass, by the LMVJV, in bottomland hardwood forests lacked spatial replication across the MAV. Our study provided a precise and contemporary estimate of invertebrate biomass in the MAV during winter. Thus, we recommend the LMVJV adopt 18.39 kg[dry]/ha as a revised estimate for invertebrate biomass in naturally flooded bottomland hardwood forests.

Water management that mimics natural hydrologic ebbs and flows in GTRs provides wet–dry pulses beneficial for invertebrate survival and reproduction (Wehrle et al. 1995; Batema et al. 2005). If fuel or other management costs preclude intentional fluctuations in water levels and durations in GTRs, a complex of GTRs that incorporates successive gravity-fed flooding between GTRs during winter may be logistically and fiscally efficient. If only a single GTR is present, removal of boards from water control structures during natural flood events and replacement of boards before flood cessation would help mimic dynamic hydroperiods. Additionally, flooding within GTRs should provide maximal coverage of depths less than 30 cm to facilitate foraging ducks' access to nektonic and benthic invertebrates, acorns, and other natural seeds (This study; Foth 2011; Hagy and Kaminski 2012).

Supplemental Material

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Table S1. Data for analysis on samples collected from forested wetlands of Arkansas, Mississippi and Missouri, winters 2008–2009 and 2009–2010. Data are organized by year, round (November, NOV; December, DEC; January, JAN; February, FEB), study site (Delta National Forest, DNF; Mingo National Wildlife Refuge/Duck Creek Conservation Area, MINGO; Sam D. Hamilton Noxubee National Wildlife Refuge, NOX; White River National Wildlife Refuge, WR), flooding regime (naturally flooded forest, NFF; greentree reservoir, GTR), survey plot, compass azimuth, and invertebrate Family (count, weight, kg/ha, and g/m^3).

Found at DOI: http://dx.doi.org/10.3996/092013-JFWM-061.S1 (69 KB XLSX)

Reference S1. Classification of Wetlands and Deepwater habitats of the United States. Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. U.S. Department of the Interior, Fish and Wildlife Service, Washington DC, USA.

Found at DOI: http://dx.doi.org/10.3996/092013-JFWM-061.S2; also available at http://www.co.monterey.ca.us/planning/major/Pebble%20Beach%20Company/Pebble_Beach_DEIR_Nov_2011/Pebble_Beach_DEIR_Admin_Records_Nov_2011/Cowardin/Cowardin_1979_%20wetland.pdf (78 KB PDF)

Reference S2. Water and habitat dynamics of the Mingo Swamp in Southeastern Missouri, Fish and Wildlife Research, 6 of series of technical reports. Heitmeyer ME, Fredrickson LH, Krause GF. 1989. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Found at DOI: http://dx.doi.org/10.3996/092013-JFWM-061.S3; also available at http://www.dtic.mil/dtic/tr/fulltext/u2/a322649.pdf (1977 KB PDF)

Reference S3. Development of objectives for waterfowl and shorebirds in the Mississippi Alluvial Valley. Loesch CR, Twedt DJ, Tripp K, Hunter WC, Woodrey MS. 2000. Pages 8–11 in USDA Forest Service Proceedings Rocky Mountain Research Station (RMRS-P) Publication 16, Ogden, Utah, USA.

Found at DOI: http://dx.doi.org/10.3996/092013-JFWM-061.S4; also available at http://www.lmvjv.org/library/research_docs/2000%20RMRS-P-16_8-11%20Loesch%20et%20al.PDF (539 KB PDF)

Reference S4. Reinecke, K. J., and R. M. Kaminski. 2007. Lower Mississippi Valley Joint Venture, waterfowl working group memorandum. Subject: Final Revision of Table 5 (Duck Energy-days:DEDS) U.S. Fish and Wildlife Service, Vicksburg, Mississippi, USA.

Found at DOI: http://dx.doi.org/10.3996/092013-JFWM-061.S5 (70 KB PDF)

Reference S5. 2007 Census of Agriculture, County Profile, Oktibbeha County, Mississippi. U. S. Department of Agriculture, National Agricultural Statistics Service,

Found at DOI: http://dx.doi.org/10.3996/092013-JFWM-061.S6; also available at http://www.agcensus.usda.gov/Publications/2007/Online_Highlights/County_Profiles/Mississippi/cp28105.pdf (378 KB PDF)

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References

Akaike H. 1974. A new look at the statistical model identification. The Institute of Electrical and Electronics Engineers Transactions on Automatic Control 19: 716–723.

Barras SC, Kaminski RM, Brennan LA. 1996. Acorn selection by female wood ducks. Journal of Wildlife Management 60:592–602.

Barras SC, Kaminski RM, Brennan LA. 2001. Effect of winter-diet restriction on prebasic molt in female wood ducks. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 55:506–516.

Batema DL, Henderson GS, Fredrickson LH. 1985. Wetland invertebrate distribution in bottomland hardwoods as influenced by forest type and flooding regime. Pages 196–202 in Dawson JO, Majeras KA, editors. Proceedings of the fifth central hardwoods conference. Urbana-Champaign: University of Illinois.

Batema DL, Kaminski RM, Magee PA. 2005. Wetland invertebrate communities and management of hardwood bottomlands in the Mississippi Alluvial Valley. Pages 173–190 in Fredrickson LH, King SL, Kaminski RM, editors. Ecology and management of bottomland hardwoods systems: the state of our understanding. Puxico, Missouri: University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication Number 10.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Fort Collins: Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University.

Cheal F, Davis JA, Growns JE, Bradley JS, Whittles FH. 1993. The influence of sampling method on the classification of wetland macroinvertebrate communities. Hydrobiologia 257:47–56.

Cowardin LM, Carter V, Golet FC, LaRoe ET. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service. (see *Supplemental Material*, Reference S1, http://dx.doi.org/10.3996/092013-JFWM-061.S2); also available: http://www.co.monterey.ca.us/planning/major/Pebble%20Beach%20Company/Pebble_Beach_DEIR_Nov_2011/Pebble_Beach_DEIR_Admin_Records_Nov_2011/Cowardin/Cowardin_1979_%20wetland.pdf (March 2014).

Dabbert CB, Martin TE. 2000. Diet of mallards wintering in greentree reservoirs in Southeastern Arkansas. Journal of Field Ornithology 71:423–428.

Davis JB, Cox RR Jr, Kaminski RM, Leopold BD. 2007. Survival of wood duck ducklings and broods in Mississippi and Alabama. The Journal of Wildlife Management 71:507–517.

Delnicki D, Reinecke KJ. 1986. Mid-winter food use and body weights of mallards and wood ducks in Mississippi. Journal of Wildlife Management 50:43–51.

Duffy WC, LaBar DJ. 1994. Aquatic invertebrate production in southeastern USA wetlands during winter and spring. Wetlands 14:88–97.

Ervin GN, Majure LC, Bried JT. 2006. Influence of long-term greentree reservoir impoundment on stand structure, species composition, and hydrophytic indicators. Journal of the Torrey Botanical Society 133:468–481.

Foth JR. 2011. Aquatic invertebrate biomass and community composition in greentree reservoirs and naturally flooded forests in the Mississippi Alluvial Valley and Interior Flatwoods. Master's thesis. Mississippi State: Mississippi State University. Available: http://sun.library.msstate.edu/ETD-db/theses/available/etd-03242011-163545/unrestricted/Final.pdf (March 2014).

Foth JR, Straub JN, Kaminski RM. 2012. Comparison of methods for processing aquatic invertebrate sweep net samples from forested wetlands. Journal of Fish and Wildlife Management 3:296–302.

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233–249.

Fredrickson LH. 2005. Contemporary bottomland hardwood systems: structure, function and hydrologic condition resulting from two centuries of anthropogenic activities. Pages 19–35 in Fredrickson LH, King SL, Kaminski RM, editors. Ecology and management of bottomland hardwoods systems: the state of our understanding. Puxico, Missouri: University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication Number 10.

Fredrickson LH, King SL, Kaminski RM. 2005. Ecology and management of bottomland hardwood systems: the state of our understanding. Puxico, Missouri: University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication Number 10.

Gray MJ, Kaminski RM, Weerakkody G, Leopold BD, Jensen KC. 1999. Aquatic invertebrate and plant responses following mechanical manipulations of moist-soil habitat. Wildlife Society Bulletin 27:770–779.

Hagy HM, Kaminski RM. 2012. Winter waterbird and food dynamics in autumn-managed moist-soil wetlands of the Mississippi Alluvial Valley. Wildlife Society Bulletin 36:512–523.

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

Heitmeyer ME, Cooper RJ, Dickson JG, Leopold BD. 2005. Ecological relationships of warmblooded vertebrates in bottomland hardwood ecosystems. Pages 281–306 in Fredrickson LH, King SL, Kaminski RM, editors. Ecology and management of bottomland hardwoods systems: the state of our understanding. Puxico, Missouri: University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication Number 10.

Heitmeyer ME, Fredrickson LH. 1990. Fatty acid composition of wintering female mallards in relation to nutrient use. Journal of Wildlife Management 54:54–61.

Heitmeyer ME, Fredrickson LH, Krause GF. 1989. Water and habitat dynamics of the Mingo Swamp in Southeastern Missouri. U.S. Department of Interior, Fish and Wildlife Resource 6:1–26. (see *Supplemental Material*, Reference S2, http://dx.doi.org/10.3996/092013-JFWM-061.S3); also available: http://www.dtic.mil/dtic/tr/fulltext/u2/a322649.pdf (March 2014).

Kaminski RM, Davis JB, Essig HW, Gerard PD, Reinecke KJ. 2003. True metabolizable energy for wood ducks from acorns compared to other waterfowl foods. Journal of Wildlife Management 67:542–550.

Kaminski RM, Pearse AT, Stafford JD, Reinecke KD. 2005. Where have all the mallards gone? Delta Wildlife 13:23–26.

Kincaid TM, Olsen AR. 2011. Spsurvey: spatial survey design and analysis. R package version 2.2. http://www.epa.gov/nheerl/arm/

King SL, Shepard JP, Ouchley K, Neal JA, Ouchley K. 2005. Bottomland hardwood forests: past, present, and future. Pages 1–17 in Fredrickson LH, King SL, Kaminski RM, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. Puxico, Missouri: University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication No. 10.

Kross JP, Kaminski RM, Reinecke KJ, Aaron TP. 2008. Conserving waste rice for wintering waterfowl in the Mississippi Alluvial Valley. Journal of Wildlife Management 72:1383–1387.

Leach AG, Straub JN, Kaminski RM, Ezell A, Hawkins TS, Leininger TD. 2012. Effect of winter flooding on mass and gross energy of bottomland hardwood acorns. Journal of Wildlife Management 76:1519–1522.

Loesch CR, Twedt DJ, Tripp K, Hunter WC, Woodrey MS. 2000. Development of objectives for waterfowl and shorebirds in the Mississippi Alluvial Valley. Pages 8–11 in USDA Forest Service Proceedings Rocky Mountain Research Station Publication 16, Ogden, Utah. (see *Supplemental Material*, Reference S3, http://dx.doi.org/10.3996/092013-JFWM-061.S4); also available: http://www.lmvjv.org/library/research_docs/2000%20RMRS-P-16_8-11%20Loesch%20et%20al.PDF (March 2014).

Lowney MS, Hill EP. 1989. Wood duck nest sites in bottomland hardwood forests of Mississippi. Journal of Wildlife Management 53:378–382.

Manley SW, Kaminski RM, Reinecke KJ, Gerard PD. 2004. Waterbird foods in winter-managed ricefields in Mississippi. Journal of Wildlife Management 68:74–83.

Merritt RW, Cummins KW, editors. 2008. An introduction to the aquatic insects of North America. 4th edition. Dubuque, Iowa: Kendall-Hunt Publishers.

Mitsch WJ, Gosselink JG. 2007. Wetlands. 4th edition. Hoboken, New Jersey: John Wiley and Sons.

Murkin HR, Wrubleski DA, Reid FA. 1994. Sampling invertebrates in aquatic and terrestrial habitats. Pages 349–369 in Bookhout TA, editor. Research and management techniques for wildlife and habitats. 5th edition. Bethesda, Maryland: The Wildlife Society.

Oli MK, Jacobson HA, Leopold BD. 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61:700–706.

Pennak RW. 1989. Fresh-water invertebrates of the United States. 3rd edition. New York, New York: John Wiley and Sons.

Pettry DE. 1977. Soil resource areas of Mississippi. Mississippi State: Department of Agronomy, Mississippi State University. Information sheet no. 1278.

R Development Core Team. 2008. R: a language and environment for statistical computing. Version 2.11.1. Vienna, Austria: R Foundation for Statistical Computing.

Reinecke KJ, Kaminski RM. 2007. Lower Mississippi Valley Joint Venture, waterfowl working group memorandum. Vicksburg, Mississippi: U.S. Fish and Wildlife Service. (see *Supplemental Material*, Reference S4, http://dx.doi.org/10.3996/092013-JFWM-061.S5); also available: http://www.lmvjv.org/library/WWG_literature/WWGTS_AllocationReport_Approved_6-5-12.PDF

Reinecke KJ, Kaminski RM, Moorehead DJ, Hodges JD, Nassar JR. 1989. Mississippi Alluvial Valley. Pages 203–247 in Smith LM, Pederson RL, Kaminski RM, editors. Habitat management for migrating and wintering waterfowl in North America. Lubbock: Texas Tech University Press.

Richardson DM, Kaminski RM. 1992. Diet restriction, diet quality, and prebasic molt in female mallards. Journal of Wildlife Management 56:531–539.

Schoenholtz SH, Stanturf JA, Allen JA, Schweitzer CJ. 2005. Afforestation of agricultural lands in the lower Mississippi Alluvial Valey: the state of our understanding. Pages 413–432 in Fredrickson LH, King SL, Kaminski RM, editors. Ecology and management of bottomland hardwoods systems: the state of our understanding. Puxico, Missouri: University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication Number 10.

Stafford JD, Kaminski RM, Reinecke KJ, Manley SW. 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. Journal of Wildlife Management 70:61–69.

Stanturf JA, Gardiner ES, Hamel PB, Devall MS, Leininger TD, Warren ME. 2000. Restoring bottomland hardwood ecosystems in the Lower Mississippi Alluvial Valley. Journal of Forestry 98:10–16.

Stenroth P, Nyström P. 2003. Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae. Freshwater Biology 48:466–475.

Sternitzke HS. 1976. Impact of changing land use on Delta hardwoods. Journal of Forestry 74:25–27.

Straub JN. 2012. Estimating and modeling red oak acorn yield and abundance in the Mississippi Alluvial Valley. Doctoral dissertation. Mississippi State: Mississippi State University. Available: http://sun.library.msstate.edu/ETD-db/theses/available/etd-11092012-101944/unrestricted/final.pdf (March 2014).

Twedt DJ, Loesch CR. 1999. Forest area and distribution in the Mississippi Alluvial Valley: implications for breeding bird conservation. Journal of Biogeography 26:1215–1224.

[USDA] U.S. Department of Agriculture. 2007. Census of agriculture, geographic area series: Oktibbeha County Mississippi. U.S.D.A. National Agricultural Statistics Service. (see *Supplemental Material*, Reference S5, http://dx.doi.org/10.3996/092013-JFWM-061.S6). also available: http://www.agcensus.usda.gov/Publications/2007/Online_Highlights/County_Profiles/Mississippi/cp28105.pdf (February 2014).

Vannote RL, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Wehrle BW, Kaminski RM, Leopold BD, Smith WP. 1995. Aquatic invertebrate resources in Mississippi forested wetlands during winter. Wildlife Society Bulletin 23:774–783.

White DC. 1985. Lowland hardwood wetland invertebrate community and production in Missouri. Archiv für Hydrobiologie 103:509–533.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology. New York, New York: R. Springer Science and Business Media.