Foraging thresholds of spring migrating dabbling ducks in central Illinois.

Technical Report · January 2011

6 authors, including:

Joshua Stafford
United States Geological Survey

Christopher J Whelan
University of Illinois at Chicago

ILLINOIS NATURAL HISTORY SURVEY
PRAIRIE RESEARCH INSTITUTE

University of Illinois at Urbana-Champaign
Prairie Research Institute
William Shilts, Executive Director

ILLINOIS NATURAL HISTORY SURVEY
Brian D. Anderson, Director
1816 South Oak Street
Champaign, IL 61820
217-333-6830

Foraging Thresholds of Spring Migrating Dabbling Ducks in Central Illinois

Randolph V. Smith, Joshua D. Stafford, Aaron P. Yetter, Christopher J. Whelan, Christopher S. Hine, and Michelle M. Horath

Submitted to:
Barbra J. Pardo
Regional Joint Venture Coordinator
Upper Mississippi River & Great Lakes Region Joint Venture
U.S. Fish & Wildlife Service
1 Federal Drive
Fort Snelling, MN 55111

INHS Technical Report 2011(37)
Date of Issue: 14 November 2011

ACKNOWLEDGEMENTS

Funding for this project was provided by a grant/cooperative agreement from the U.S. Department of the Interior, Fish and Wildlife Service (USFWS) through the Upper Mississippi River and Great Lakes Region Joint Venture (UMRGLRJV). We are grateful for the help of B. Pardo (UMRGLRJV) and G. Soulliere (UMRGLRJV) in project development and support. Conversations with J. Brown (University of Illinois-Chicago) contributed to project quality. We thank Illinois Department of Natural Resources (IDNR) site personnel (S. Weimer), USFWS site personnel (L. Albright), The Nature Conservancy site personnel (D. Blodgett, T. Hobson, and J. Beverlin), and private land owners (D. Fornoff, D. Hahn, and E. Yetter) who allowed us access to study wetlands.

DISCLAIMER

Any opinions, findings, and conclusions or recommendations expressed in this report are those of the authors and do not necessarily reflect the views of the USFWS, INHS, IDNR, or the University of Illinois.

EXECUTIVE SUMMARY

The Upper Mississippi River and Great Lakes Region Joint Venture (hereafter, JV) endeavors to model energetic carrying capacity to inform conservation planning in the JV region. Currently, carrying capacity models use estimates of food production (e.g., moist-soil plant seeds) and habitat availability (area). However, estimates of the amount of food exploited by ducks with respect to availability are lacking. The JV currently assumes a conservative foraging threshold of 50% of gross food abundance can be exploited by foraging ducks. Giving-up densities (GUDs), which express the amount of food that remains after organisms cease foraging, can be used to estimate foraging thresholds. We endeavored to provide information to refine the JV's foraging-threshold estimate through field experiments. We used experimental foraging patches, placed in wetlands used by spring-migrating dabbling ducks (*Anas* spp.) along the central Illinois River valley (IRV), to estimate the GUD in relation to experimentally manipulated seed density, seed size, seed depth in the substrate, substrate type, and predation risk.

We conducted 7 foraging trials in 2010 (March and April) and 10 in 2011 (February–April), beginning immediately following spring ice-out. Trials were comprised of a series of plastic pans (foraging patches) filled with a combination of substrate (e.g., sand, clay) and seed (Japanese millet and red rice) and placed in wetlands near dabbling duck concentration areas. We monitored trial plots daily for duck use and conducted behavioral observations of ducks near trial plots. Once plots were abandoned by foraging ducks, we removed experimental patches, sorted seed from substrate, and dried and weighed remaining seed to estimate the GUD.

Our results differed greatly between years. We had difficulty attracting ducks to trial plots in 2010, and use and seed exploitation was correspondingly low. On average, 521.4 kg/ha

(20% removed) of seed remained following duck abandonment in 2010. We had greater success attracting ducks to plots in 2011, and this was reflected by lower average GUD (35.8 kg/ha, 94% removed). Ducks foraged more efficiently in sand than clay substrates, and better exploited shallowly buried over deeply buried seeds; however, we only collected data on the latter in 2010. Initial seed density decreased the GUD in 2010, but not in 2011, whereas predation risk increased the GUD in 2011 but not in 2010. Finally, ducks favored small seeds in 2010, but large seeds in 2011.

Although our annual results contrasted, several of these differences may be explained by foraging theory and variation in migration chronology. Indeed, local food abundance likely varied considerably between years. Other food sources represent missed opportunities to ducks; thus, we expect the GUD to vary with respect to missed opportunity costs. When missed opportunity costs are high (i.e., high local food abundance outside of our test plots), the GUD in experimental patches should be correspondingly high, whereas the GUD will be lower when missed opportunity costs are also lower (i.e., relatively low local food abundance). Additionally, ice-out was nearly 1 month later than average (15 March) in 2010, and approximately average (15 February) in 2011. This difference may have shortened the stopover duration of large-bodied dabbling ducks (e.g., mallard [*Anas platyrhynchos*]) at our study sites, potentially altering the GUDs. Despite these interannual differences, our results demonstrate that ducks are capable of removing substantially more seed from wetland habitats than the estimate currently used by the JV. Therefore, we suggest the JV consider incorporating the GUD estimates generated by this study into future energetic carrying capacity models. However, revising carrying capacity models would lead to revision of habitat protection and enhancement goals and should be approached cautiously. Perhaps carrying capacity estimates based on the results of our study could be considered as alternate or competing models to the current approach. In this scenario, consideration of formally revising the estimates based on lowered foraging thresholds might be framed in the context of adaptive resource management, whereby support for formal revision could be based on the weight of evidence as our study is replicated or results otherwise supported or refuted.

INTRODUCTION

Wetlands in mid-migration and wintering areas of North America provide critical food resources for migratory birds during important times of the annual cycle. Correspondingly, waterfowl conservation planning in these regions is typically based on energetic carrying capacity (ECC; e.g., daily ration models). In fact, a majority of habitat Joint Ventures under the North American Waterfowl Management Plan rely on estimates of available food energy to set waterfowl population objectives.

Precise and reliable estimates of food available to migratory birds are needed for sound energy-based conservation planning. Considerable effort in recent years has improved our knowledge of abundance of many waterfowl foods, such as waste rice in the Mississippi Alluvial Valley (MAV; Stafford et al. 2006, Kross et al. 2008*a*, Greer et al. 2009), waste corn in Ontario, Canada (Barney 2008) and Tennessee (Foster et al. 2010), and moist-soil plant seeds in several regions (Naylor 2002 [California], Penny 2003 [Mississippi], Stafford et al. 2006, 2011 [Illinois], Kross et al. 2008b [MAV], Johnson 2008 [Utah]). Using data on food abundance, daily energetic requirements, and land area estimates has allowed Joint Ventures to compute approximate ECCs of large regions critical to migratory waterfowl.

Although estimates of food abundance have improved conservation planning for waterfowl, the relationship between forage biomass and exploitation is complex and variable. Optimal foraging theory suggests waterfowl and other organisms likely feed in areas until food is depleted to a level where a decision must be made to cease foraging and move elsewhere. These foraging thresholds are referred to as giving-up densities (GUD) and may be considered as the level of food abundance at which foraging is no longer profitable (Brown 1988). Information on the GUD of waterfowl in important wetland foraging habitats (e.g., moist-soil wetlands) is critical to conservation planning based on ECC. Many ECC-based conservation plans assume all forage is available or make somewhat arbitrary, but conservative, assumptions about the abundance of food at which waterfowl cease foraging (i.e., 50% of gross estimates; Soulliere et al. 2007). Model-predicted carrying capacity may be particularly sensitive to estimates of forage abundance (Miller and Eadie 2006), and ECC is likely over- or under-estimated without reliable information on the GUD. Further, the GUDs may influence other factors important to estimating ECC, such as the length of time birds spend refueling at a site during migration (i.e., stopover duration). Nolet and Drent (1998) reported that Bewick's Swans (*Cygnus columbianus bewikii*) staging in Russia during spring increased stopover duration as forage was depleted, which may reduce fitness if swans subsequently arriving later on breeding areas secured poor territories (Nolet and Drent 1998). Schaub et al. (2008) reported migratory passerines in Europe that accumulated fuel stores at intermediate rates stayed longer at stopover sites than birds that either lost or accumulated fuel stores quickly. Thus, understanding when the GUD is reached may provide important information to help conservation planners understand the fitness consequences to waterfowl of management actions.

Despite their importance to conservation planning, few investigations have documented the GUD for waterfowl foraging habitats, and those that exist are largely for agricultural grains. Further, existing GUD estimates for waterfowl have been variable and often products of other efforts to estimate food abundance. For example, Baldassarre and Bolen (1984) determined that mallards (*Anas platyrhynchos*) wintering in Texas feeding in harvested corn fields ceased foraging when waste grain densities were <20 kg/ha. In Ontario, Canada, Barney (2008) found mallards depleted waste corn below 20 kg/ha in 66–74% of harvested fields. Other studies suggested that waterfowl depleted 80% of initial waste corn before abandoning fields

(Baldassarre and Bolen 1987, Clark and Greenwood 1987). Experiments in harvested rice fields suggested that waterfowl cease foraging and depart when abundance of waste grain reaches about 50 kg/ha (Reinecke et al. 1989, Greer et al. 2009). An example for natural seed comes from Naylor (2002), who estimated 30–160 kg/ha of moist-soil plant seed remained in wetlands after waterfowl departed the Central Valley of California and suggested these values represented the GUDs.

Brown (1988) formalized the concept of the GUD with a simple patch-use theory, which states that a forager should leave a patch when its harvest rate equals the sum of its foraging costs:

$$H=C+P+MOC$$

Here, H = the quitting harvest rate, C = the metabolic or physiological costs of foraging, P = the cost of predation, and MOC = costs of missed opportunities (e.g., cost of not foraging in a better patch or engaging in other fitness enhancing activities, such as preening). The density of food at which a forager quits a patch, the GUD, serves as a surrogate for the quitting harvest rate, and provides a tool to assess foraging costs. In areas with increased risk of predation (perhaps owing to obstructed visibility), P will increase thereby increasing the GUD, relative to safer areas (all else equal). Seed searching and handling time will increase C, which will also be reflected by an increase in the GUD. Although these factors can be difficult to disentangle through direct observation, they can be readily identified with manipulative experiments.

Studies using experimental food patches to quantify GUDs have been conducted with many species representing a wide variety of taxa, including mammals, birds, and insects. Jedlicka (*in* Whelan and Jedlicka 2007) found that the GUDs of fox squirrels (*Sciurus niger*) and eastern chipmunks (*Tamias striatus*) increased 4-fold during an oak (*Quercus* spp.) mast year when all other foraging costs were held constant. In this case, the high GUDs during the mast-production event reflected the high abundance of background food available (missed opportunities) within the environment. Whelan and Maina (2005) found that the GUDs of woodpeckers (Family Picidae) foraging near forest edges were significantly greater than those from interior forest. In this example, the high GUDs at the forest edge reflected increased predation risk from accipiter hawks (*Accipiter* spp.) in thick vegetation, which reduced visibility. They found that the GUDs were greatest during winter, when physiological costs were greatest due to colder ambient temperatures (Whelan and Maina 2005).

An alternative approach to measure GUDs uses observation and sampling natural environments as they are exploited. Most experiments involving waterfowl have been of this nature (Lovvorn 1987, Nolet et al. 2006, Greer et al. 2009, Hagy 2010). For instance, Nolet et al. (2006) found that energetic foraging cost, food accessibility, and foraging strategy (e.g., stop-over or over-wintering) affected the GUDs of Bewick's swans foraging for buried pondweed tubers. Hagy (2010) examined foraging thresholds of dabbling ducks (*Anas* spp.) wintering in the lower MAV, and found that dabbling ducks quickly reduced seed abundance to a forage availability threshold. However, observations indicated that ducks continued to forage in wetlands despite their inability to further deplete seed resources (Hagy 2010). This threshold varied little across initial seed density and type of habitat manipulation (Hagy 2010).

Experimental patches allow investigators to isolate or test variables that cannot be controlled in natural systems. Herein, we describe research using experimental foraging patches and direct observation to quantify how a variety of factors affected the giving-up density of seeds for spring-migrating dabbling ducks in moist-soil (i.e., nonpersistent emergent; Cowardin et al. 1979) wetlands of central Illinois. Our objective was to estimate the GUD for spring-migrating dabbling ducks in relation to seed density, seed size, substrate type, seed depth in substrate, and predation risk. These factors will further our understanding of ECC and how it relates to management of waterfowl resources. Elucidating the relationships among ECC, GUD, and waterfowl management was an explicit research objective of the Upper Mississippi River and Great Lakes Region Joint Venture (hereafter JV; Soulliere et al. 2007).

STUDY AREA

Our study sites included backwater lakes and wetlands associated with the La Grange Pool of the Illinois River (river miles 80.2–157.6) in Fulton, Mason, and Tazewell counties, Illinois (Figure 1). We also included Sand Lake, an isolated semi-permanent marsh, and 2 additional isolated seasonal wetlands east of Havana in Mason County, Illinois. The importance of these floodplain wetlands to migratory waterbirds has been described in detail (Bellrose et al. 1983, Havera and Bellrose 1985, Havera 1999). These wetlands were readily used by mallards and other dabbling ducks, were accessible by all-terrain vehicle (to deploy and remove experimental foraging patches), and could be observed from a distance without disturbing the study plots. Thus, in 2010 we conducted 3 trials at Spring Lake Bottoms State Fish and Wildlife Area (Illinois Department of Natural Resources) in Tazewell County, 3 trials at Sand Lake (privately owned) in Mason County, and 1 trial at The Emiquon Preserve (The Nature Conservancy) in Fulton County. In 2011, we conducted 1 trial at Spring Lake Bottoms, 1 trial at The Emiquon Preserve, and 2 trials at the South Globe unit of Emiquon National Wildlife Refuge (NWR; U.S. Fish and Wildlife Service), in Fulton County. In Mason County, we conducted 2 trials at Sand Lake and 4 trials at 2 other privately owned wetlands.

Wetland habitats varied by site and year. Spring Lake Bottoms consisted of a series of 4 impoundments seasonally managed to promote moist-soil vegetation. Plant communities in both years contained a mix of seed producing annual grasses and forbs, and seed production was likely above average (i.e., >580 kg/ha; Stafford et al. 2011). The Emiquon Preserve was a large (~2,000 ha) restored backwater wetland that contained a mix of habitat types. In 2010, we selected a site at Emiquon Preserve with emergent moist-soil vegetation, whereas in 2011 we selected an open marsh site adjacent to moist-soil vegetation due to water depth. At the South Globe Unit of Emiquon NWR, we located our trials within moist-soil patches. One trial location was surrounded by harvested corn stubble, whereas the other was surrounded by cattail (*Typha* spp.). Sand Lake was an isolated semi-permanent wetland. In 2010, Sand Lake increased in size and inundated unharvested corn that had lodged due to wind, wave, and ice action. In contrast, water levels at Sand Lake receded in 2011, which developed open marsh and mudflat habitat types. The other 2 isolated wetlands became inundated during spring and summer 2010. In spring 2011, 3 trial sites contained unharvested standing corn, and a 4th site contained corn stubble with developing open-marsh habitat. The Illinois River flooded extensively during both springs, thereby precluding use of additional backwater lakes and wetlands, because water levels were inappropriate to attract foraging dabbling ducks or to access potential study sites.

METHODS

In 2010, we initiated trials on 17 March (i.e., immediately after ice receded) and concluded on 12 April, after most dabbling ducks departed central Illinois. Ice-out was considerably later than normal in 2010, which lead to a compressed spring migration period and a relatively short amount of time to conduct experiments. In 2011, we initiated trials on 22 February, as ice receded, and concluded on 13 April. Date of ice-out was average in 2011, and allowed nearly an additional month to conduct trials than in 2010. Individual trials lasted 6–21 days in 2010 and 2–25 days in 2011, depending on duck use of the plot and concern about seed germination as ambient temperatures increased.

To make each experimental foraging patch (pan), we mixed the treatment-specific amount of seed with the treatment-specific amount and type of substrate(s) and a pre-determined amount of water until the mixture was the desired consistency. We covered the surface of the substrate in each experimental patch with wet straw to mimic natural plant debris found in moist-soil wetlands. Unfortunately, the process of compiling and mixing experimental patches was time and labor intensive, requiring ~32 person-hours to produce the 34 experimental foraging patches required for one trial (33 experimental pans and 1 control). Further, we mixed experimental pans ≤1 day prior to deployment to minimize chances of seed degradation or germination. To improve efficiency and minimize redundancy, we reduced the number of experimental patches (pans) in the 4th and 5th trials of 2010 to 31 and 28, respectively, and used 31 pans in all 2011 trials.

In the field, we placed pans in a grid pattern in shallow water (15–35 cm) near duck concentrations within wetlands, and randomized patch distributions within plots using a random-numbers table. We monitored plots daily for duck use or abandonment by conducting 1 hr of behavioral observation in the morning or evening. We used scan sampling (Altmann 1974) to quantify behavior of all dabbling and wood ducks (*Aix sponsa*) within 100 m of study plots. We typically conducted 5 consecutive scans, lasting 1 to 10 minutes each depending on duck abundance, over the course of 1 hr and used the following 6 behavioral categories: feeding, resting, social, locomotion, alert, and other (e.g., comfort and preening). We recorded behavior by sex and estimated the overall species composition of ducks included in each scan. Behavior observations were used to quantify use of study plots or the surrounding area, and we recorded the presence of ducks occupying or feeding in trial plots at the beginning of each scan. Additionally, we deployed motion-sensitive "trail-cameras" to photograph experimental plots hourly to aid in documenting use or abandonment.

2010–For each trial, we deployed 28–33 plastic pans (36.8 cm diameter by 8.9 cm depth) consisting of 1 of 11 different treatments (Table 1) that manipulated seed density, seed size, substrate type, seed depth in the substrate, and predation risk. To evaluate how ducks depleted patches, we deployed pans with various seed densities, representing low (350 kg/ha), average (580 kg/ha), and high (1,120 kg/ha) estimates used for conservation planning by Soulliere et al. (2007:34). We evaluated the influence of seed size on depletion by using trays with large (red rice; *Oryza sativa* var.; hereafter rice) or small (Japanese millet; *Echinochloa crus-galli*; hereafter millet) seeds only, as well as trays with equal masses of each seed size. The relationship between substrate firmness and foraging success by dabbling ducks is largely unknown. Thus, we used 3 substrate types (firmnesses) to evaluate the GUD in relation to difficulty of accessing seed. We classified substrates as: 1) clay; a dense mixture of bentonite clay (2000 cm^3 dry volume) and water (2000 ml); 2) clay-sand; 60% silica sand and 40% bentonite clay mixed until homogenous when dry (2000 cm^3) and then mixed with a pre-determined amount of water (2000 ml) to create a moderately-dense substrate, and; 3) sand; composed entirely of 2400 cm^3 (dry volume) silica sand (2010), or bank sand washed through a 1.4 mm sieve (2011). These 3 substrates were intended to reflect a range of benthic substrates encountered by foraging ducks from relatively easy to relatively difficult foraging conditions. We predicted that seeds buried in sand would require the least effort to consume (i.e., least GUD), followed by seeds in the clay-sand, and then clay substrates (i.e., greatest GUD). To investigate the influence of seed depth on foraging thresholds, we deployed trays with known amounts of seed that were: 1) mixed homogenously through 7.6 cm of substrate; 2) mixed throughout the upper 3.8 cm only (0–3.8 cm depth), and; 3) mixed throughout only the lower 3.8 cm (3.8–7.6 cm depth). Finally, we evaluated predation risk by creating 4 seed and substrate combinations for visual obstruction trials (Table 1). Each combination was replicated 3 times, and a replicate was placed in each of 3 groups of pans located 1 m, 5 m, and 10 m from a 2.4 m by 1.5 m commercially available woven grass mat suspended vertically just above the water on metal conduit poles driven into the substrate.

In each trial, with the exception of predation risk trials, we placed a control patch enclosed in fine wire mesh, to prevent seed loss or entry, within the study plot to estimate seed decomposition during trials. To make control patches, we mixed equal masses of millet and rice to make a high density (1,120 kg/ha) patch in sand-clay substrate. We treated control patches similar to all other patches, adding straw before deployment and placing them randomly within plots.

2011–We reevaluated our treatments in 2011 due to difficulty attracting ducks to plots, and the overall time required to deploy complicated treatments in 2010. The most notable differences were the elimination of substrate depth and clay substrate as variables; thus, in all patches, seeds were pre-soaked to prevent floating, and pressed into the substrate surface to increase detection probability and use in either sand or clay-sand substrate. Methods for evaluating seed density, seed size, substrate type, and predation risk did not change. We reduced the number of patches in each trial from 34 to 31, to speed patch preparation and handling time after trial removal (Table 2).

In both years we removed experimental foraging patches from wetlands when observations and/or photos indicated that ducks were no longer feeding in trial plots. Following plot removal, we transported patches to the laboratory and rinsed contents through a #14 (1.4 mm) sieve that retained experimental rice and millet seeds but allowed the passage of substrate. We dried seeds to constant mass at 80° C and weighed them (± 1 mg).

Statistical Procedures

We applied 2 corrections to post-experiment dry mass values. First, seeds were not dried and weighed prior to deploying treatments. To account for moisture in seeds at deployment, we dried 1 g and 5 g samples of red rice and millet at 80° C to a constant mass. The percent of mass lost during drying was consistent among 3 replicates, and we used these values as correction factors for post-experiment dry mass values. Thus, we increased the dry mass of recovered millet seeds by 11.2% and recovered rice seeds by 9.9%. Second, recovery of seeds from control pans indicated that masses (dry-mass corrected) of rice were essentially unchanged since deployment, whereas millet masses were lower than expected unless decomposition occurred. Because each set of treatment and control patches were deployed on different dates and for different lengths of time, we estimated the rate of mass loss of millet seeds in control patches for each deployment date. Then, we corrected for decomposition by using the number of days treatments were exposed and the estimated decomposition rate (from control patches). We used only these corrected values in evaluating the proportion of food consumed and the amount left when abandoned (GUD). Finally, corrected mass values indicated that ducks did not forage in all experimental patches. Thus, unless noted otherwise, results include data only from patches where corrected seed-mass values were less than the amount deployed.

We summarized the annual GUD estimates in relation to starting seed density, seed size, substrate type, depth seed occurred in the substrate, and predation risk using the MEANS procedure in SAS v9.2 (SAS Institute 2004). We report results as the mean GUD ± standard error (SE) in kilograms per hectare remaining after ducks abandoned trials.

RESULTS

We conducted 5 full trials (28–33 patches each) and 2 predation risk (visual obstruction) trials (12 patches each) in 2010, and 7 full (31 patches each) trials and 3 predation risk trials (12 patches each) in 2011.

Seed Density–There was considerable variation in the depletion of foods in experimental patches within and between years. In 2010, the overall pattern of depletion generally supported our hypothesis in a step-wise fashion. That is, more seed was consumed from high than medium density patches, and more from medium than low density patches (Figure 2). However, the pattern of depletion was markedly different in 2011. All patches were extensively depleted, with high density patches of large seed depleted to a similar level (25.4 ± 12.3 kg/ha) as low density patches (25.5 ± 12.9 kg/ha and 29.4 ± 12.2 kg/ha for large and small seed, respectively; Figure 3). Interestingly, the proportion of seed consumed was similar across the 3 density classes ($\bar{x} =$ 92.5%; Figure 4).

Seed Size–Dabbling ducks generally consumed more small than large seed in 2010 (Figure 2), and seed-size selection appeared to be related to seed density, as the high-density small-seed treatment experienced the most consumption (705.4 ± 58.9 kg/ha, 63.0%). Likewise, more small seed was also consumed from medium and low density patches than those with large seed.

In 2011, the pattern of consumption relative to seed size was opposite of 2010; that is, more large seed was consumed than small seed in each of the density classes (Figure 5). Interestingly, the GUD was least in the medium-density large-seed treatment (11.2 ± 6.3 kg/ha), and slightly greater in high- (25.4 ± 12.3 kg/ha) and low- (25.5 ± 12.9 kg/ha) density large-seed treatments (Figure 4). The GUD was least for the low-density small-seed treatment (29.4 ± 12.2 kg/ha), followed by the high- (57.5 ± 26.6 kg/ha) and medium- (65.7 ± 36.6 kg/ha) density small-seed patches.

Substrate Type–In 2010, the GUD was similar among sand- (GUD = 519.8 ± 23.3 kg/ha), clay-sand- (524.3 ± 28.9 kg/ha), and clay- (560.5 ± 42.8 kg/ha) substrate patches (Figure 6). In 2011, the GUD was less (43.3 ± 11.6 kg/ha) in sand-substrate than clay-sand-substrate (83.0 ± 27.2 kg/ha; Figure 7). Ducks also appeared to consume more rice from sand than clay-sand patches, but millet consumption was similar between substrates (Figure 7).

Substrate Depth–In 2010, ducks consumed about 30% of food (GUD = 415.7 kg/ha) in patches where seeds were only in the upper portion of the pans (shallow depth; 0–3.8 cm). However, we did not detect any consumption in patches where all seeds were deeply buried (3.8–7.6 cm; Figure 8), which led us to remove this treatment from our experiment in trials 4 and 5 in 2010 and all 2011 trials. Although our results are not conclusive, we found little evidence that ducks foraged beyond the first few cm of the substrate.

Predation-risk–Results of predation-risk trials were inconclusive. No trend emerged between GUD and the distance from the visual barrier in 2010 (Figure 9); however, in 2011, a clear pattern of depletion emerged where ducks consumed more from 10 m patches than 5 m patches, and more from 5 m patches than 1 m patches (Figure 10). Ducks consumed more seed from sand than clay-sand substrate in 2010 (Figure 9), but more from clay-sand substrate than sand in 2011 (Figure 9). Ducks consumed more millet than rice in both years (Figures 9 and 10). Overall, ducks consumed considerably more seed from patches in 2011 (average GUD 21.7 ± 16.8 kg/ha) than in 2010 (average GUD 818.0 ± 178.7 kg/ha).

Waterfowl Behavior–We conducted 284 and 255 behavioral observations of trial plots during 2010 and 2011, respectively. We recorded ducks foraging in study plots 85 times (29.9%) in 2010 and 33 times (12.9%) in 2011. We observed ducks in trial plots that were not foraging during 2 (0.7%) additional scans in 2010 and during 26 (10.1%) additional scans in 2011. Dabbling ducks spent most (52.7–59.4%) of their time foraging near trial plots during 2010, but spent less (32.1–49.4 %) time foraging in 2011 (Table 3). Interestingly, behavior generally did not differ between trials 1–5 and the visual obstruction trials during 2010 (Table 3). However, during 2011, ducks spent slightly less time foraging near visual obstruction plots than near 5 full trial plots where behavior observations were conducted (Table 3). Time spent alert was similar at visual-obstruction and full trial plots during both years (Table 3).

Migration Chronology–In both years trials began immediately after ice-out (17 March 2010, 22 February 2011) and ceased when most dabbling ducks departed our study area (mid-April). Therefore, we evaluated the GUD in relation to migration chronology. In both years, no clear trend emerged, and the GUD varied throughout spring migration (Figures 11 and 12). In 2011, the lowest GUD was recorded on a trial beginning 25 March (5.2 ± 2.0 kg/ha), and the highest on a trial beginning 16 March (668.6 ± 125.8 kg/ha). We did not detect a trend in seed size preference throughout migration in either year.

DISCUSSION

The Illinois River valley (IRV) was identified by the JV as an important staging area for migrating waterfowl (Soulliere et al. 2007). Additionally, moist-soil wetlands throughout the JV region support migrating waterfowl during spring and fall, and may provide a large percentage of the non-agricultural food available to migrants. Estimates of food availability have increased our understanding of the forage value these wetlands provide (e.g., Bowyer et al. 2005, Stafford et al.

2011), but the amount of food waterfowl are capable of exploiting remains largely unknown. The JV currently uses a conservative estimate of 50% of gross food abundance as the amount of food available to foraging waterfowl. We attempted to refine this estimate through experimentation. Our results indicated that although exploitation may be variable, waterfowl were capable of removing substantially more seed from wetland habitats than the estimate currently assumed by the JV. Refining these estimates may have important implications for energetic carrying capacity based conservation planning in the JV region.

Annual Variation

Weather plays an important role in waterfowl migration, as evidenced by this study. Spring thaw in 2010 was nearly 1 month later than in most years (i.e., 15 March 2010 vs. the long term average of 15 February). This lead to a temporally-compressed migration, and many large-bodied, early-nesting dabbling ducks (e.g., mallard, northern pintail [*Anas acuta*]) moved through our study area quickly in 2010. Additionally, several of our study wetlands became inundated during late fall 2009 or early winter 2010. Wetlands that became inundated earlier received consistent disturbance throughout fall (i.e., hunting), which prevented or reduced exploitation of food resources. Several of these study sites were agricultural fields where unharvested corn became flooded, providing a very strong attractant to migrating dabbling ducks. Other wetlands were intensively managed for moist-soil plants, and likely had above average (e.g., >580 kg/ha) seed production. Although we placed our experimental plots near or within these areas, we suspect there was little incentive for ducks to extensively exploit the additional food resources our plots provided. In contrast, date of ice-out in spring 2011 was average (Havera 1999), which appears to have led to a more prolonged migration chronology. Wetlands in agricultural fields at our study sites had been inundated for a full growing season, almost assuredly resulting in reduced abundance of grain. Seed abundance in managed moist-soil wetlands were likely similar between years, but the earlier spring thaw allowed more time for ducks to exploit these wetlands and forage in our patches.

We found that developing an appropriate experimental study patch that allowed for accurate estimation of the GUD was difficult. We speculate that our patch design in 2010 was too difficult for ducks to accurately evaluate and exploit (e.g., seeds too deep, substrates too firm). In 2011, we modified patches to make them easier for ducks to evaluate and exploit, which may have positively influenced use. This combination of factors (migration chronology, food availability, patch design) may have discouraged ducks from using patches in 2010, which in turn resulted in relatively high GUD values compared to 2011 (Figure 13). We believe, therefore, that the GUD estimates from 2011 probably represent those that might be observed under more natural conditions. Nonetheless, estimates from 2010 provide interesting trends that may be applicable in certain situations and should not be entirely disregarded. For instance, 2010 results may demonstrate that ducks used a high quitting harvest rate (Brown and Morgan 1995). That is, patches were abandoned despite high food abundance because missed opportunity costs were also great.

Factors Influencing GUD

Seed Density–We designed foraging patches with 1 of 3 biologically relevant densities of seed. We hypothesized that ducks would forage in patches and the GUDs would relate to initial seed density; that is, the GUD would be greater in patches with more food. This was the general pattern we observed in 2010. However, in 2011 ducks foraged all patches extensively, to the point where the GUDs did not show a clear trend with initial seed density. It appears that all starting densities were foraged to a fairly consistent GUD, as only a small amount of seed remained. Averaged across initial densities, 94.0% of seed was consumed in 2011 and the GUD varied by only 55 kg/ha (11–66 kg/ha, $\bar{x}$ = 35.8 kg/ha) across density classes. Thus, results from 2011 trials were similar to those of Greer et al. (2009), who reported a very consistent amount of rice remaining (48.7 ± 3.5 (SE) kg/ha) after waterfowl ceased foraging in flooded fields of the MAV. Therefore, we suggest our 2011 average estimate of the GUD may best represent spring dabbling duck GUD in the IRV.

Seed Size–Interestingly, ducks favored small seeds in 2010 and large seeds in 2011. We speculate this difference may have been due to differences in the availability of other food resources in study wetlands. For instance, in 2010 several trials were conducted in wetlands where unharvested corn became flooded, providing abundant, high-calorie food for dabbling ducks. However, agricultural grains do not contain all the essential nutrients necessary for ducks to maintain optimal condition (Baldassarre et al. 1983, Loesch and Kaminski 1989, Havera 1999). Therefore, ducks may have actively selected millet seeds from trial patches in order to obtain nutrients not found in corn, and thereby maintain a balanced diet (Loesch and Kaminski 1989). In contrast, our observations indicated that less corn was available in these wetlands in 2011; therefore, ducks may have favored higher-energy and larger-reward rice over millet. We note, however, that a far greater proportion of both seed types were consumed in 2011 than in 2010. As such, small differences in consumption between seed sizes preclude us from drawing strong conclusions regarding seed-size selectivity.

Substrate Type–We anticipated that the GUD would vary with substrate type, and that patches with less dense, sandy substrates would have lower GUDs (Santamaría and Rodríguez-Gironés 2002). Indeed, our results generally followed this pattern, although the trend was less pronounced in 2010. Ducks consumed more seed from sand substrate in both years, as opposed to mixed clay-sand substrates in both years, or clay-only substrates in 2010. As with other variables, differences between years were far greater than differences between substrates. Nonetheless, ducks appeared to favor less-dense substrates. We removed clay substrate from trials in 2011 due to the low amount of use it received in 2010, and to reduce the complexity of our patches. We also suspect that clay and mixed clay-sand substrates were too similar for foraging ducks to recognize differences, so including both was duplicative. We note that the observed pattern of use may have been related to the specific materials we used to make our clay-sand and clay substrates. We encountered difficulty finding a material that effectively mimicked natural substrates. We could not use natural substrates because they likely contained naturally occurring seed, which we could not quantify without additional expense and time, and because it would have been difficult to maintain consistency among substrates, seeds, patches, trials, and years. Therefore, we used commercially available bentonite clay, which was readily available in powdered form and could be manipulated to different consistencies by mixing with sand and varying amounts of water when preparing patches. We tested these substrates using simple trials with captive mallards. When a small number of mallards foraged in patches, the substrate maintained its consistency, which was sticky and thick. However, when use increased, additional mixing took place and the substrate became flocculent. Thus, results of trials with wild birds may have varied with respect to substrate type depending on the amount of use the patches received. As duck use increased, patches may have become easier to deplete. We are uncertain if this characteristic affected our final GUD values, but it may have effectively mimicked natural conditions in which foraging ducks disturb and redistribute sediments.

Our results may have implications for conservation planning, given that the GUD likely varies among substrate types. Therefore, the GUD may be lower for ducks foraging in wetlands with firm, sandy bottoms, as opposed to those foraging in heavy silt substrates. Including substrate type in models of forage abundance could complicate conservation planning, but such categories would likely be broad, and closely tied to habitat or wetland types. For example, wetlands associated with large rivers would likely contain silt-laden substrates, whereas those associated with lakes and reservoirs would have sandy substrates. We suggest further exploration of these patterns, perhaps with captive waterfowl and replicated in a natural setting, may provide parameter estimates useful for future ECC model refinement.

Substrate Depth–We attempted to evaluate the ability of ducks to exploit seeds buried up to 7.6 cm in 2010, but use of patches with shallowly (i.e., 0–3.8 cm) and deeply (i.e., 3.8–7.6 cm) buried seed was consistently low. Thus, we revised patch design in 2011, wherein we pressed seeds into the substrate surface instead of burying them (i.e., mimicking seed-rain from annual production), with the goal of improving attractiveness to ducks by allowing them to evaluate patch quality without extensive searching (Klaassen et al. 2007). Our change of patch design resulted in our inability to evaluate the relationship between substrate depth and the GUD in 2011. Nonetheless, the contrast of results from each year of study tentatively supports the notion that ducks were considerably more effective at foraging on and depleting (i.e., GUD < 65 kg/ha) seeds near the surface compared to those buried more deeply. We suggest this finding generally supports our hypothesis that the depth of seeds in the substrate would affect the GUD, and that the GUD would likely be much lower for seeds attained near the substrate surface.

The apparent relationship between seed depth and the GUD may have important implications for research design and conservation planning. Typically, 10 cm deep soil cores are used to estimate seed availability for foraging waterfowl in wetlands (Naylor 2002, Penny 2003, Stafford et al. 2006, 2011, Kross et al. 2008b). However, seeds from the current growing season should lie near the soil's surface and likely comprise the largest percentage of seeds in the entire soil core (Olmstead 2010). Additionally, ducks may not be able to forage on deeply-buried seeds due to anatomical constraints such as bill length (e.g., ~4.0 cm in mallard; Nudds and Kaminski 1984, Drilling et al. 2002), physical constraints such as substrate firmness, or because doing so exposes the forager to heightened predation risk. Moreover, the additional time and energy required to find and exploit buried seeds may make them a less efficient food source (Santamaría and Rodríguez-Gironés 2002). If, as our results suggest, ducks cannot forage below a certain depth (e.g., 5 cm), deeper core samples will lead to overestimates of available food resources (Sherfy et al. 2000). Because of changes to our study design and clear interannual variation, our results must be considered somewhat equivocal. Nonetheless, we believe additional work to understand the ability of ducks to forage on seeds in relation to substrate depth is important, but will require targeted investigations. Such an endeavor might include foraging patches with seeds pressed into substrate surface, making them profitable and attractive enough for ducks to initiate foraging, as well as deeply and shallowly buried seeds, to evaluate their willingness or ability to forage for deeply buried seeds and how the GUD is influenced by low and high quality patches.

Predation Risk–We predicted that the GUD would decrease as foraging patches were placed farther from the visual obstruction (i.e., assumed greater risk of predation near the obstruction), that the GUD would be lower in patches with sand than clay-sand substrate, and that the GUD would be lower in patches with large seeds. Results of predation-risk trials varied between years, but some patterns followed our predictions. For instance, no pattern emerged in the GUD with respect to the distance patches were placed from the obstruction in 2010 (Figure 9). However, a clear trend appeared in 2011, where the GUD was lowest for patches placed 10 m from the obstruction, 5 m were intermediate, and 1 m were greatest (Figure 10). We believe the discrepancy between years is likely due to overall use of trial plots. In 2010, plots received little use; most patches were foraged in, but not substantially depleted, and it was difficult to draw strong conclusions about the affects of a visual barrier on the GUD. However, results from 2011 may have interesting implications for habitat management. For example, ducks appeared to avoid patches closest to a visual obstruction, presumably because this represented increased predation risk from undetected predators. Ducks commonly forage in wetlands with tall vegetation interspersed within and around them. Thus, perhaps the predation threat is only perceived when visual obstruction is patchy. Managers might conclude that wetlands designed to attract foraging ducks (e.g., moist-soil impoundments) should remain clear of interspersed patches of tall, dense vegetation such as persistent forbs or shrubs. However, effects of visual obstruction on the GUD were small in terms of seed density (17.1 kg/ha) and spatial scale (10 m). Thus, the benefits of irregular vegetation (e.g., wind break, thermal refugia, and pair isolation) may outweigh any negative change in the GUD. We suggest future studies examining additional habitats (e.g., flooded forest) to elucidate relationships between foraging efficiency and vegetation may be warranted to refine ECC models.

Interestingly, the GUD was lower in clay-sand than in sand substrate during 2011 in visual obstruction trials. This is contrary to results from visual obstruction trials in 2010, full trials in both years, and other published research (Nolet et al. 2001, 2006). In fact, clay-sand substrate in visual obstruction trials from 2011 had the lowest GUD of any variable in our study (7.4 kg/ha). We can think of few explanations for this result and suggest that because the magnitude of difference was relatively small, it may not be ecologically important. Clay-sand substrate was considerably thicker, stickier, and more dense than sand substrate and, anecdotally, more difficult for researchers to recover seeds from. Perhaps the most important implication of this result is that waterfowl were capable of depleting seeds to very low densities despite substrates that we perceived as difficult to forage in.

Finally, the GUD of millet was lower than the GUD of rice in visual obstruction trials during both years. These results coincide with results from full trials in 2010, in which millet had a lower GUD, but contrast 2011 results, in which rice had a lower GUD. For full trials in 2010, we speculate that millet may have been favored due to an abundance of recently flooded agricultural crops; therefore, millet may have offered a nutritious supplement to agricultural grain (Baldassarre et al. 1983, Loesch and Kaminski 1989, Havera 1999). However, flooded crops may not have been as abundant in the area in 2011. Our visual obstruction may have effectively created low- and high-risk habitats, which Brown and Morgan (1995) showed affected the GUD as well as diet selection. Dabbling ducks are capable of food selection during spring (Pederson and Pederson 1983, Miller 1987, Manley et al. 1992, Smith 2007); therefore, if millet was favored, and ducks do perceive a predation risk, they may attempt to deplete millet more quickly than rice before moving away from the perceived risk. Although we cannot positively identify the mechanism leading to reduced millet GUD in predation-risk trials, we suggest it further supports the notion that waterfowl can exploit large percentages of available seed regardless of seed size.

Behavior–Our results were consistent with other behavioral studies conducted during spring in which waterfowl spent the largest proportion of their time foraging (Paulus 1984, 1988). Time spent foraging was lower in 2011 than in 2010 at full trials and visual obstruction trials. These results were somewhat surprising, given that duck use of trial plots was low in 2010 but extensive in 2011. A possible explanation is that in 2010 several study wetlands were recently inundated agricultural wetlands with abundant food (i.e., corn), which created a strong attractant to foraging ducks. Thus, most ducks in the vicinity of the plots were foraging and had little incentive to visit trial plots given the abundance of grain in the immediate area. Newly flooded corn was not as abundant in 2011, perhaps leading to reduced time spent foraging. Similarly, Benoy (2005) found that ducks using manipulated wetlands spent more time actively foraging when food abundance was greater than when it had been reduced. In general, ducks did not appear to adjust their behavior near visual obstructions (e.g., more time alert) or exploit high density plots (e.g., hyperphagia, agonistic interactions competing for patches) as a result of our trials; therefore, we believe our results documented typical spring migration behavior. Had ducks altered their behavior due to experimental activities, our results would not accurately represent the GUD, thereby reducing their meaningfulness to conservation planning.

Migration Chronology–Although we did not specifically intend to evaluate the effects of migration chronology on the GUD, it was a convenient addition to our study design. During both years, we could not identify a trend of depletion associated with deployment date, and the GUD was similar among trial start dates (Figures 11, 12). In 2011, a trial beginning 16 March (trial 5) was an outlier; ducks immediately abandoned the wetland following trial deployment. Subsequent observation confirmed abandonment, and the trial was removed over concerns about seed germination. Thus, this apparently unused trial may not be meaningful in our dataset. The remaining 6 trials received extensive use by feeding ducks in 2011, and the GUD was similar among them regardless of trial deployment date (Figure 12).

Conservation Planning

Estimates of available forage during migration periods are not well documented in many areas (Calicutt et al. 2011), including the JV region (Soulliere et al. 2007), and particularly during spring (Arzel et al. 2006). Additionally, waterfowl researchers and managers largely lack an understanding of the GUD as it relates to waterfowl and have used incomplete information to estimate forage availability. For example, Soulliere et al. (2007) summarized estimates of energy available in broad habitat classes found in the JV region. Because estimates of the GUD for waterfowl are unavailable, energy estimates are subsequently reduced by 50% to account for potentially inaccessible food and reduced foraging efficiency as resources are depleted (Soulliere et al. 2007). Based on our 2011 findings, we suggest this underestimates available forage by as much as 44%, inasmuch as ducks removed 94% of seeds from our experimental patches. However, this estimate does not consider seeds that were deeply buried; thus, all were likely available in our trial patches (i.e., not representative of “seed bank” forage), seed taxa were known to be readily consumed by waterfowl (i.e., some naturally-occurring seeds may not be readily consumed), and our results are only applicable to moist-soil and shallow-marsh habitats. Despite these limitations, we suggest that it may be appropriate for the JV to consider revising their estimate of energy available to waterfowl (50% of gross food abundance). Because ducks depleted 89–98% (i.e., GUD of 11.2–65.7 kg/ha) of seeds in experimental patches during 2011, reducing the JV’s estimated percentage of unavailable food to an average (i.e., 6.1%, 35.8 kg/ha) or conservative (i.e., 11.3%, 65.7 kg/ha) value may be a more appropriate representation of spring GUD for use in conservation planning.

Other research results support a seed density-based or constant threshold GUD for waterfowl. For instance, Greer et al. (2009) reported that waterfowl foraging in rice fields in the MAV reduced waste-rice density to a relatively consistent 48.7 kg/ha, and suggested the Lower Mississippi Valley Joint Venture use a GUD of 50 kg/ha for waste rice in that region. Similarly, Hagy (2010) experimentally manipulated and evaluated managed moist-soil impoundments throughout winter in the MAV and reported that foraging ducks depleted seeds to an average threshold of 220 kg/ha. However, this estimate may have been confounded with seeds avoided by foraging ducks and potentially inaccessible seeds in the seed bank. Naylor (2002) found that the proportion of seeds depleted in wetlands of California's Central Valley was closely related to initial seed density, but remaining seed density was not. Remaining seed density varied between years in relation to overall seed production in the region, indicating that the GUD is likely a constant threshold that varies with missed opportunity cost (Naylor 2002). We believe that this body of research (Naylor 2002, Greer et al. 2009, Hagy 2010, this study) generally support our notion that the GUD of dabbling duck foods may be relatively constant in certain circumstances, and perhaps not closely related to initial food abundance. That is, ducks appeared to be capable of depleting seeds to low densities, yet this density may vary among years in relation to missed opportunity costs. For conservation planning, a conservative, constant threshold could be used with the understanding that the threshold may not be reached in all years.

In contrast, van Gils et al. (2004) cautioned against using fixed prey density thresholds to estimate carrying capacity. All systems are open and individuals can leave the system entirely or move to new patches or sites within a system. Therefore, most studies do not estimate true carrying capacity (i.e., all individuals reach starvation), as individuals would emigrate or move before starving. Thus, van Gils et al. (2004) suggested using behavioral ecology and rates of energy expenditure for all patches within a study area to model carrying capacity. We contend that at scales as large as the JV region, accurately estimating variables influencing carrying capacity for the diversity of species and habitats in the region would be impractical. Currently, average threshold values may represent the most realistic, and perhaps conservative, estimates of the GUD to incorporate in waterfowl conservation plans.

Other recent studies have used experimental habitat manipulation and observation, paired with extensive sampling of habitats, to estimate the GUD for waterfowl (Greer et al. 2009, Hagy 2010). We chose to use experimental foraging patches in order to precisely manipulate several variables simultaneously while endeavoring to hold non-experimental variables constant within each trial (Brown 1988). Whole-wetland manipulations would not have allowed substrate manipulation, and manipulation of seed density and predation risk would have been much more difficult. Additionally, cost was reduced by sorting only one sample (i.e., the experimental patch) as opposed to the many samples that would have been required with whole-wetland manipulations. Finally, experimental trials allowed for several replications within a migration period in the same wetland. Our results offer proof that duck foraging ecology may be successfully evaluated using an experimental approach in a field setting.

Foraging Strategy–The GUD may vary by region and season because of differences in physiological needs of ducks throughout the annual cycle, as well as by the physical variables manipulated during this study. For instance, wintering waterfowl are likely resource satisfiers, whereas migrating waterfowl may be resource maximizers (Nolet et al. 2006). That is, during winter, maintaining body condition to survive may be the primary purpose of foraging decisions. Feeding activity, movements, and food requirements, may be reduced to those necessary to maintain a basic metabolic rate and maximize survival (Davis and Afton 2010). In contrast, physiological needs during spring may be greater to meet the demands of migration and subsequent preparation for breeding (Krapu 1981). Differences in foraging strategies between winter and spring likely influence the GUD (Nolet et al. 2006). In winter, ducks may continue to forage to a critical food density, despite poor success, because the amount of food obtained is sufficient to maintain their basic needs, and other factors, such as predation risk, may influence patch use (Nolet et al. 2006, Hagy 2010). During spring, however, increased energetic demands may increase missed opportunity costs and enhance the likelihood that ducks will abandon a patch at a higher GUD in search of more favorable patches or to pursue other fitness-enhancing activities (Olsson and Molokwu 2007). Hagy (2010) provides an example of this phenomenon during winter. Ducks foraging in wetlands quickly depleted seeds to a threshold level, yet ducks continued to forage in patches despite the fact that no additional depletion of seeds was documented (Hagy 2010). During spring, we would expect ducks to abandon patches once thresholds were approached. Consequently, we anticipate the GUD measured in other regions and annual cycle periods may not be applicable to the JV, although they do provide ranges of the GUDs in waterfowl. Furthermore, we expect the GUDs to vary temporally and spatially as factors influencing foraging costs also vary.

Ideal Free Distribution/Optimal Foraging Theory–Seed depletion from our experimental patches differed between years. In 2010, patches were sampled but not substantially depleted and seed reduction was proportionally similar ($\bar{x}$ = 19.8%) among initial seed densities. Conversely, patches were exploited extensively in 2011 and were reduced to similar seed densities ($\bar{x}$ = 35.8 ± 17.8 kg/ha) and proportions ($\bar{x}$ = 94%) across treatments. Initial interpretation of these results may indicate that ducks used drastically different foraging strategies between years or sites at the same latitude. However, we contend our data may represent ducks foraging in an ideal free fashion (Fretwell and Lucas 1970). That is, when food densities in surrounding wetlands were great (i.e., 2010), missed opportunity costs were also large and ducks spent little time foraging in patches, which were comparatively difficult to exploit, resulting in high GUD. Alternatively, when food resources were likely average (i.e., 2011), missed opportunity costs were lower, affording ducks more time to utilize our experimental patches (Olsson and Molokwu 2007). Whelan and Jedlicka (2007) provide an example of this, wherein the GUD in experimental patches increased 400% when natural foods in the surrounding area increased substantially from one study year to the next. Results such as this highlight the ability of ducks to sample and assess habitats, and successfully exploit available resources. This also validates using waterfowl abundance and behavior as indicators of habitat quality, since ducks appear to be able to find and use the most profitable patches.

Conservation and Management Implications

The JV endeavors to use accurate and current habitat information to model energetic carrying capacity (Soulliere et al. 2007). Although contemporary estimates of food production from various habitats in the JV region have improved, much uncertainty remains about how waterfowl exploit foods in these habitats, hence the conservative GUD estimate used by the JV (Soulliere et al. 2007: 34). Recent research investigating food density thresholds (GUDs) in the Mississippi Flyway suggest that constant thresholds, rather than proportions of food consumed, may best characterize the GUDs in ducks (Greer et al. 2009, Hagy 2010, this study). Although our results varied greatly between years, 2011 results indicated that ducks were capable of depleting seeds near the soil surface, intended to simulate seed production from the current growing season, to a low density ($\bar{x}$ = 35.8 kg/ha). We anticipate that this GUD would not be reached in all years, particularly when local food resources are abundant (i.e., 2010), in which case we assume food availability is not limiting and is sufficient to support ducks staging in the region. Conversely, ducks may be able to exploit seeds to a lower GUD when food resources are scarce. Although the use of constant thresholds in energetic carrying capacity models has received recent support, considering a proportion-based threshold may also be appropriate. For example, our 2011 results show average seed depletion of 94% (range 89–98%); thus, using a conservative proportion of 85–90% may yield similar results and be easier to interpret and implement. Therefore, we suggest that any potential revision of current carrying capacity models should reflect conservative estimates generated by this study. Additionally, habitat- or region-specific carrying capacity models could include variables such as substrate type or average seed production, as the GUD varied among experimental treatments (e.g., initial seed density, substrate type; Figures 3 and 6). However, these differences were small compared to the total amount of seed consumed (Figure 4) and may contribute little to ECC model refinement.

Finally, revising carrying capacity estimates for the JV region may necessarily require revision of habitat protection and enhancement goals. If reducing the GUD increases estimates of available forage, then wetland habitat deficits may be reduced or eliminated. For instance, if the JV revised carrying capacity estimates using a proportion-based GUD of 75% of available forage (for ease of interpretability) estimated energy available in wet mudflat/moist-soil habitats in the JV region would increase by 50%, from 3,629,321 kJ/ha to 5,443,981.5 kJ/ha (Soulliere et al. 2007:34). Extrapolating these changes to habitat restoration and enhancement goals for wet mudflat/moist-soil habitat in Illinois, the desired area would decline from 458 ha to 229 ha (Soulliere et al. 2007:38). Of course, changes to conservation plans that reduce habitat objectives in the JV region should be approached cautiously. Due to the potential to dramatically change habitat objectives in the JV region, perhaps refined energetic carrying capacity estimates could be considered as alternate or competing models to the current approach. In this scenario, consideration of formally revising the estimates based on lowered foraging thresholds might be viewed in the context of adaptive resource management, whereby support for formal revision could be based on the weight of evidence as our study is replicated or results otherwise supported or refuted. Nonetheless, if reductions are warranted it would allow for reallocation of resources to other critical needs, such as habitat management to increase productivity or diversity (Stafford et al. 2007).

Literature Cited

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

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

Baldassarre, G. A., R. J. Whyte, E. E. Quinlan, and E. G. Bolen. 1983. Dynamics and quality of waste corn available to postbreeding waterfowl in Texas. Wildlife Society Bulletin 11: 25–31.

Baldassarre, G. A., and E. G. Bolen. 1984. Field-feeding ecology of waterfowl wintering in the Southern High Plains of Texas. Journal of Wildlife Management 48:63–71.

Baldassarre, G. A., and E. G. Bolen. 1987. Management of waste corn for waterfowl wintering on the Texas High Plains. Department of Range and Wildlife Management, Management Note 13. Lubbock, Texas, 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, The University of Western Ontario, London, Ontario, Canada.

Bellrose, F. C., S. P. Havera, F. L. Paveglio, Jr., and D. W. Steffeck. 1983. The fate of lakes in the Illinois River Valley. Illinois Natural History Survey Biological Notes 119.

Benoy, G. A. 2005. Variation in tiger salamander density within prairie potholes affects aquatic bird foraging behaviour. Canadian Journal of Zoology 83:926–934.

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 15:331-341.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Brown, J. S., and R. A. Morgan. 1995. Effects of foraging behavior and spatial scale on diet selectivity: a test with fox squirrels. Oikos 74:122–126.

Calicutt, J. T., H. M. Hagy, and M. L. Schummer. 2011. The food preference paradigm: A review of autumn–winter food use by North American dabbling ducks (1900–2009). Journal of Fish and Wildlife Management 2:29–40.

Clark, R. G., and H. Greenwood. 1987. A circular “ring-angel” movement by field-feeding waterfowl. Wilson Bulletin 99:722–723.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildl. Serv. FWS/OBS 79/31. Government Printing Office, Washington, District of Columbia, USA.

Davis, B. E., and A. D. Afton. 2010. Movement distances and habitat switching by female mallards wintering in the lower Mississippi Alluvial Valley. Waterbirds 33:349–356.

Drilling, N., R. Titman, and F. Mckinney. 2002. Mallard (*Anas platyrhynchos*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.proxy2.library.illinois.edu/bna/species/658

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.

Fretwell, S. D., and H. L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

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.

Hagy,H. M. 2010. Winter food and waterfowl dynamics in managed moist-soil wetlands in the Mississippi Alluvial Valley. Dissertation. Mississippi State University, Mississippi State, Mississippi, USA.

Havera, S. P. and F. C. Bellrose. 1985. The Illinois river: a lesson to be learned. Wetlands 4:29–42.

Havera, S. P. 1999. Waterfowl of Illinois: status and management. Illinois Natural History Survey Special Publication 21, Urbana, IL, USA.

Johnson, A. M. 2008. Food abundance and energetic carrying capacity for wintering waterfowl in the Great Salt Lake Wetlands. M.S. Thesis. Oregon State University, Corvallis, OR, USA.

Klaassen, R. H., B. A. Nolet, and C. H. 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. 1981. The role of nutrient reserves in mallard reproduction. Auk 98:29-38.

Kross, J. P., 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.

Loesch, C. R. and R. M. Kaminski. 1989. Winter bodyweight patterns of female mallards fed agricultural seeds. Journal of Wildlife Management 53:1081–1087.

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

Manley, S. W., W. L. Hohman, J. L. Moore, and D. Richard. 1992. Food preferences of spring migrating blue-winged teal in southwestern Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 46:46-56.

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

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, CA, USA.

Nolet, B. A., and R. H. Drent. 1998. Bewick's Swans refueling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. Journal of Avian Biology 29:574–581.

Nolet, B. A., O. Langevoord, R. M. Bevan, K. R. Engelaar, M. Klaassen, R. J. W. Mulder, and S. Van Dijks. 2001. Spatial variation in tuber depletion by swans explained by difference in net intake rates. Ecology 82:1655–1667.

Nolet, B. A., A. Gyimesi, and R. H. Klaassen. 2006. Prediction of bird-day carrying capacity on a staging site: a test of depletion models. Journal of Animal Ecology 75:1285–1282.

Nudds, T. D. and R. M. Kaminski. 1984. Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. Can. J. Zool. 62:2009-2012.

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.

Olsson, O., and M. N. Molokwu. 2007. On the missed opportunity cost, GUD, and estimating environmental quality. Israel Journal of Ecology and Evolution 53:263–278.

Paulus, S. L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. Journal of Wildlife Management 48:371-380.

Paulus, S. L. 1988. Time-activity budgets of nonbreeding Anatidae: a review. Pages 135-149 *in* M. W. Weller, editor. Waterfowl in winter. University Minnesota Press, Minneapolis, Minnesota, USA.

Pederson, G. B. and R. L. 1983. Feeding ecology of mallards and pintails in the lower Klamath Marshes. USFWS Final Report Contract # 14-16-0001-79106. Humboldt State University, Humboldt, California, USA.

Penny, E. J. 2003. Estimating moist-soil plant seed availability in the Mississippi Alluvial Valley. Thesis. Mississippi State University, Mississippi State, Mississippi, USA.

Reinecke, K. J., R. M. Kaminski, K. J. Moorehead, J. D. Hodges, and J. R. Nassar. 1989. Mississippi Alluvial Valley. Pages 203–247 *in* L.M. Smith, R.L. Pederson, and R.M. Kaminski, editors. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, Texas, USA.

Santamaría, L., and M. A. Rodríguez-Gironés. 2002 Hiding from swans: optimal burial depth of sago pondweed tubers foraged by Bewick's swans. Journal of Ecology 90:303–315.

SAS Institute. 2004. SAS/STAT 9.1 User's Guide. SAS Institute Inc., Cary, North Carolina.

Schaub, M., L. Jenni, and F. Bairlein. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657–666.

Sherfy, M. H., R. L. Kirkpatrick, and K. D. Richkus. 2000. Benthos core sampling and Chironomid vertical distribuion: implications for assessing shorebird food availability. Wildlife Society Bulletin 28:124–130.

Soulliere, G. J., B. A. Potter, J. M. Coluccy, R. C. Gatti, C. L. Roy, D. R. Luukkonen, P. W. Brown, and M. W. Eichholz. 2007. Upper Mississippi River and Great Lakes Region Joint Venture Waterfowl Habitat Conservation Strategy. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

Smith, R. V. 2007. Evaluation of waterfowl habitat and spring food selection by mallard and lesser scaup on the Swan Lake, Illinios habitat rehabilitation and enhancement project. M.S. Thesis. Southern Illinois University, Carbondale, USA.

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.

Stafford, J. D., M. M. Horath, A. P. Yetter, R. V. Smith, and C. S. Hine. 2007. Historical and contemporary characteristics of Illinois River valley wetlands: a geospatial database for conservation planning and evaluation. Final Report. U.S. Fish and Wildlife Service, Upper Mississippi River and Great Lakes Region Joint Venture. INHS Technical Report 2007 (51). October. 64 p.

Stafford, J.D., A. P. Yetter, C. S. Hine, R. V. Smith, and M. M. Horath. 2011. Seed abundance for waterfowl in wetlands managed by the Illinois Department of Natural Resources. Journal of Fish and Wildlife Management 2:3–11.

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.

Whelan, C. J., and G. G. Maina. 2005. Effects of season, understory vegetation density, habitat edge and tree diameter on patch-use by bark-foraging birds. Functional Ecology 19:529–239.

Whelan, C. J., and D. M. Jedlicka. 2007. Augmenting population monitoring programs with behavioral indicators during ecological restorations. Israel Journal of Ecology and Evolution 53:279–295.

Table 1. Treatment combinations used to create experimental foraging patches deployed in trials to evaluate factors influencing foraging thresholds by dabbling ducks in central Illinois during March–April 2010.

						Trial Number						
Name	Replicates	Seed Size	Seed Density (kg/ha)	Seed Depth (cm)	Substrate	1	2	3	4	5	Vis Obs 1[a]	Vis Obs 2
Control	1	Both	580	0–7.6	Clay-sand	X	X	X	X	X		
Deep Depth	3	Both	580	3.8–7.6	Clay-sand	X	X	X				
Shallow Depth	3	Both	580	0–3.8	Clay-sand	X	X	X	X	X		
Mixed Depth	3	Both	580	0–7.6	Clay-sand	X	X	X	X	X		
Clay Substrate	3	Both	580	0–7.6	Clay	X	X	X	X	X		
Sand Substrate	3	Both	580	0–7.6	Sand	X	X	X	X	X		
High Density Large Seed	3	Large	1,120	0–7.6	Clay-sand	X	X	X	X	X		
High Density Small Seed	3	Small	1,120	0–7.6	Clay-sand	X	X	X	X	X		
Low Density Large Seed	3	Large	350	0–7.6	Clay-sand	X	X	X	X	X		
Low Density Small Seed	3	Small	350	0–7.6	Clay-sand	X	X	X	X	X		
Medium Density Large Seed	3	Large	580	0–7.6	Clay-sand	X	X	X	X			
Medium Density Small Seed	3	Small	580	0–7.6	Clay-sand	X	X	X	X	X		
High Density Mixed Millet	3	Small	1,120	0–7.6	Clay-sand						X	X
High Density Mixed Rice	3	Large	1,120	0–7.6	Clay-sand						X	X
High Density Sand Millet	3	Small	1,120	0–7.6	Sand						X	X
High Density Sand Rice	3	Large	1,120	0–7.6	Sand						X	X

[a] visual obstruction

Table 2. Treatment combinations used to create experimental foraging patches deployed in trials to evaluate factors influencing foraging thresholds by dabbling ducks in central Illinois during February–April 2011.

Name	Replicates	Seed Size	Seed Density (kg/ha)	Seed Depth (cm)	Substrate	Trial Number 1	2	3	4	5	6	7	Vis Obs 1[a]	Vis Obs 2	Vis Obs 3
Control	1	Both	1,120	0–1	Clay-sand	X	X	X	X	X	X	X			
High Density Large Seed Mix	3	Large	1,120	0–1	Clay-sand	X	X	X	X	X	X	X			
High Density Large Seed Sand	3	Large	1,120	0–1	Sand	X	X	X	X	X	X	X			
High Density Small Seed Mix	3	Small	1,120	0–1	Clay-sand	X	X	X	X	X	X	X			
High Density Small Seed Sand	3	Small	1,120	0–1	Sand	X	X	X	X	X	X	X			
Low Density Large Seed Mix	3	Large	350	0–1	Clay-sand	X	X	X	X	X	X	X			
Low Density Large Seed Sand	3	Large	350	0–1	Sand	X	X	X	X	X	X	X			
Low Density Small Seed Mix	3	Small	350	0–1	Clay-sand	X	X	X	X	X	X	X			
Low Density Small Seed Sand	3	Small	350	0–1	Sand	X	X	X	X	X	X	X			
Medium Density Large Seed Sand	3	Large	580	0–1	Sand	X	X	X	X	X	X	X			
Medium Density Small Seed Sand	3	Small	580	0–1	Sand	X	X	X	X	X	X	X			
High Density Mixed Millet	3	Small	1,120	0–1	Clay-sand								X	X	X
High Density Mixed Rice	3	Large	1,120	0–1	Clay-sand								X	X	X
High Density Sand Millet	3	Small	1,120	0–1	Sand								X	X	X
High Density Sand Rice	3	Large	1,120	0–1	Sand								X	X	X

[a] visual obstruction

Table 3. Waterfowl behavior (mean percent time) at GUD trial plots (2010; *n* = 5, 2011; *n* = 7) and visual obstruction plots (2010; *n* = 2, 2011 *n* = 3) during springs 2010 and 2011.

		Trials			Visual Obstruction Trials		
	Activity	Total	Male	Female	Total	Male	Female
2010	Feed	55.5	52.7	59.4	56.0	53.8	59.0
	Rest	16.4	17.0	15.6	16.5	15.6	17.7
	Other	6.6	7.1	5.8	5.9	6.1	5.5
	Social	1.9	2.2	1.4	2.8	3.5	1.9
	Motion	12.8	13.6	11.6	13.9	14.9	12.4
	Alert	6.9	7.4	6.2	5.0	6.1	3.5
2011	Feed	45.9	43.4	49.4	35.0	32.1	38.9
	Rest	22.1	21.7	22.7	30.9	29.0	33.5
	Other	8.6	9.0	8.1	8.4	9.2	7.4
	Social	2.1	2.5	1.5	4.1	5.4	2.4
	Motion	17.3	18.5	15.6	17.1	18.9	14.7
	Alert	3.9	4.8	2.7	4.4	5.4	3.2

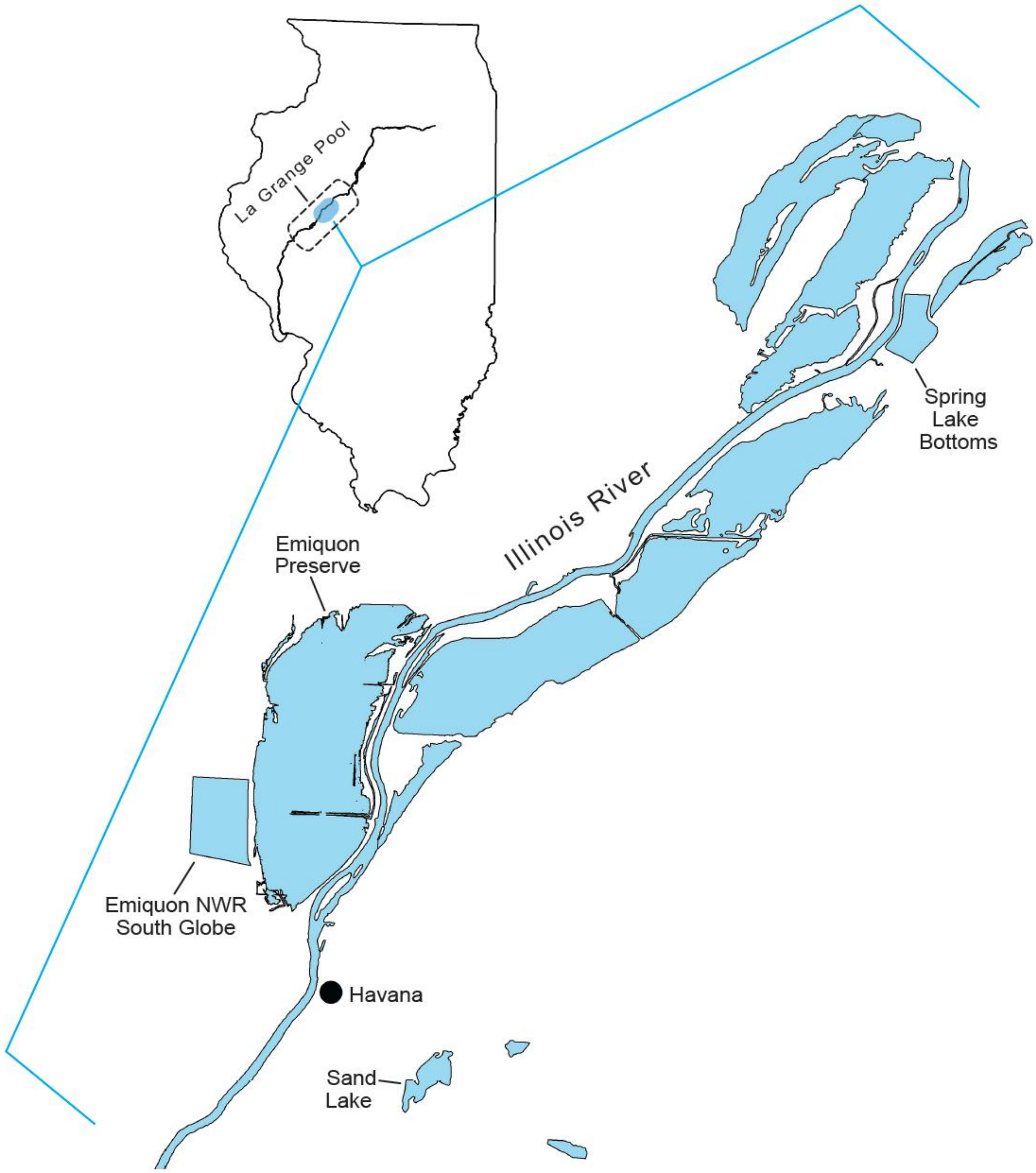

Figure 1. Map depicting our study area along La Grange Pool (dotted line) of the Illinois River, and specific study wetlands (labeled).

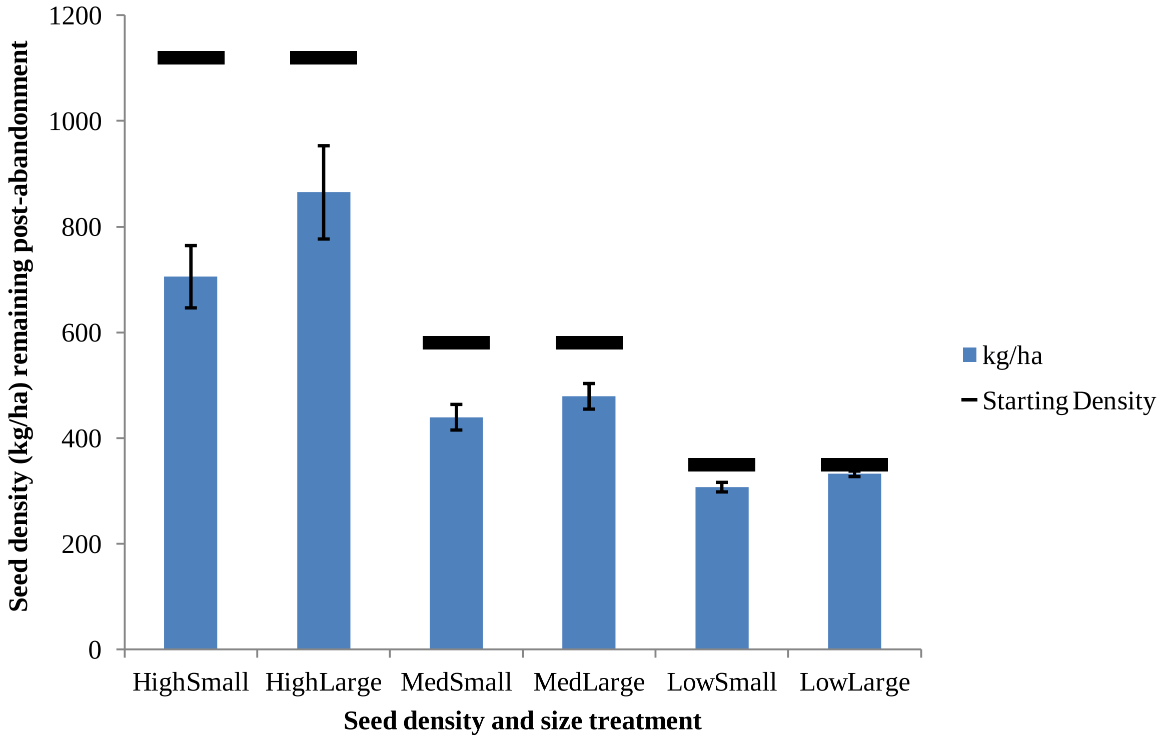

Figure 2. Mean seed density (kg/ha) following dabbling duck abandonment by density and seed size during spring in central Illinois 2010. Horizontal lines indicate initial seed densities (1,120, 580, and 350 kg/ha). Vertical bars are ± 1 standard error.

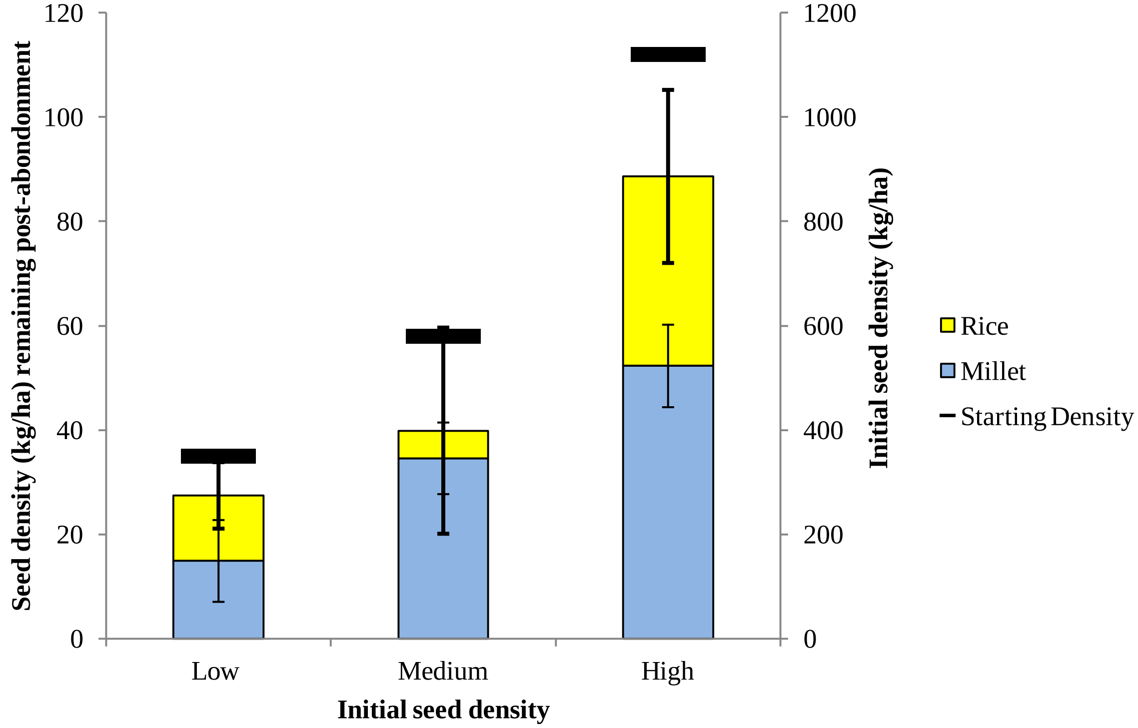

Figure 3. Mean seed density (kg/ha) following dabbling duck abandonment of foraging patches by initial seed density during spring 2011 in central Illinois. Horizontal lines indicate initial seed densities (1,120, 580, and 350 kg/ha) on the right-hand vertical axis. Vertical bars are ± 1 standard error.

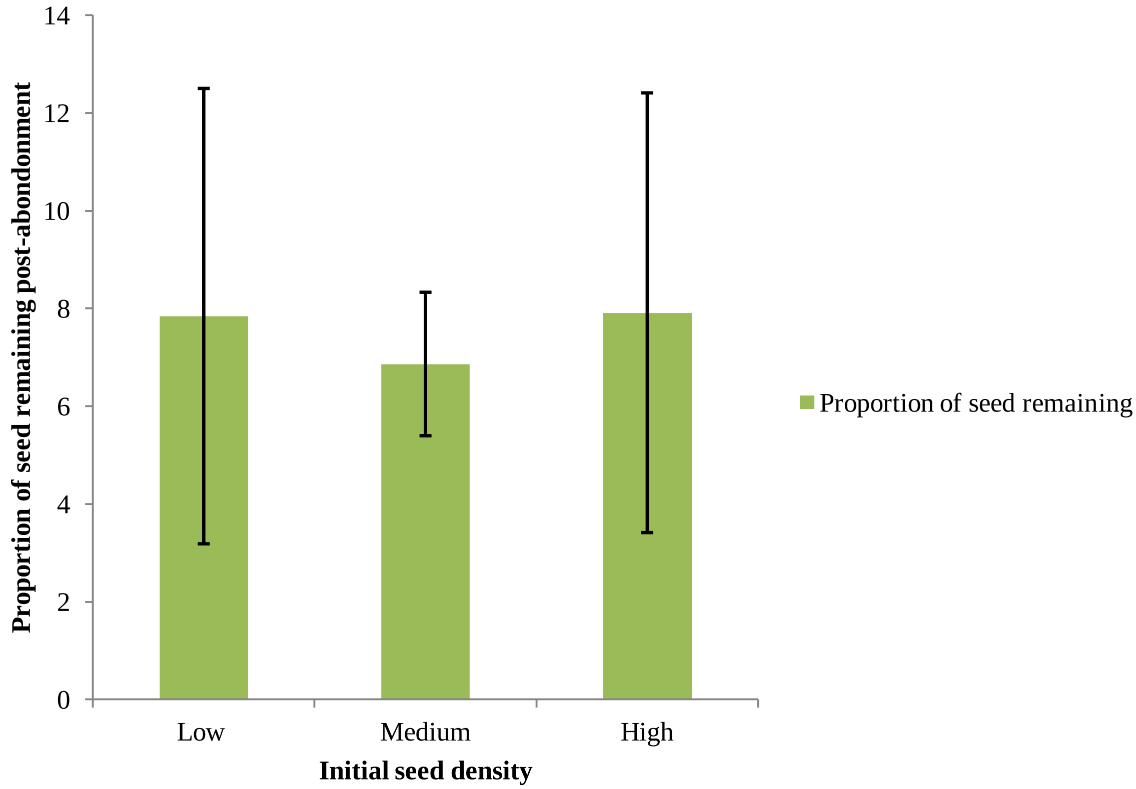

Figure 4. Mean proportion of seed remaining following dabbling duck abandonment of foraging patches by initial seed density during spring 2011 in central Illinois. Vertical bars are ± 1 standard error.

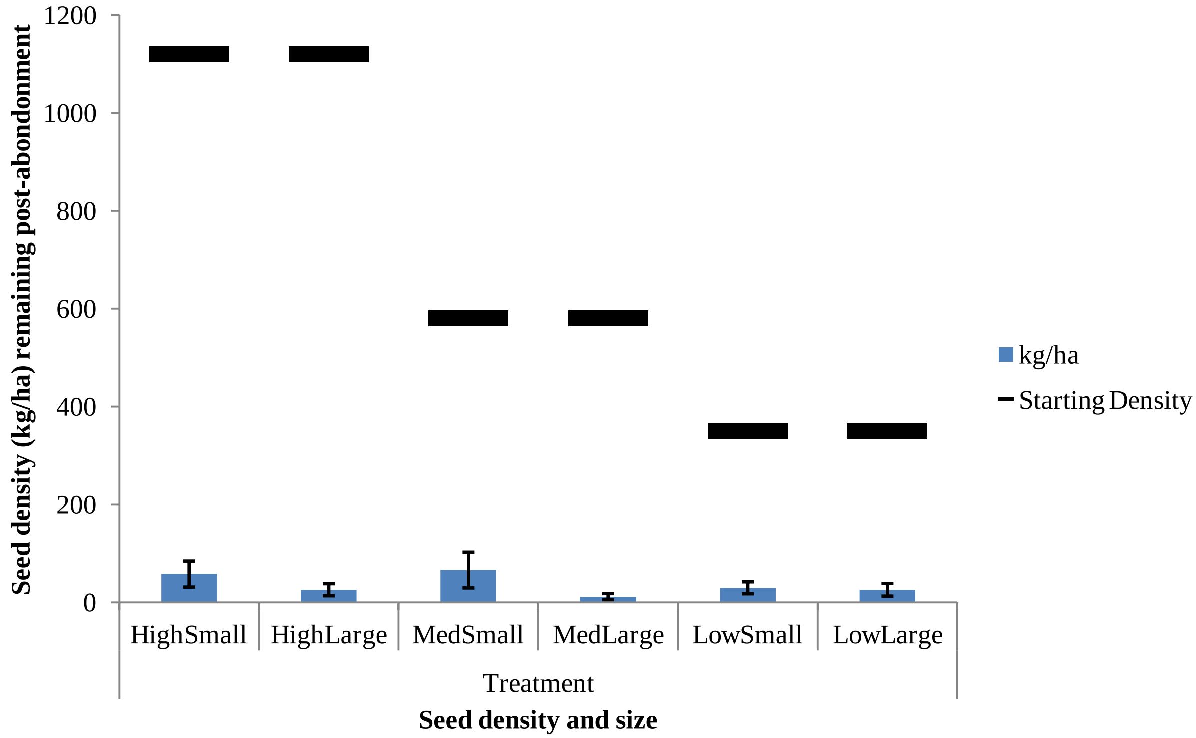

Figure 5. Mean seed density (kg/ha) following dabbling duck abandonment by density and seed size during spring 2011 in central Illinois. Horizontal lines indicate initial seed densities (1,120, 580, and 350 kg/ha). Vertical bars are ± 1 standard error.

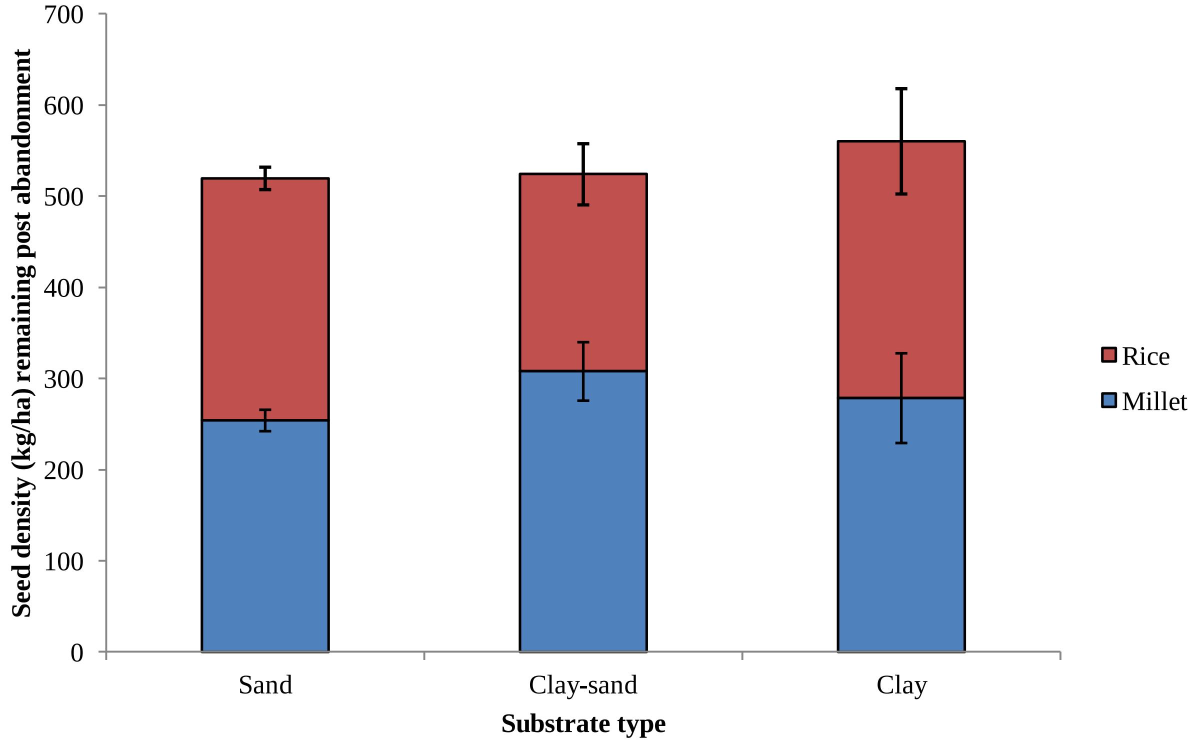

Figure 6. Mean seed densities (kg/ha) following dabbling duck abandonment of foraging patches by substrate type during March–April 2010 in central Illinois. Vertical bars are ± 1 standard error.

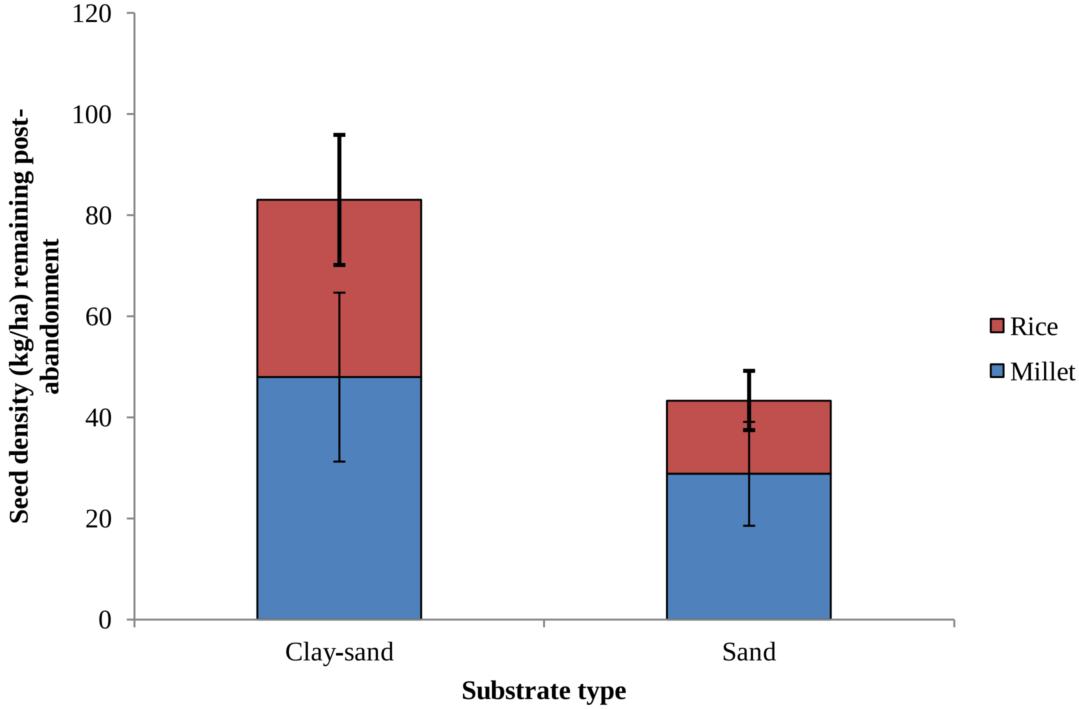

Figure 7. Mean seed density (kg/ha) following dabbling duck abandonment of foraging patches by substrate type during spring 2011 in central Illinois. Vertical bars are ± 1 standard error.

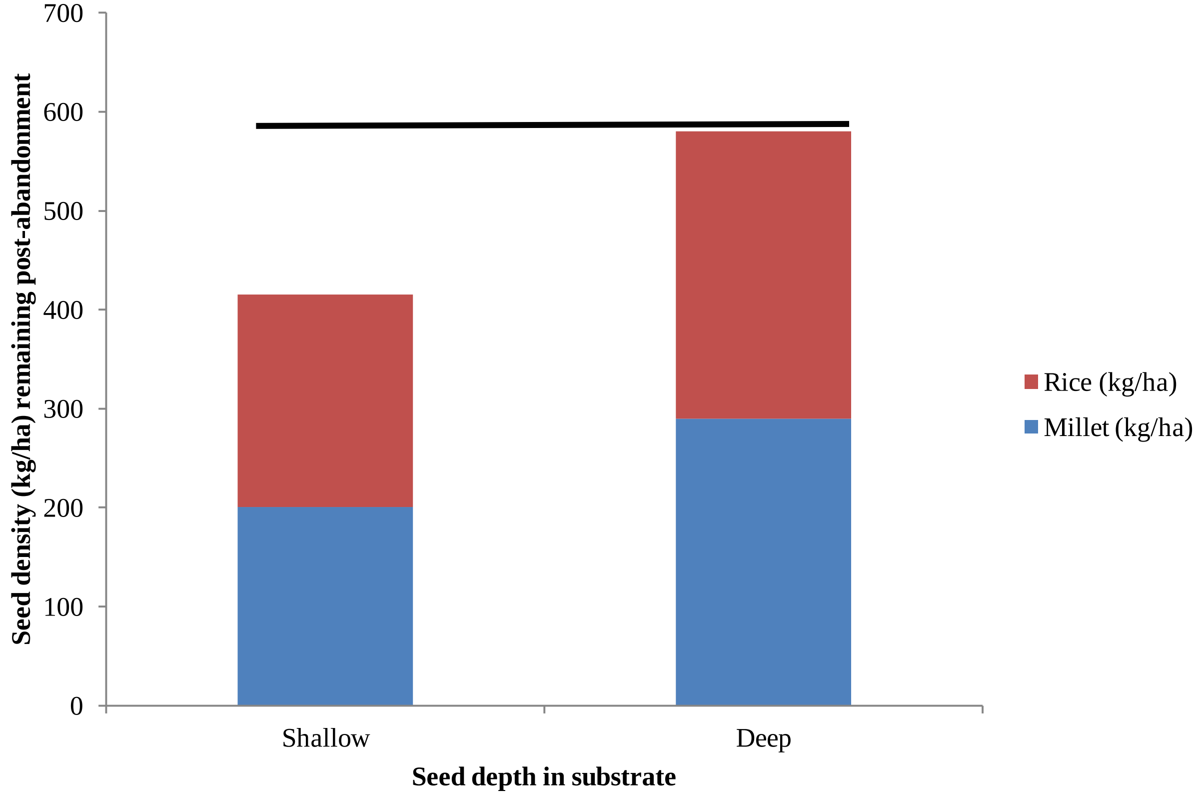

Figure 8. Mean seed density (kg/ha) following dabbling duck abandonment in patches with deep (3.8–7.6 cm) and shallowly (0–3.8 cm) buried seeds during spring 2010 in central Illinois. Horizontal line indicates initial seed density of 580 kg/ha.

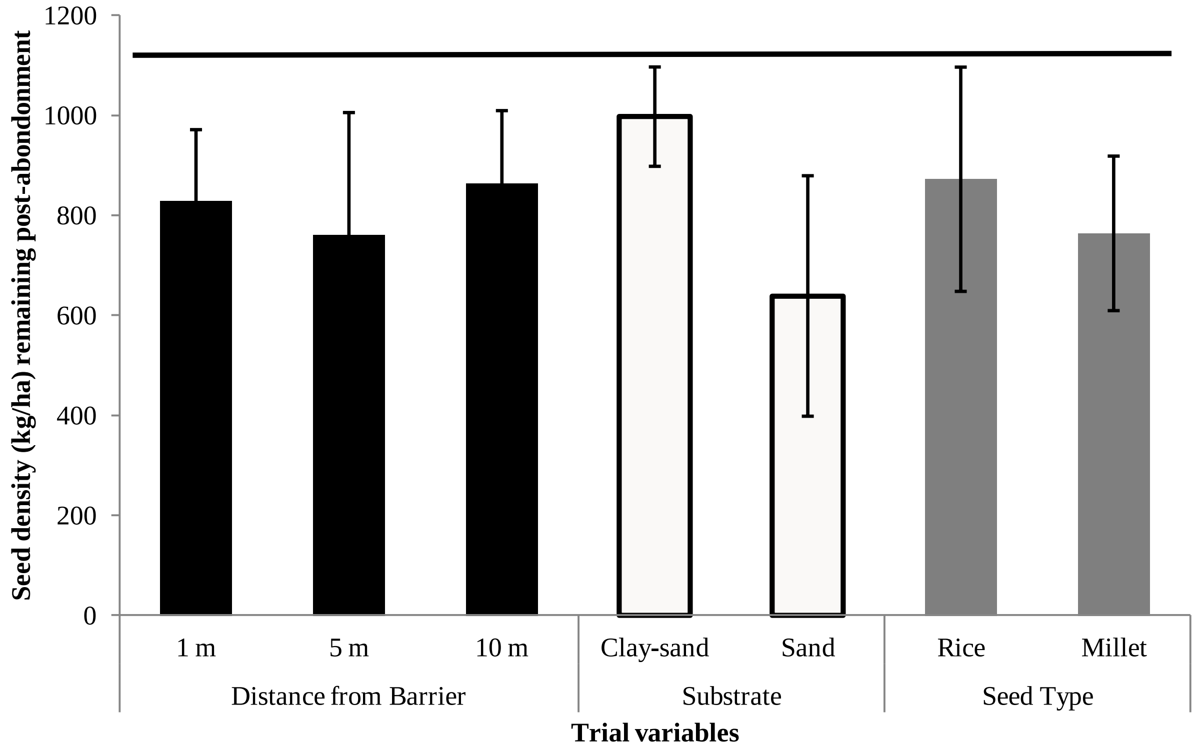

Figure 9. Mean seed density (kg/ha) following dabbling duck abandonment in visual obstruction trials during spring 2010 in central Illinois. Horizontal line indicates initial seed density (1,120 kg/ha). Vertical bars are ± 1 standard error.

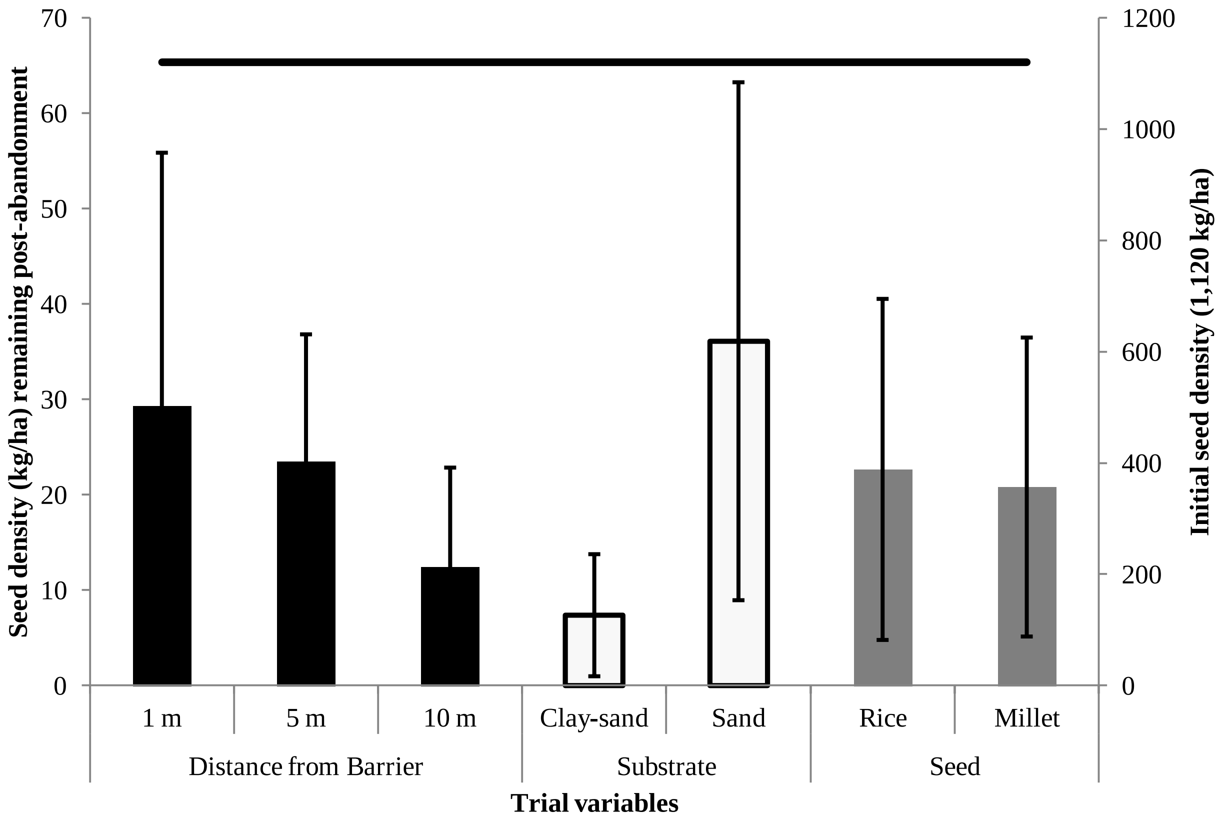

Figure 10. Mean seed density (kg/ha) following dabbling duck abandonment in visual obstruction trials during spring 2011 in central Illinois. Horizontal line indicates initial seed density (1,120 kg/ha, right axis). Vertical bars are ± 1 standard error.

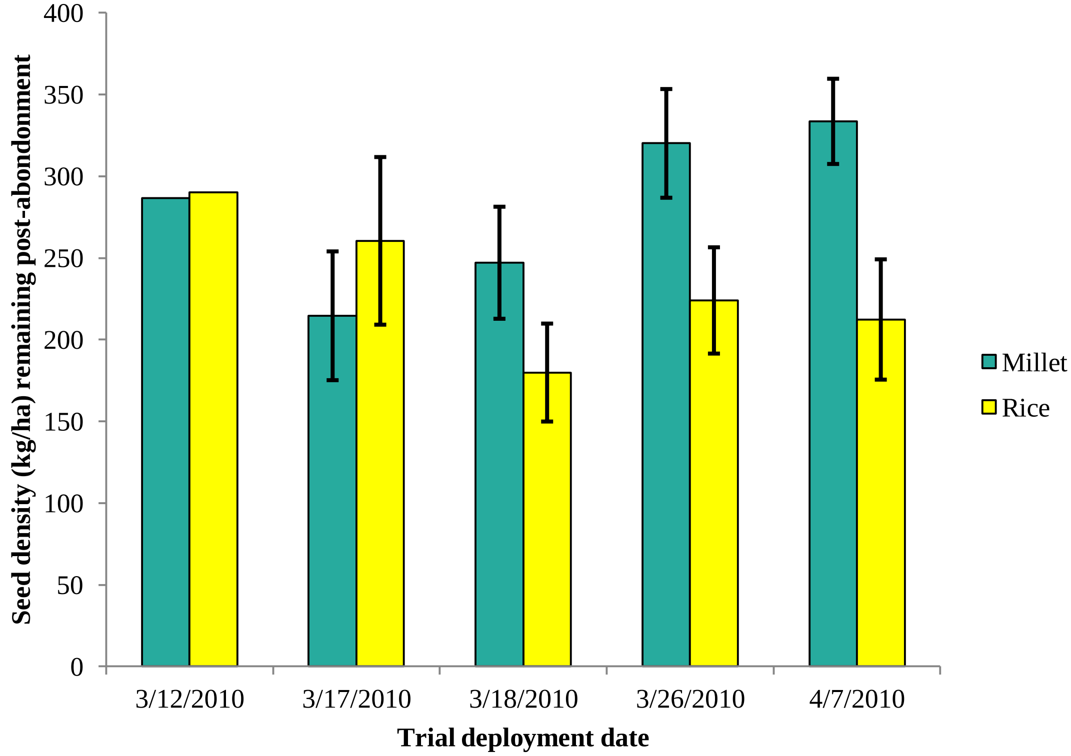

Figure 11. Mean seed density (kg/ha) following dabbling duck abandonment by trial deployment date during spring 2010 in central Illinois. Vertical bars are ± 1 standard error.

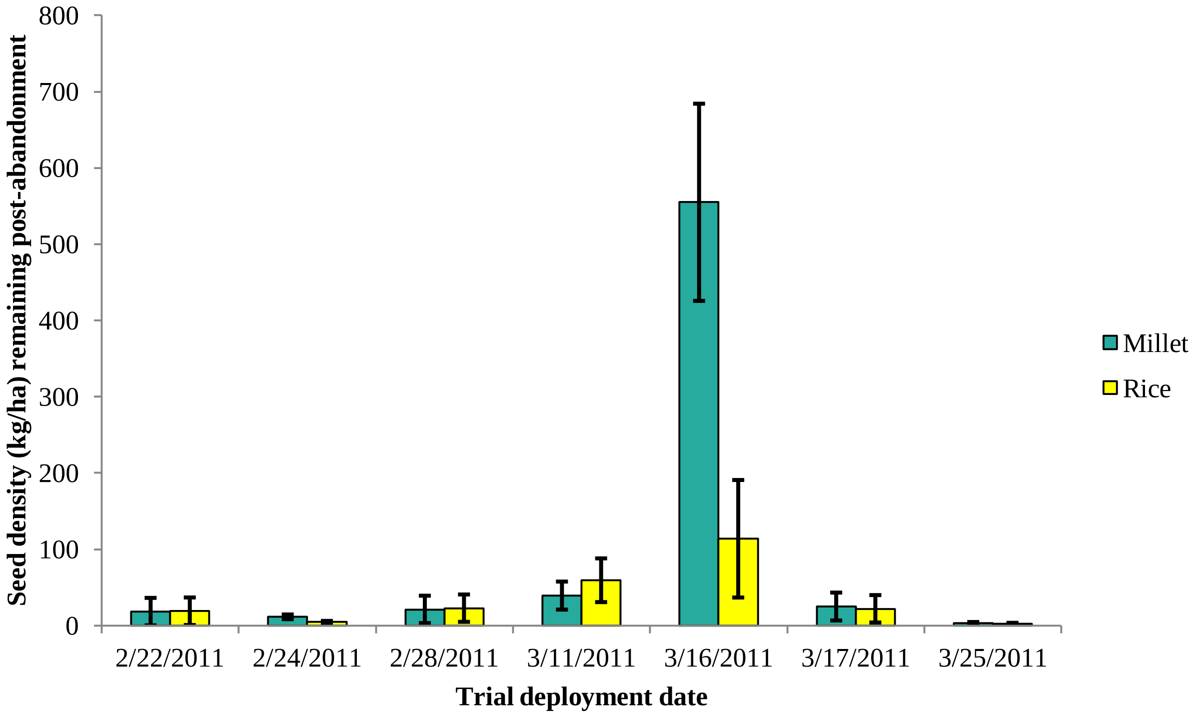

Figure 12. Mean seed density (kg/ha) following dabbling duck abandonment by trial deployment date during spring 2011 in central Illinois. Vertical bars are ± 1 standard error.

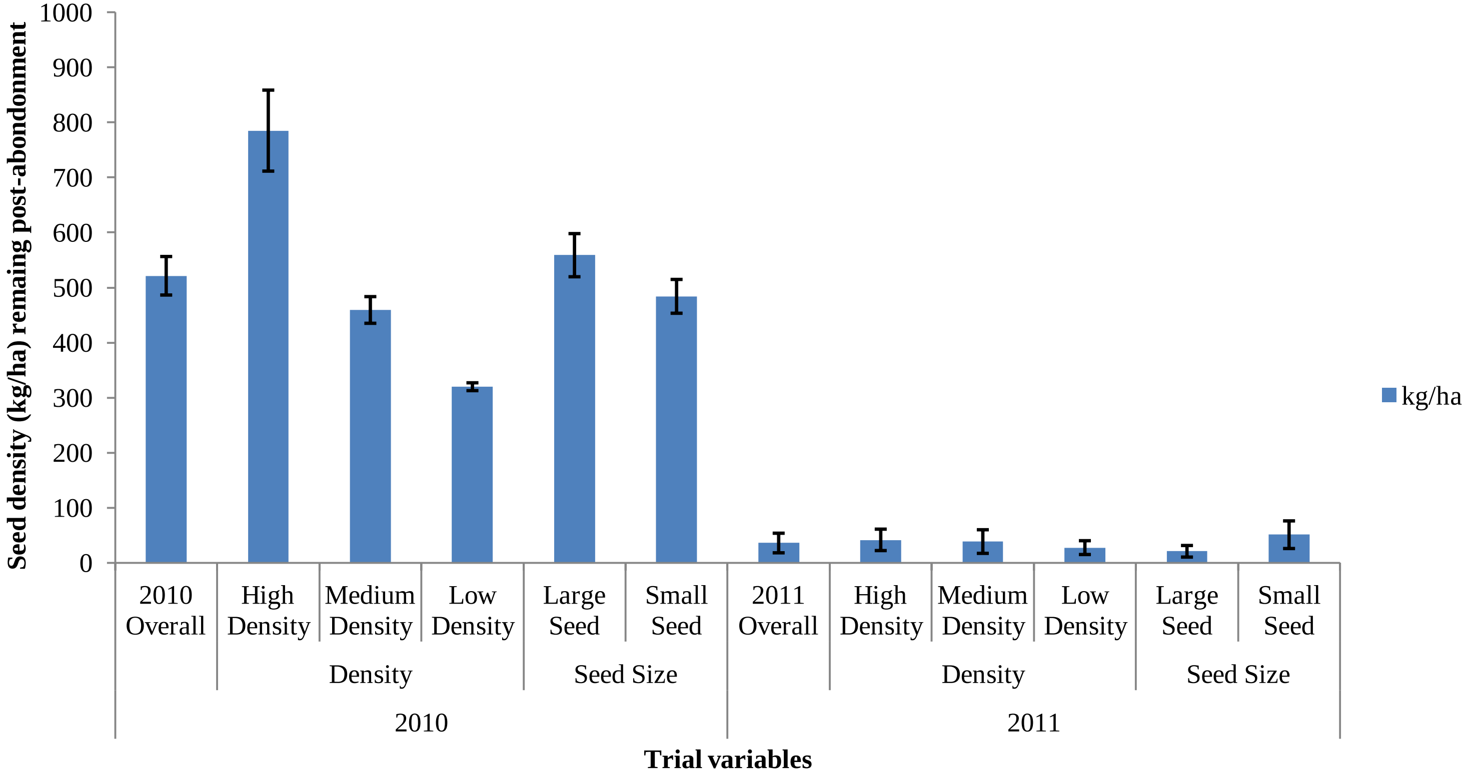

Figure 13. Mean seed density (kg/ha) following dabbling duck abandonment of foraging patches by year, initial seed density, and seed size in central Illinois. Vertical bars are ± 1 standard error.

Submitted by:

Joshua D. Stafford, PhD.
Assistant Unit Leader
U.S. Geological Survey
South Dakota Cooperative Fish and Wildlife Research Unit
South Dakota State University

Date: 15 November 2011 .