Depletion of Rice as Food of Waterfowl Wintering in the Mississippi Alluvial Valley

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ABSTRACT Waterfowl habitat conservation strategies in the Mississippi Alluvial Valley (MAV) and several other wintering areas assume carrying capacity is limited by available food, and increasing food resources is an effective conservation goal. Because existing research on winter food abundance and depletion is insufficient to test this hypothesis, we used harvested rice fields as model foraging habitats to determine if waste rice seed is depleted before spring migration. We sampled rice fields ($n = 39$ [winter 2000–2001], $n = 69$ [2001–2002]) to estimate seed mass when waterfowl arrived in late autumn and departed in late winter. We also placed exclosures in subsets of fields in autumn ($n = 8$ [2000–2001], $n = 20$ [2001–2002]) and compared seed mass inside and outside exclosures in late winter to estimate rice depletion attributable to waterfowl and other processes. Finally, we used an experiment to determine if the extent of rice depletion differed among fields of varying initial abundance and if the seed mass at which waterfowl ceased foraging or abandoned fields differed from a hypothesized giving-up value of 50 kg/ha. Mean seed mass was greater in late autumn 2000 than 2001 (127.0 vs. 83.9 kg/ha; $P = 0.018$) but decreased more during winter 2000–2001 than 2001–2002 (91.3 vs. 55.7 kg/ha) and did not differ at the end of winter (35.8 vs. 28.3 kg/ha; $P = 0.651$). Assuming equal loss to deterioration inside and outside exclosures, we estimated waterfowl consumed 61.3 kg/ha (48.3%) of rice present in late autumn 2000 and 21.1 kg/ha (25.1%) in 2001. When we manipulated late-autumn rice abundance, mean giving-up mass of rice seed was similar among treatments (48.7 kg/ha; $P = 0.205$) and did not differ from 50 kg/ha ($P = 0.726$). We integrated results by constructing scenarios in which waterfowl consumed rice at different times in winter, consumption and deterioration were competing risks, and consumption occurred only above 50 kg/ha. Results indicated waterfowl likely consumed available rice soon after fields were flooded and the amount consumed exceeded our empirical estimates but was $\leq$48% (winters pooled) of rice initially present. We suggest 1) using 50 kg/ha as a threshold below which profitability limits waterfowl feeding in MAV rice fields; 2) reducing the current estimate (130 kg/ha) of rice consumed in harvested fields to 47.2 kg/ha; and 3) increasing available rice by increasing total area of fields managed, altering management practices (e.g., staggered flooding), and exploring the potential for producing second or ratoon rice crops for waterfowl. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1125–1133; 2009)

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Historically, the Mississippi Alluvial Valley (MAV) was the largest forested wetland in North America (approx. 10 million ha; Reinecke et al. 1989). However, construction of >1,500 km of levees along the Mississippi River, wetland drainage, and clear-cutting of timber for agricultural development removed approximately 80% of original bottomland hardwood forests (Twedt and Loesch 1999). Despite these changes, the MAV still supports continentally significant waterfowl populations, because several species have adapted to the agricultural landscape by consuming rice and other grains in harvested fields (Reinecke et al. 1989). Waste rice, or rice grain remaining in fields after harvest, is an important agricultural food for migrating and wintering waterfowl in the MAV. Rice is more resistant to deterioration when flooded (Nelms and Twedt 1996) and provides more metabolizable energy than most grains and natural foods (Kaminski et al. 2003). Additionally, the MAV is a major rice-producing area in the United States and harvests nearly 900,000 ha annually (U.S. Department of Agriculture National Agricultural Statistics Service 2007).

Waterfowl habitat conservation in the MAV is guided by the Lower Mississippi Valley Joint Venture (LMVJV) and is based on the assumption that carrying capacity of habitats for wintering waterfowl is limited by food availability (Reinecke and Loesch 1996). Consequently, area of flooded fields, abundance of waste rice when waterfowl use fields, and the extent to which waterfowl can deplete rice are important considerations for conservation planning in the MAV. Surveys conducted during 1992–1995 revealed 80,830 ha of harvested rice were flooded during winter (Uihlein 2000), whereas recent analysis of satellite images indicated area of flooded fields increased to 126,515 ha by January 2003 (T. E. Moorman, Ducks Unlimited Inc., unpublished data). Sampling of harvested fields throughout the MAV during 2000–2002 indicated rice abundance in early December varied among years from 54 kg/ha to 116 kg/ha (Stafford et al. 2006*a*) and was substantially less than assumed by the LMVJV (180 kg/ha; Reinecke et al. 1989, Loesch et al. 1994). Despite increased knowledge concerning area of managed habitat and abundance of food, no data are available regarding depletion of rice in winter, extent of depletion attributable to waterfowl, or abundance thresholds limiting profitability of foraging.

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Documenting food depletion is important for estimating habitat carrying capacity (Gill et al. 1996, Krapu et al. 2004, Nolet et al. 2006) and understanding abundance, movement, distribution, and habitat use of wintering and migrating waterfowl (e.g., Sutherland and Allport 1994, Percival et al. 1996, Guillemain et al. 2000*b*, Nolet et al. 2001). By constraining food intake, depletion may decrease body mass or nutrient reserves (Krapu et al. 2004), increase movements and vulnerability to hunting mortality (Hepp et al. 1986), increase predation risk by altering foraging methods and vigilance behavior (Guillemain et al. 2000*a*, Fritz et al. 2002), and ultimately decrease survival and breeding potential (Krapu 1981, Goss-Custard et al. 2006). Thus, understanding food depletion is critical to the structure and parameterization of theoretical models of population and habitat dynamics for wintering waterfowl (Goss-Custard et al. 2002, 2003).

We used rice fields as model foraging habitats to investigate the extent of food depletion in winter, amount of depletion attributable to waterfowl, and possible existence of an abundance threshold limiting foraging profitability. We assumed available rice seed primarily determined depletion dynamics because alternative foods, such as invertebrates and moist-soil seeds, were limited to 6–7 kg/ha (Manley et al. 2004). Our objectives were to 1) use sample surveys to estimate abundance of waste rice in late autumn and late winter and extent of depletion during winter, 2) use exclosures to estimate amount of rice consumed by waterfowl and lost to deterioration, and 3) experimentally determine if a threshold or giving-up abundance of rice seed exists and limits further consumption by waterfowl. Finally, we integrated results to determine the amount of waste rice potentially consumed by wintering waterfowl to assist conservation planning by the LMVJV.

STUDY AREA

The MAV was >800 km long, varied in width from 32 km to 128 km, and encompassed approximately 10 million ha in Arkansas, Illinois, Kentucky, Louisiana, Mississippi, Missouri, and Tennessee (USA; Reinecke et al. 1989). Agriculture was the dominant land use in the MAV. Principal crops during 2000–2002 included soybean (1,965,000 ha), cotton (1,380,000 ha), rice (885,000 ha), corn (415,000 ha), winter wheat (405,000 ha), and grain sorghum or milo (240,000 ha; U.S. Department of Agriculture National Agricultural Statistics Service 2007). During winters 1992–1993 through 1994–1995, harvested rice was the dominant habitat managed by private landowners for waterfowl (55%; Uihlein 2000). Dates of waterfowl hunting varied by state but generally coincided with our data collection.

Weather patterns differed between the 2 years of our study. Cumulative precipitation during September 2000–February 2001 (64.2 cm) was near normal (62.1 cm), whereas September 2001–February 2002 (87.2 cm) was wetter than normal (National Oceanic and Atmospheric Administration, Midwestern and Southern Regional Climatic Data Centers). Mean minimum temperatures were near normal during September–October of both years but were among the coldest on record during November 2000–January 2001. During this cold period, Arkansas experienced 2 major ice storms and temperatures below normal for 25 consecutive days (11 Dec 2000–4 Jan 2001), including 10 days with daily maxima below freezing. In contrast, temperatures during November 2001–January 2002 were above normal.

METHODS

Surveys and Experiments

To estimate waste rice depletion in fields managed (i.e., flooded) for waterfowl during winter, we sampled fields at the onset of flooding (i.e., Oct–Dec; hereafter late autumn) and after they were drained (i.e., generally Feb; hereafter late winter). We used a multistage sample design (e.g., Thompson 1992) to estimate rice mass during each time period and included 3 hierarchical stages of random selection: landowners, rice fields managed by landowners, and soil cores within fields. Because we did not have a sample frame of all landowners in the MAV who managed fields each winter, we used as a surrogate a database of landowners enrolled in habitat management programs with Ducks Unlimited (cf. Stafford et al. 2006*a*, *b*). We believe the subset of landowners in the program was representative of all owners managing fields because net income from rice production was their primary objective and managing for waterfowl was secondary, many landowners managed more fields than they enrolled, and methods of managing fields are well-known (Reinecke et al. 1989) and have limited effect on rice seed available to waterfowl (Kross et al. 2008).

After selecting landowners, we chose 1 or 2 fields for sampling from among those each landowner planned to manage for waterfowl. In winter 2000–2001, we selected 26 landowners and 40 fields (AR [18], LA [5], MS [9], MO [8]), and in 2001–2002 we selected 36 landowners and 72 fields (AR [38], LA [12], MS [10], MO [12]; Fig. 1). The many fields sampled in Arkansas reflected the large area of rice managed for waterfowl in that state (Uihlein 2000). In each time period and field, we collected 2 soil cores 10 cm in diameter and depth along each of 5 equally spaced parallel transects ($n = 10$ cores/field) and selected sample sites along transects by pacing distances drawn from a random numbers table.

Each year, we installed exclosures in a random subset of fields from our sample survey to obtain separate estimates of rice consumed by waterfowl and lost to seed deterioration (germination and decomposition combined) during winter. We placed 5 2 × 2-m exclosures in each of 8 fields (AR [4], LA [1], MS [1], MO [2]) in late autumn 2000 and 10 1 × 1-m exclosures in each of 20 fields (AR [10], LA [3], MS [4], MO [3]) in 2001. In 2000, we randomly placed one exclosure along each transect used in the sample survey, whereas in 2001 we randomly placed 2 exclosures along each transect. We collected 2 core samples from each of the 5 exclosures/field in late winter 2000–2001 ($n = 10$ cores/field) and 1 core from each of the 10 exclosures/field in late winter 2001–2002 ($n = 10$ cores/field).

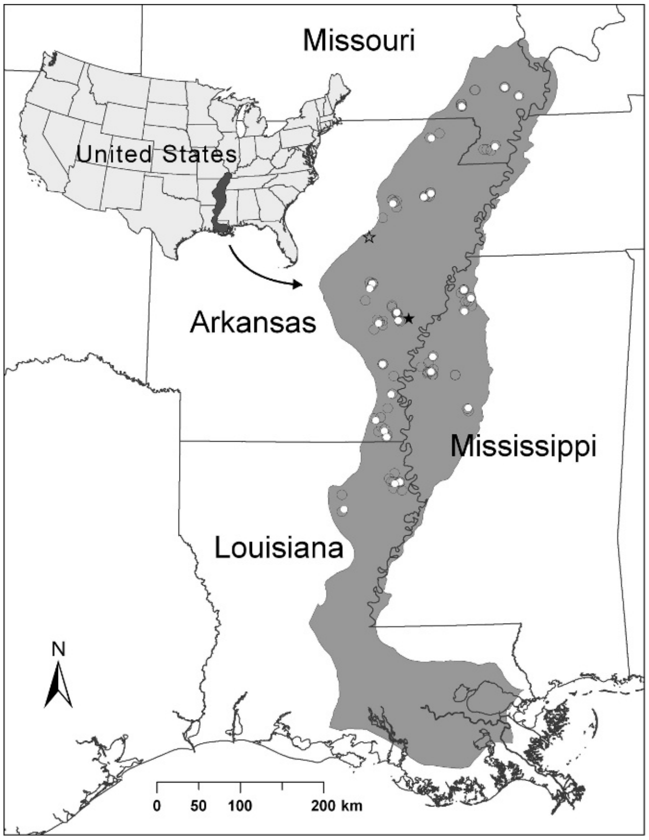

Figure 1. Rice fields in the Mississippi Alluvial Valley, USA, flooded in winter to attract waterfowl and used as study sites during late autumn 2000–late winter 2001 and late autumn 2001–late winter 2002. We sampled harvested fields on private land (open and white filled circles) in late autumn and late winter to estimate decreases in rice abundance during winter, and installed exclosures in a subset of the fields (white filled circles) in late autumn to sample in late winter and estimate decreases in rice attributable to feeding by waterfowl and other factors. We varied rice abundance in late autumn in plots at White River (closed star) and Bald Knob (open star) National Wildlife Refuges to estimate rice abundance when waterfowl stopped feeding and determine if the final or giving-up density was related to initial density.

We conducted an experiment to estimate rice seed mass remaining after waterfowl stopped feeding in fields (i.e., giving-up density [GUD]) and determine if GUD differed from a hypothesized threshold of 50 kg/ha (Reinecke et al. 1989). In the experiment, we used rice fields that were managed by tenant farmers using normal agricultural practices and located at 5 sites over 2 winters (one at White River National Wildlife Refuge [NWR] in 2000–2001 and 2 each at White River NWR and Bald Knob NWR in 2001–2002). Each site comprised 2 or 3 plots that ranged in size from 2 ha to 4 ha. We assigned plots within sites to 1 of 3 treatments to vary postharvest rice abundance from low (normal harvest) to medium (partial harvest) and high (no harvest). We created partially harvested plots by adjusting combine settings to allow approximately 50% of seed to pass through during harvest. Plots within sites were adjacent and near a 6-m-high observation blind. Refuge staff rolled rice straw using a cleated stubble roller and flooded plots during autumn. Because shallow flooding was maintained during autumn–winter and the only treatment applied to rice stubble was rolling, most waste rice should have remained accessible on the soil surface. We monitored seed mass and waterfowl use to determine the amount of rice remaining when waterfowl stopped feeding in plots. We collected core samples (n = 12 [2000–2001]; n = 10 [2001–2002]) from each plot 1–2 times/week throughout winter using methods described for the sample surveys and visited plots several times per week to record number and behavior of waterfowl present.

We washed core samples from surveys and experiments through a series of sieves (mesh sizes 10 [2.0-mm aperture], 14 [1.4-mm], 18 [1.0-mm]) and manually separated rice seeds (domestic rice plus the weedy variant red rice) from soil and organic matter. We classified seeds as 1) unsprouted, 2) short-sprouted, with emerging coleoptile and radicle less than seed length, and 3) long-sprouted, with coleoptile or radicle greater than seed length. We report selected results for long-sprouted seeds but considered only unsprouted and short-sprouted seeds as potential waterfowl food because we found no long-sprouted seeds among foods consumed by mallards (*Anas platyrhynchos*; K. J. Reinecke, United States Geological Survey, unpublished data). We dried samples to constant mass at 50° C and measured mass to the nearest 0.0001 g.

Data Analysis

Before analyzing data from the sample survey, we omitted one field sampled only in late autumn 2001 and excluded as outliers 2 landowners (one each winter) with mean seed mass in late autumn >4 standard errors from the overall mean. Then, we estimated mean mass and standard errors for unsprouted, short-sprouted, and long-sprouted seeds by year (1 [winter 2000–2001], 2 [winter 2001–2002]) and time period (late autumn, late winter) using methods appropriate for the 3-stage structure of the sample design (PROC SURVEYMEANS; SAS Institute Inc. 1999). We also estimated mean mass for the sum of unsprouted and short-sprouted seeds and considered this the best estimate of potential waterfowl food.

We tested factors affecting variation in rice mass (unsprouted plus short-sprouted seeds) using repeated-measures analysis of variance (ANOVA). We used ANOVA despite some nonnormality and heterogeneity of variances, because ANOVA is robust to nonnormality and plots indicated sample distributions and residuals were similar among treatments (Littell et al. 2002). The dependent variable in the model (PROC MIXED; SAS Institute Inc., Cary, NC) was mean seed mass computed by year, time period, and landowner (kg/ha; n = 10 or 20 soil cores [subsamples]) because landowners were the primary sample unit in the survey design. For consistency, we weighted field means with the sample weights used in the SURVEYMEANS procedure. Fixed effects were year, time period, and their interaction; landowner nested within years was a random effect. The subject of repeated measures was mean rice mass of landowners between time periods within years. Because of inherent variability associated with large-scale field sampling, we considered tests with $P < 0.10$ as significant. When comparing selected means a posteriori, we adjusted significance levels with the Bonferroni method to control experiment-wise Type I error rates.

Before analyzing data from exclosures, we excluded one field where exclosures failed. Because fields selected for exclosures were a subset of those in the sample survey, we adjusted sample weights before using PROC SURVEYMEANS to estimate mean rice mass computed by year and treatment, where the 3 treatments comprised late autumn, late winter outside exclosures, and late winter inside exclosures. We assumed decreases in mean rice mass between late autumn and late winter inside exclosures represented deterioration, and decreases outside exclosures represented combined effects of deterioration and feeding by waterfowl. We estimated amount of rice consumed by waterfowl as the difference in rice mass inside and outside exclosures in late winter. Implicit in our method of estimating consumption were assumptions that rice loss from deterioration during winter was equal inside and outside exclosures and waterfowl consumed rice only in late winter after deterioration occurred. We used repeated-measures ANOVA to test factors affecting variation in mean rice mass per field and weighted the dependent variable as in PROC SURVEYMEANS. Fixed effects were year, treatment, and their interaction; field (or landowner) was a random effect within years; and the repeated measure was rice mass in fields over treatments within years. We treated assumptions of ANOVA, a posteriori comparisons, and alpha level as described previously.

For the foraging threshold experiment, we estimated rice mass initially present in plots as simple means of data collected during the 2 sample periods preceding waterfowl use (n = 24 soil cores [2000–2001]; n = 20 soil cores [2001–2002]). Similarly, we estimated seed mass after abandonment as means over the 2 periods following intensive foraging. We used a one-way ANOVA to test if rice mass following waterfowl use varied among treatments differing in initial abundance. Then, we used a one-sample t-test to determine if mean GUD over treatments differed from the hypothesized threshold of 50 kg/ha.

Finally, we knew rice consumption estimates from the exclosure experiment were negatively biased because our methods required the unrealistic assumption that waterfowl consumed rice only during late winter. To determine the extent of this potential bias, we simulated 3 contrasting scenarios that showed how variation in temporal patterns of foraging during a hypothetical 100-day winter affected estimates of consumption. For each scenario, we assumed seeds deteriorated at a constant daily rate (Nelms and Twedt 1996) and estimated this value as the rate needed to account for the decrease in seed mass inside exclosures between late autumn and late winter for data pooled over years. We also assumed rice available to waterfowl each day was the mass of seeds exceeding the value identified in our foraging threshold experiment. The scenarios simulated were 1) rice deteriorated until day 99 and on day 100 waterfowl consumed remaining available seeds (i.e., as assumed in the exclosure experiment), 2) rates of consumption and deterioration were equal from day 1 until all available rice was consumed and rice deteriorated thereafter, and 3) waterfowl consumed all available rice on day 1 and rice deteriorated thereafter.

RESULTS

Sample Survey of Rice Abundance

Median dates of late-autumn sampling were 12 November (range = 8 Nov–5 Dec) in 2000 and 30 November (range = 21 Oct–14 Dec) in 2001. In autumn 2000, we sampled 80% of fields within 2 weeks of the onset of flooding, and, in autumn 2001, we sampled >80% of fields within 1 week of flooding. Median dates of late-winter sampling were 23 February (range = 29 Jan–28 Feb) in 2001 and 21 February (range = 11–27 Feb) in 2002, and we sampled nearly all fields within 1 week of drainage. Mean size of sampled fields was 24.9 ha (range = 4.1–113.5 ha; n = 39) in year 1 and 26.8 ha (range = 5.0–90.9 ha; n = 69) in year 2. Overall, we collected and processed 2,160 core samples (n = 780 [2000–2001], 1,380 [2001–2002]) from 108 fields.

During all time periods, unsprouted rice grains contributed most (63.6–96.9%) of the seed mass recovered from samples (Table 1). However, sprouted seeds (both short and long) contributed a greater percentage of mass in year 2 than year 1 in both late autumn (36.4% vs. 17.6%) and late winter (14.4% vs. 3.1%). Within sprouted seeds, long-sprouted seeds contributed limited mass in late autumn (7.4–9.6 kg/ha [5.5–10.3%]) and were mostly gone by late winter whether or not protected by exclosures. Mass of rice in late autumn was 127.0 kg/ha (SE = 25.2) in 2000, 83.9 kg/ha (21.8) in 2001, and 102.1 kg/ha (20.0) when we pooled data (Table 1). In late winter, mass was 35.8 kg/ha (5.2) in 2001, 28.3 kg/ha (3.4) in 2002, and 31.4 kg/ha (3.0) when we pooled data. Rice mass decreased 91.3 kg/ha in winter 2000–2001, 55.7 kg/ha in winter 2001–2002, and 70.7 kg/ha overall.

Year and time period interacted ($F_{1,\,58} = 3.01$, $P = 0.088$) in the repeated-measures ANOVA, suggesting main effects were not additive. We examined 5 selected a posteriori contrasts with the adjusted significance level $\alpha = 0.10/5 = 0.02$. We found strong evidence that seed mass decreased between late autumn and late winter in both year 1 ($t_{58} = 5.81$, $P < 0.001$) and year 2 ($t_{58} = 4.15$, $P < 0.001$). Within time periods, seed mass was greater in late autumn 2000 than 2001 ($t_{58} = 2.43$, $P = 0.018$), but we did not detect a difference in late winter ($t_{58} = 0.46$, $P = 0.651$). Finally, we failed to reject the hypothesis that decreases between late autumn and late winter differed between years ($t = 1.74$, $P = 0.088$).

Sample Exclosures

Mean seed mass in late autumn 2000 was 158.3 kg/ha; in late winter 2001, mass was 88.9 kg/ha inside exclosures and 27.6 kg/ha outside exclosures (Table 2). Mean seed mass in late autumn 2001 was 87.1 kg/ha; in late winter 2002, mass was 46.2 kg/ha inside exclosures and 25.1 kg/ha outside exclosures. Decreases attributed to seed deterioration were 69.4 kg/ha (43.8%) in year 1 and 40.9 kg/ha (47.0%) in year

Table 1. Means (kg/ha; SE), percentages, and changes over time in mass of waste rice seeds classified as unsprouted, short-sprouted, and long-sprouted in harvested fields managed for waterfowl wintering in the Mississippi Alluvial Valley, USA. Estimates are from a 3-stage sample in which we collected 10 soil cores during each of 2 time periods from 39 fields managed by 25 landowners in 2000–2001 and 69 fields managed by 35 landowners in 2001–2002.

	Late autumn			Late winter				
Seed type[a]	$\bar{x}$	SE	%[b]	$\bar{x}$	SE	%[b]	Diff[c]	%Diff[d]
2000–2001								
UN	110.8	22.2	82.5	35.0	5.2	96.9	75.9	68.4
SH	16.2	4.9	12.1	0.8	0.3	2.2	15.4	95.1
LO	7.4	2.2	5.5	0.3	0.2	0.9	7.0	95.5
UN+SH	127.0	25.2	94.5	35.8	5.2	99.1	91.3	71.8
2001–2002								
UN	59.5	15.7	63.6	24.6	3.0	85.4	34.9	58.7
SH	24.4	6.7	26.1	3.6	0.6	12.6	20.8	85.1
LO	9.6	2.8	10.3	0.5	0.2	1.8	9.1	94.5
UN+SH	83.9	21.8	89.7	28.3	3.4	98.2	55.7	66.3
Yr pooled								
UN	81.2	16.0	73.3	28.9	2.8	90.9	52.2	64.4
SH	21.0	5.1	18.9	2.4	0.5	7.7	18.5	88.3
LO	8.7	2.3	7.8	0.4	0.2	1.4	8.2	94.9
UN+SH	102.1	20.0	92.2	31.4	3.0	98.6	70.7	69.3

[a] UN were unsprouted seeds showing no evidence of germination; SH were short-sprouted seeds having radicle and coleoptile less than seed length; LO were long-sprouted seeds having radicle or coleoptile greater than seed length.
[b] Mass of seed type *i* divided by total mass of seeds within yr and time period.
[c] $\bar{x}_{\text{Late autumn}} - \bar{x}_{\text{Late winter}}$.
[d] $100 \times \text{Diff}/\bar{x}_{\text{Late autumn}}$.

2. Decreases attributed to waterfowl were 61.3 kg/ha (38.7%) in year 1 and 21.1 kg/ha (24.3%) in year 2.

Year and treatment interacted in the repeated-measures ANOVA ($F_{2,\ 50} = 2.49$, $P = 0.093$). We suspected the interaction resulted from lack of a difference between years in late winter outside exclosures, and a contrast between years within this treatment (late winter inside exclosures) supported our inference ($t_{50} = 0.34$, $P = 0.739$). Further, when we excluded data from within this treatment and repeated the ANOVA, we found no evidence of interaction ($F_{1,\ 25} = 0.37$, $P = 0.551$), and year ($F_{1,\ 25} = 5.84$, $P = 0.023$) and treatment ($F_{1,\ 25} = 5.47$, $P = 0.028$) were significant. Thus, rice abundance was greater in late autumn 2000 than 2001 and the difference persisted through late winter inside exclosures. We additionally conducted 3 a posteriori contrasts with the full model (adjusted $\alpha = 0.10/3 = 0.033$). Rice abundance outside exclosures was less than inside in late winter 2001 ($t_{50} = 2.68$, $P = 0.010$) but not 2002 ($t_{50} = 1.59$, $P = 0.117$), and the difference between inside and outside exclosures was similar between years ($t_{50} = 1.52$, $P = 0.135$).

Foraging Threshold Experiment

Species observed feeding in experimental plots included mallard, northern pintail (*Anas acuta*), green-winged teal (*A. crecca*), snow goose (*Chen caerulescens*), gadwall (*A. strepera*), and northern shoveler (*A. clypeata*). Once foraging was initiated at a site, large numbers of waterfowl fed in plots for

Table 2. Means (kg/ha; SE), percentages, and changes over time in mass of waste rice seeds classified as unsprouted, short-sprouted, and long-sprouted from sites accessible to foraging and sites protected by exclosures in harvested fields managed for waterfowl in the Mississippi Alluvial Valley, USA. Estimates are from an experiment in which we collected 10 soil cores (subsamples) in each of 3 time periods (or treatments) in 8 fields in 2000–2001 and 19 fields in 2001–2002.

				Late winter											
	Late autumn			Inside exclosures					Outside exclosures						
Seed type[a]	$\bar{x}$	SE	%[b]	$\bar{x}$	SE	%[b]	Diff_I[c]	$\%\text{Diff}_\text{I}$[d]	$\bar{x}$	SE	%[b]	Diff_O[e]	$\%\text{Diff}_\text{O}$[f]	$\text{Diff}_{\text{I}-\text{O}}$[g]	$\%\text{Diff}_{\text{I}-\text{O}}$[h]
2000–2001															
UN	144.3	36.4	86.5	85.0	29.0	95.1	59.3	41.1	26.6	7.8	96.0	117.7	81.5	58.4	40.5
SH	14.0	4.4	8.4	3.9	1.1	4.3	10.1	72.5	0.9	0.6	3.4	13.0	93.2	2.9	20.8
LO	8.5	2.6	5.1	0.5	0.3	0.6	8.0	93.8	0.2	0.2	0.6	8.4	98.1	0.4	4.2
UN+SH	158.3	36.9	94.9	88.9	28.9	99.4	69.4	43.8	27.6	8.2	99.4	130.7	82.6	61.3	38.7
2001–2002															
UN	68.8	18.4	70.3	40.6	8.5	87.0	28.2	41.0	23.0	2.3	91.1	45.7	66.5	17.6	25.5
SH	18.3	7.4	18.7	5.6	2.4	12.0	12.7	69.4	2.0	0.8	8.1	16.3	88.9	3.6	19.5
LO	10.7	3.7	11.0	0.5	0.3	1.0	10.3	95.6	0.2	0.1	0.9	10.5	98.0	0.2	2.3
UN+SH	87.1	24.4	89.0	46.2	9.8	99.0	40.9	47.0	25.1	2.5	99.1	62.0	71.2	21.1	24.3
Yr pooled															
UN	88.6	19.1	76.4	51.8	10.8	90.2	36.8	41.6	23.9	2.6	92.4	64.7	73.0	27.8	31.4
SH	17.2	5.3	14.8	5.2	1.8	9.0	12.0	69.9	1.8	0.6	6.8	15.4	89.7	3.4	19.8
LO	10.2	2.6	8.8	0.5	0.2	0.8	9.7	95.2	0.2	0.1	0.8	10.0	98.0	0.3	2.7
UN+SH	105.8	22.7	91.2	56.9	11.6	99.2	48.8	46.2	25.7	2.8	99.2	80.1	75.7	31.2	29.5

[a] UN were unsprouted seeds showing no evidence of germination; SH were short-sprouted seeds having radicle and coleoptile less than seed length; LO were long-sprouted seeds having radicle or coleoptile greater than seed length.
[b] Mass of seed type *i* divided by total mass of seeds within corresponding yr, time period, and treatment.
[c] Mass lost absent waterfowl foraging: $\text{Diff}_\text{I} = \bar{x}_{\text{Late autumn}} - \bar{x}_{\text{Late winter inside exclosures}}$.
[d] $100 \times \text{Diff}_\text{I}/\bar{x}_{\text{Late autumn}}$.
[e] Mass lost to waterfowl foraging and all other factors: $\text{Diff}_\text{O} = \bar{x}_{\text{Late autumn}} - \bar{x}_{\text{Late winter outside exclosures}}$.
[f] $100 \times \text{Diff}_\text{O}/\bar{x}_{\text{Late autumn}}$.
[g] Rice consumed by waterfowl: $\text{Diff}_{\text{I}-\text{O}} = \bar{x}_{\text{Late winter inside exclosures}} - \bar{x}_{\text{Late winter outside exclosures}}$.
[h] $100 \times \text{Diff}_{\text{I}-\text{O}}/\bar{x}_{\text{Late autumn}}$.

several days to 3 weeks and then departed abruptly. Because foraging was intense and of short duration, our behavioral observations provided qualitative descriptions of use patterns but not quantitative estimates of waterfowl densities or cumulative use-days. To summarize, plots at one site were used by >6,000 mallards and other species for 1 week in late November 2000 and by ≤1,000 ducks during the following 2 weeks in December. At 2 other sites, northern pintails and other species numbering >120,000 birds fed in plots for 2 weeks in mid-November 2001. The last 2 sites were used by >2,000 snow geese for daily morning and evening feeding bouts for 2–3 weeks in December 2001–January 2002.

Because of early use of experimental sites by waterfowl, we were able to estimate rice seed mass before waterfowl arrived in only 6 of 12 plots. Before arrival, rice mass averaged 138.9 kg/ha (SE = 19.1) in 3 harvested plots, 1,553 kg/ha in one partially harvested plot, and 6,030 kg/ha (range = 5,600–6,460 kg/ha) in 2 unharvested plots. We sampled 7 of 12 plots immediately after abandonment by waterfowl but, because of ice cover in year 1 and severe flooding in year 2, we could not sample the remaining 4 plots until 23 days (n = 2), 6 weeks, and 8 weeks after abandonment. We did not estimate rice mass at abandonment for one harvested plot because we were uncertain about timing of waterfowl use. Mean rice mass at abandonment ranged from 42.8 kg/ha (6.6) in 4 harvested plots to 43.0 kg/ha (9.8) in 2 partially harvested plots and 55.7 kg/ha (3.2) in 5 unharvested plots. We did not detect any variation among treatments ($F_{2,8}$ = 1.94, P = 0.205) nor did the mean across treatments (48.7 kg/ha, SE = 3.5) differ from the hypothesized threshold of 50 kg/ha (t_{10} = −0.36, P = 0.726).

Rice Consumption by Waterfowl

In simulating effects of temporal variation in foraging on estimates of rice consumption, we assumed an initial mean rice mass of 105.8 kg/ha (Table 2), waterfowl consumed rice only in excess of 50 kg/ha, and rice mass deteriorated at a rate of 0.63%/day (105.8–56.9 kg/ha; Table 2). In scenario 1, waterfowl consumed rice at the end of winter after 99 days of deterioration had decreased seed mass inside and outside exclosures from 105.8 kg/ha to 56.9 kg/ha (Fig. 2). On day 100, waterfowl consumed the 6.9 kg/ha of seed remaining above the threshold of 50 kg/ha and the difference in mass inside and outside exclosures was an accurate estimate of consumption. In scenario 2, rice consumption and deterioration occurred at equal rates and each reduced seed mass by 27.9 kg/ha before the threshold was reached on day 59 (Fig. 2). Thereafter, deterioration decreased seed mass outside exclosures to 38.6 kg/ha and, at the end of winter, the difference in mass inside and outside exclosures (56.9 − 38.6 = 18.3 kg/ha) underestimated the true consumption of 27.9 kg/ha by 9.6 kg/ha or 34.4%. In scenario 3, waterfowl ate all 55.8 kg/ha (105.8 − 50 kg/ha) of available rice on day 1, then deterioration decreased rice remaining outside exclosures to 26.9 kg/ha (Fig. 2). At the end of winter, the difference in mass inside and outside exclosures (56.9 − 26.9 = 30.0 kg/ha) underestimated the true consumption of 55.8 kg/ha by 25.8 kg/ha or 46.2%.

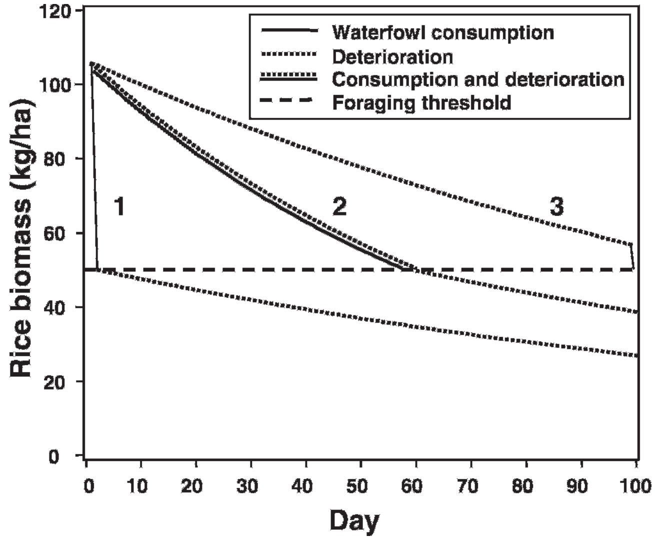

Figure 2. Hypothetical scenarios depicting the extent to which waste rice was consumed by waterfowl and lost to other factors during winters 2000–2001 and 2001–2002 in the Mississippi Alluvial Valley, USA. We based scenarios on samples collected in late autumn and inside and outside exclosures in late winter and assumed 105.8 kg/ha of seed was present in late autumn and 50 kg/ha was a threshold below which feeding no longer occurred. Scenarios indicated waterfowl feeding 1) in late autumn before seeds deteriorated consumed 55.8 kg/ha (53%) of rice, 2) gradually during winter at the same rate deterioration occurred consumed 27.9 kg/ha (26%), and 3) at the end of winter after seeds deteriorated consumed 6.9 kg/ha (7%).

Consistent with field observations of waterfowl foraging behavior (Rutka 2004), we believed our empirical estimate of rice consumption from fields with exclosures should be modified to reflect results of simulation scenarios 2 and 3, where waterfowl depleted rice in early to mid winter. We concluded that adding the mean bias of 17.7 kg/ha from scenarios 2 and 3 to the original estimate of 31.2 kg/ha provided the most representative estimate of rice consumed. The adjusted estimate (48.9 kg/ha) then revealed that waterfowl consumed 46.2% of rice available in late autumn, which equaled 58.7 kg/ha in year 1, 38.8 kg/ha in year 2, and 47.2 kg/ha for years pooled when calculating 46.2% of rice available in fields of our sample survey.

DISCUSSION

Sample Survey of Rice Abundance

Difference in late-autumn abundance of rice seed between 2000 and 2001 probably resulted, in part, from greater rainfall during October–November 2001, which saturated soils in rice fields and increased postharvest losses to decomposition and germination (McGinn and Glasgow 1963, Stafford et al. 2006*a*). Consistent with this explanation, sprouted seeds comprised a larger percentage of rice mass in year 2 than year 1. Both late-autumn estimates were in agreement with recent work indicating waste rice abundance has declined in the MAV (Manley et al. 2004, Stafford et al. 2006*a*). Our pooled estimate of rice mass in late autumn (102.1 kg/ha) was greater than the late-autumn estimate of 78.4 kg/ha reported by Stafford et al. (2006*a*), who sampled the same set of fields. However, because study objectives were different, we sampled fields relative to flooding date, whereas Stafford et al. (2006*a*) sampled based on calendar date. Consequently, our sampling efforts began earlier than the late-autumn period of Stafford et al. (2006*a*), and, because earlier sampling permits less time for deterioration and consumption by waterfowl, we anticipated our estimate would be greater.

Although many studies have reported depletion of local waterfowl food sources (e.g., Percival et al. 1996, Amano et al. 2006, Nolet et al. 2006, Greer et al. 2007), ours is the first to document depletion of a food in an area the size of the MAV. Regional depletion of an important food source is not unequivocal evidence that wintering waterfowl populations are limited by food availability, but it is consistent with the hypothesis. Also consistent is our finding that estimates of rice mass were similar between years in late winter despite an initial difference in late autumn. Rice depletion is consistent with conservation strategies that emphasize management of foraging habitats in the MAV, but LMVJV energetics models also need to quantify how much of the decrease results from consumption by waterfowl.

Sample Exclosures and Simulations

Our estimate of rice loss by deterioration was considerably less than the 99% reported by McGinn and Glasgow (1963) and greater than estimates from several other studies after 90 days inundation (19–20%; Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996). We speculate differences among studies resulted, in part, from differences in experimental design and definitions of deterioration. Most previous studies (Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996) were limited in spatial scale and, by initiating experiments with only sound, unsprouted seeds, did not account for germination or enhanced susceptibility to decomposition resulting from exposure to ambient conditions during autumn. McGinn and Glasgow (1963) measured deterioration as percentage of rice seeds no longer whole and firm at the end of the exposure period, whereas our study and others measured deterioration as percentage of initial mass lost during exposure.

Use of exclosures indicated waterfowl consumed substantially <130 kg/ha, the value used by the LMVJV to estimate food consumption in rice fields (Reinecke and Loesch 1996). We attribute this difference to a combination of decreased abundance of waste rice in late autumn (Stafford et al. 2006*a*, this study) and the method we used to account for losses to deterioration and consumption by waterfowl. In estimating consumption, we necessarily assumed equal masses of rice deteriorated inside and outside exclosures. However, the mass of rice exposed and percent lost to deterioration was greater inside exclosures than outside because waterfowl consumed rice outside exclosures and decreased the mass at risk to deterioration. Thus, loss to deterioration depended on amount and timing of rice consumption during winter, and estimates of consumption based exclusively on data from exclosures were negatively biased and conservative.

Empirical data support our simulated scenarios 1 and 2, which confined waterfowl foraging to early and mid-winter. Evidence of early depletion consistent with scenario 1 includes observations of foraging behavior from the threshold experiment, where waterfowl fed for a short period in 9 of 11 experimental plots as soon as they were flooded and then abandoned sites for the remainder of winter. In addition, data collected by Stafford et al. (2006*a*) indicated rice mass decreased by 18% in 2000 and 41% in 2001 between the time we collected samples in late autumn and their final sampling period (27 Nov–7 Dec). The magnitude of this loss is greater than predicted from deterioration alone. Other evidence, consistent with scenario 2, suggests rice consumption continued beyond early winter. Diurnal and nocturnal behavioral observations (D. M. Greer, Southern Illinois University, unpublished data) and aerial surveys (Reinecke et al. 1992) documented significant use of rice fields persisting into January, and the difference between the foraging threshold of 50 kg/ha and mean seed mass at the end of winter (31.4 kg/ha) suggests consumption was followed by further deterioration. Taken together, these observations suggest most rice in fields managed for waterfowl in the MAV is depleted in early to mid winter.

Foraging Threshold Experiment

Depletion of waste rice by waterfowl was density-dependent, because loss of rice mass during the period of waterfowl foraging increased with initial rice mass and GUD in all treatments did not differ statistically from 50 kg/ha. Density-dependent depletion is consistent with predictions from optimal foraging theory (Charnov et al. 1976, Sutherland 1996) and has been demonstrated empirically for waterfowl in recent studies by Nolet et al. (2006), Amano et al. (2006), and van Gils and Tijsen (2007). Also, patch selection in our experiment followed predictions from spatial-depletion models in that waterfowl used unharvested plots before moving to partially and then completely harvested plots (D. M. Greer, unpublished data).

Physical conditions that can affect profitability in a foraging patch include soil type and water depth (Nolet et al. 2001), predation risk (Guillemain et al. 2001), disturbance (Amano et al. 2004, van Gils and Tijsen 2007), travel distance (van Gils and Tijsen 2007), and foraging strategy adopted by the consumer (Nolet et al. 2006). We cannot quantify how physical constraints and profitability contributed to our mean GUD of 50 kg/ha. However, we believe most rice in our threshold experiment was accessible and suggest changes in profitability were most important. Goss-Custard et al. (2003) described an alternative strategy for estimating foraging thresholds from data on daily energy requirements and functional responses of predators to prey. Using predicted energy requirements (Miller and Eadie 2006) and functional responses of green-winged teal to rice densities (Arzel et al. 2007), we calculated a foraging threshold consistent with our field estimates (K. J. Reinecke, unpublished data).

Assuming profitability was the primary determinant of mean GUD of rice fields, foraging theory predicts interpretable variation of GUDs should occur among fields, years, and foraging habitats (Charnov et al. 1976, van Gil and Tijsen 2007). Recently, van Gils et al. (2004) demonstrated that using a fixed GUD to assess foraging habitats can over- or underestimate carrying capacity, and they advocated using complex models that allow foraging thresholds to vary. Given precise estimates, deviations in late-winter rice abundance among fields within years should reflect effects of disturbance, isolation, and other factors on GUDs. However, we doubt failure to use site-specific GUDs will systematically bias estimates of carrying capacity in systems as large as the MAV and are skeptical researchers can estimate GUDs and measure relevant ecological variables for enough sites to build predictive models of GUDs. Waterfowl in the MAV also feed in seasonal herbaceous wetlands and flooded hardwood forests (Reinecke et al. 1989), where prey abundance, distribution, energy value, and presumably profitability and GUDs differ from rice fields (e.g., Heitmeyer 2006). Additional work is needed to estimate GUDs in those habitat types.

Carrying Capacity in the MAV

Joint Venture energetics models correspond to daily ration models where carrying capacity in bird-days equals the amount of consumable food divided by the daily food requirement (Goss-Custard et al. 2003). Subtracting the GUD from our pooled estimate of late-autumn rice abundance indicated a maximum of 52.1 kg/ha of rice was available (i.e., potentially consumable) for waterfowl. However, our field experiments and simulations that accounted for deterioration indicated amount actually consumed was somewhat less. Food abundance and depletion are presumably linked to demographic and physiological parameters (survival and body condition) of interest to managers. Decreased quality of rice fields as foraging habitat has significant implications for the carrying capacity of the MAV and may have demographic consequences for wintering waterfowl.

MANAGEMENT IMPLICATIONS

The LMVJV assumes waterfowl consume 130 kg/ha of 180 kg/ha of rice present in harvested fields and depart when densities reach 50 kg/ha. We suggest the LMVJV continue using 50 kg/ha as the GUD for waterfowl feeding on rice. However, averaging over years and adjusting for bias resulting from seed deterioration, we estimated waterfowl consumed only 47.2 kg/ha of rice and recommend the LMVJV reduce estimates of carrying capacity accordingly. Further, given the difference in rice consumption between years (58.7 kg/ha vs. 38.8 kg/ha), we recommend conservation planners determine the sensitivity of habitat objectives to this variation and consider if managing for mean rice abundance is the best strategy. Because rice consumption was directly related to initial density, managers can expect waterfowl to respond and benefit when management actions increase food densities in foraging habitats. Finally, research is needed to develop innovative ways to reverse the declining value of rice fields for waterfowl; 2 such options include implementing a staggered regime of flooding fields during autumn–winter and exploring the potential for producing second or ratoon rice crops.

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