Research Article

Energetic Carrying Capacity of Actively and Passively Managed Wetlands for Migrating Ducks in Ohio

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ABSTRACT Habitat conservation strategies of the North American Waterfowl Management Plan (NAWMP) are guided by current understanding of factors that limit growth of waterfowl populations. The 1998 implementation plan of the Upper Mississippi River and Great Lakes Region Joint Venture (UMR and GLRJV) assumed that availability of foraging resources during autumn in wetlands actively managed for waterfowl was the primary limiting factor for duck populations during the nonbreeding season. We used multistage sampling during autumn and spring 2001–2004 to estimate energetic carrying capacity (ECC) of actively and passively managed wetlands in Ohio, USA, and examine this assumption. Energetic carrying capacity during autumn was similar between actively and passively managed wetlands each year. Averaged across years, energetic carrying capacity was 3,446 and 2,047 duck energy-days (DED)/ha for actively and passively managed wetlands, respectively. These estimates exceeded the UMR and GLRJV assumption that 1,236 DED/ha were provided by managed wetland habitats. Energetic carrying capacity declined each year by >80% between autumn and spring migration. Consequently, ECC of actively and passively managed wetlands was low during spring ($\bar{x} = 66$–242 DED/ha). These results suggested that duck foraging resources in actively and passively managed wetland habitats are abundant during autumn, but overwinter declines may create food-limiting environments during spring. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2532–2541; 2007)

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Conservation and management of waterfowl populations in North America have been guided since 1986 by goals and objectives of the North American Waterfowl Management Plan (NAWMP). Success of the NAWMP is predicated on identifying factors limiting population growth, and mitigating their effect through landscape-scale habitat conservation and management (Williams et al. 1999). Diet quality and wetland habitat conditions may affect waterfowl body condition, survival, and subsequent recruitment (Heitmeyer and Fredrickson 1981, Delnicki and Reinecke 1986, Reinecke et al. 1987). Consequently, the Upper Mississippi River and Great Lakes Region Joint Venture (UMR and GLRJV) assumed that availability of foraging resources was the factor during migration and winter most likely to limit waterfowl populations. The UMR and GLRJV thus established habitat objectives for migrating and wintering waterfowl from bioenergetic models that estimate quantities of habitats necessary to satisfy seasonal energy demands of waterfowl (NAWMP Plan Committee 2004).

A hallmark of the NAMWP is its recognition that conservation objectives and strategies should be based on existing knowledge of waterfowl ecology and refined subsequently with contemporary science. The 1998 NAWMP update (NAWMP Plan Committee 1998) advocated explicitly for evaluations of biological foundations. This stimulated several examinations of the assumptions and parameter values of Joint Venture bioenergetic models (e.g., Naylor 2002, Olson 2003, Penny 2003, Greer 2004, Rutka 2004). We designed this study to evaluate selected assumptions of a bioenergetics model for the UMR and GLRJV.

Habitat objectives of the UMR and GLRJV were derived under the following assumptions: 1) average energetic carrying capacity (ECC) of nonagricultural, managed wetlands equals 1,236 duck energy-days (DED)/ha, where 1 DED represents the daily energy requirement of a mallard-sized duck (*Anas platyrhynchos*; Prince 1979, Reinecke et al. 1989); 2) ducks satisfy energy demands principally from wetlands managed for waterfowl; 3) availability of foraging resources is more limiting during autumn than spring; and 4) meeting habitat objectives to support waterfowl during autumn migration is sufficient to support waterfowl during spring migration (UMR and GLRJV Management Board 1998). The UMR and GLRJV implicitly assumed that unmanaged or passively managed wetlands on private land would not contribute substantially to meeting energy demands of migrating waterfowl. However, wetland restoration and creation in the United States have been promoted successfully through federal and state conservation programs (Heard et al. 2000). Many restoration and creation efforts occur on private land, and management activities may be infrequent, nonexistent, or inconsistent with traditional waterfowl management practices (e.g., moist-soil management [Fredrickson and Taylor 1982]). Yet few attempts have been made to document the potential for restored and

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created wetlands on private land to satisfy energy demands of waterfowl during migration and winter.

We estimated energetic carrying capacity of actively and passively managed wetlands in Ohio, USA; during autumn and spring to test assumptions of the UMR and GLRJV waterfowl bioenergetic model. Our specific objectives were to 1) estimate and compare ECC between actively and passively managed wetlands prior to autumn and spring duck migration, and 2) estimate and compare overwinter depletion rates of ECC between actively and passively managed wetlands.

STUDY AREA

We defined actively managed wetlands as those annually affected by mechanical manipulations of water levels or vegetation with the primary goal of improving habitat for waterfowl and whose management was guided by their occurrence in a larger system of managed wetlands. We defined passively managed wetlands as those restored or created through federal or state conservation programs, disassociated with a larger system of managed wetlands, and not regularly receiving active manipulation of water levels or vegetation to improve habitat for waterfowl.

We studied actively managed wetlands at 3 wetland complexes in central Ohio (i.e., Big Island, Killbuck Marsh, and Killdeer Plains Wildlife Areas) and 2 in the southwest Lake Erie coastal region of Ohio (i.e., Pickerel Creek Wildlife Area and Winous Point Marsh; Fig. 1). Big Island, Killbuck Marsh, Killdeer Plains, and Pickerel Creek were owned and managed by the Ohio Division of Wildlife (ODW). The Winous Point Marsh was located at the southwestern end of Sandusky Bay, and was the largest privately owned coastal wetland complex in Ohio. Wetlands on these areas included natural or restored basins in which water levels were managed through a system of dikes, pumps, and water control structures. Management activities included seasonal draw-downs to promote growth of moist-soil vegetation (Fredrickson and Taylor 1982), stabilization of water levels to promote interspersion of vegetation and open water (i.e., hemi-marsh), and planting of agricultural crops (e.g., buckwheat [*Fagopyrum esculentum*]) and seed-producing wetland plants (e.g., Japanese millet [*Echinochloa crusgalli* var. *frumentacea*]; Bookhout et al. 1989). Primary management goals were to enhance wetland habitat for migrating and wintering waterfowl and provide waterfowl hunting opportunities.

Big Island and Killdeer Plains were located in Marion and Wyandot counties in the Central Lowland Till Plains physiographic region of Ohio (Brockman 1998). Surrounding land use was primarily grain agriculture and restored grasslands. Killbuck Marsh was located in Wayne and Holmes counties in the Glaciated Allegheny Plateaus (Brockman 1998). Land use near Killbuck Marsh comprised grain agriculture, pasture, and mixed upland deciduous forests. Pickerel Creek and Winous Point were located in Ottawa and Sandusky counties in the Huron–Erie Lake Plains physiographic region (Brockman 1998). Surrounding land use consisted primarily of grain agriculture and privately and publicly owned wetlands managed to enhance habitat for waterfowl and provide waterfowl-hunting opportunities.

We studied passively managed wetlands on privately owned land in 19 counties of central and northwest Ohio (Fig. 1). Surrounding land use varied among sites, but generally included grain agriculture, restored grasslands, and mixed upland deciduous forests. Passively managed wetlands were restored or created through federal or state conservation programs including the Conservation Reserve, Wetlands Reserve, Wildlife Habitat Incentives, and ODW Private Lands Wetlands Restoration Programs.

METHODS

Sampling Design

We used multi-stage sampling (MSS) to estimate ECC of actively and passively managed wetlands in Ohio during autumn and spring 2001–2004 (Levy and Lemeshow 1999; Stafford et al. 2003, 2006). We treated wetlands as primary sampling units and plots within wetlands as secondary sampling units. We stratified wetlands by management regime (active and passive) to ensure adequate representation of actively and passively managed wetlands and facilitate planned comparisons. Our target population for actively managed wetlands included those on the 5 wetland complexes selected for study. Our target population for passively managed wetlands included those restored or created in 19 selected counties of Ohio and matching our criteria for passive management. A list of passively managed wetlands for our study areas did not exist, so we adopted a database maintained by the Ohio Division of Wildlife (L. Miller, ODW, unpublished data) of such wetlands as our sampling frame. We sampled only passively managed wetlands during 2003–2004 because they have been studied less frequently than actively managed wetlands, and we desired a broader assessment of spatio-temporal variability in ECC among them. We visually inspected wetlands and conversed with landowners to verify management regime of wetlands selected from the ODW database. We excluded wetlands that did not match our criteria for passive management, and we reduced the target population size (i.e., wetlands in ODW database) proportionally.

We used stratified random sampling at the second stage (i.e., plots within wetlands) to maximize precision of ECC estimates for individual wetlands and to meet requirements of MSS. We considered vegetation zones within wetlands as strata and proportionally allocated 12–15 0.0625-m^2 plots (i.e., 25 × 25-cm sampling frame) among them (Levy and Lemeshow 1999). However, we imposed a minimum secondary sample size of 2 plots per stratum in our proportional allocation strategy to facilitate analyses. Thus, our samples were not truly self-weighting (Levy and Lemeshow 1999). We manually weighted sample plots (i.e., second-stage sampling wt) by the proportional coverage of their respective vegetation zone. We measured wetland size and estimated proportional coverage of

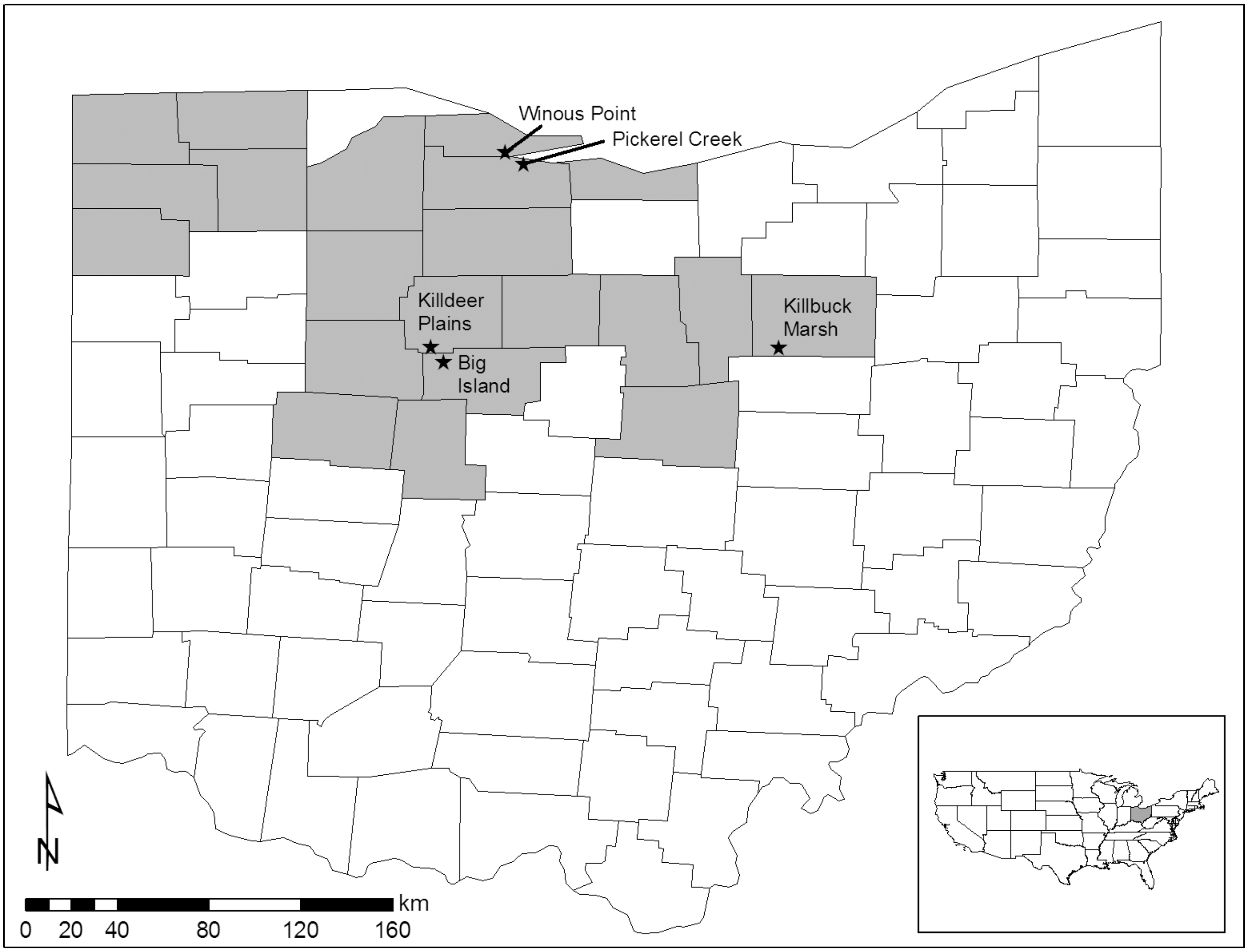

Figure 1. Locations of actively managed wetlands (★) and counties containing passively managed wetlands (shaded) in central and northwest Ohio, USA, from which autumn and spring energetic carrying capacity were estimated, 2001–2004.

vegetation zones with ArcView Geographic Information System 3.2 and color, aerial photos (image resolution <2 m/pixel) collected by county auditors and the National Agricultural Imagery Program during spring of our study years. We ground-truthed coverage of vegetation zones during visits to study wetlands. We stratified vegetation within wetlands by the following zones: moist-soil, consisting primarily of annual grasses and forbs (e.g., *Echinochloa* spp., *Leersia* spp., *Polygonum* spp.); emergent marsh, consisting primarily of persistent and nonpersistent aquatic macrophytes (e.g., *Alisma plantago*, *Sagittaria* spp., *Typha* spp.); submergent marsh, consisting of submerged or floating aquatic vegetation (*Najas* spp., *Potamogeton* spp.); and unvegetated open water, where water depth or turbidity prevented growth of vegetation. We recorded locations of plots with Global Positioning Systems and hand-drawn maps to ensure consistency in placement of plots between autumn and spring sampling periods.

Autumn ECC

We estimated ECC by sampling standing seed, below-ground tubers, and submerged aquatic vegetation of plant species commonly consumed by ducks (Farney 1975, Hoffman and Bookhout 1985; Table 1). We selected sampling dates that coincided with periods of maximum seed maturation and minimal seed drop or consumption (i.e., 17 Aug–6 Oct). We estimated standing seed biomass (kg/ha) within plots by counting numbers of inflorescences of relevant species (Table 1) and collecting a representative inflorescence to measure seed production per inflorescence. In the laboratory we threshed seeds from inflorescences and removed chaff with forceps and mesh sieves. We estimated tuber biomass by excavating soil in plots to a depth of 10 cm, but we sampled for tubers only in wetlands where we observed the growth of tuber-producing species (Table 1). We rinsed excavated soil through sieves (mesh sizes 5 [4.0 mm] and 18 [1.0 mm]) to expose and facilitate removal of tubers. We collected by hand all submerged aquatic vegetation in the water column of our plot when located in standing water. We sorted submerged aquatic vegetation to identify and retain only plant parts and species valued as food resources for ducks (Table 1).

We dried seeds, tubers, and submerged aquatic vegetation to constant mass at 50° C and weighed to nearest 0.01 g. We

Table 1. Published estimates of true metabolizable energy (TME; kcal/g dry mass) of moist-soil seeds, tubers, and submerged aquatic vegetation and TME values used in this study to estimate autumn energetic carrying capacity of actively and passively managed wetlands in central and northwest Ohio, USA, 2001–2004.

Food type	Published TME estimates[a]					
Plant species	Mallard	Northern pintail	Blue-winged teal	Canada goose	Reference	TME value this study
Moist-soil seeds						
Bidens spp.	[b]		0.55		Sherfy 1999	0.55[c]
Echinochloa colonum	2.54				Reinecke et al. 1989	2.54[c]
E. crusgalli	2.61				Checkett et al. 2002	2.64[d]
			2.67		Sherfy 1999	
E. walteri	2.86	2.82			Hoffman and Bookhout 1985	2.78[d]
			2.67		Sherfy 1999	
Leersia oryzoides	3.00	2.82			Hoffman and Bookhout 1985	2.91[d]
Fagopyrum esculentum						3.26[e]
Panicum dichotomiflorum	2.75				Checkett et al. 2002	2.65[d, f]
			2.54		Sherfy 1999	
Polygonum lapathafolium	1.52				Checkett et al. 2002	1.52[c]
P. pensylvanicum	1.08	1.25			Hoffman and Bookhout 1985	1.21[d]
			1.59		Sherfy 1999	
P. spp.						1.29[g]
Setaria lutescens	2.88					2.88[c,h]
Tubers						
Cyperus esculentus				4.03	Petrie et al. 1998	4.03[c]
Sagittaria latifolia	3.06				Hoffman and Bookhout 1985	3.06[c]
Submerged aquatic vegetation						
Ceratophyllum demersum						0.49[i]
Najas spp.						0.82[j]
Potamogeton spp.						0.82[j]

[a] Published estimates reported for waterfowl species from which they were derived (i.e., mallard [*Anas platyrhynchos*], northern pintail [*A. acuta*], blue-winged teal [*A. discors*], Canada goose [*Branta canadensis*]).
[b] Blanks indicate unavailable data.
[c] Value equals published estimate.
[d] Value equals $\bar{x}$ of published estimates.
[e] Value equals $\bar{x}$ of estimates of agricultural grain species as calculated by Kaminski et al. (2003).
[f] *Panicum dichotomiflorum* estimate substituted for other *Panicum* species.
[g] Value equals $\bar{x}$ of estimates for *Polygonum lapathafolium and P. pensylvanicum.*
[h] *Setaria lutescens* estimate substituted for other *Setaria* species.
[i] Value estimated by assuming 22.3% digestibility (i.e., estimate reported by Ballard et al. [2004] for northern pintail digestion of shoalgrass [*Halodule wrightii*] foliage) of gross energy content of *Ceratophyllum demersum* (2.18 kcal/g; Hoffman 1983).
[j] Value estimated by assuming 22.3% digestibility (Ballard et al. 2004) of gross energy content of *Potamogeton crispus* (3.67 kcal/g; Hoffman 1983).

derived species-specific seed biomass estimates for each plot by multiplying the number of inflorescences by the dry mass of seed collected from the representative inflorescence. We converted seed, tuber, and submerged aquatic vegetation biomass estimates to energetic carrying capacity (DED/ha) as described by Reinecke et al. (1989). We used 292 kcal per day as the daily energy requirement for a representative (i.e., mallard-sized) duck. We used published estimates and modified values of true metabolizable energy (TME) for moist-soil seeds, tubers, and submerged aquatic vegetation when calculating energetic carrying capacity (Table 1).

Spring ECC

We sampled wetlands immediately following thaw in late winter (1–21 Mar 2002–2004) to estimate spring ECC. High water levels and overwinter dispersal of seeds rendered sampling methods used during autumn impractical for spring. We sampled during spring moist-soil seed, tuber, and submerged aquatic vegetation biomass by vertically positioning a 30-cm-diameter stovepipe at each plot (Feddersen 2001) and using repeated sweeps with a 0.541-mm mesh net to extract plant material from the sampled water column and wetland substrate. We discontinued sweeps when recovery of vegetation and seeds became inefficient (i.e., when 4 consecutive sweeps produced no additional material; usually 10–20 total sweeps). We combined in a plastic storage bag the contents of all sweeps collected from a plot and stored it at −2° C until processing. We rinsed samples through mesh sieves and removed intact seeds, tubers, and submerged aquatic vegetation. We dried and weighed samples following procedures described for autumn. We did not sort seeds or tubers by species and were, thus, unable to use species-specific TME values to estimate ECC. We used instead TME values of 2.5 kcal/g for seeds (Checkett et al. 2002) and 3.55 kcal/g for tubers (i.e., $\bar{x}$ of chufa [*Cyperus esculentus*] and broad-leaved arrowhead [*Sagittaria latifolia*]; Table 1). Senescence of submerged aquatic vegetation during winter precluded our encounter and collection of it during spring sampling. Procedures for estimating per plot ECC during spring were similar to those described for autumn. We visually estimated percent inundation of actively and passively managed wetlands weekly during 24 September–31 December 2001–2003 and 9 March–5 May 2002–2004.

Statistical Analyses

We analyzed data separately by year because our sample of wetlands differed annually. We used PROC SURVEYMEANS in SAS Version 9.1 to estimate autumn and spring ECC of actively and passively managed wetlands (SAS Institute 2004). For autumn and spring separately, we used the CONTRAST option in PROC SURVEYREG to test for differences in ECC attributable to management regime (i.e., active vs. passive) during 2001–2003 (SAS Institute 2004). Our decision to sample only passively managed wetlands during 2003–2004 precluded comparisons between management regime for autumn and spring 2003–2004. We used PROC SURVEYMEANS and stratified random sampling at the second stage of cluster sampling to generate precise estimates of ECC for individual wetlands.

Reinecke et al. (1989) and Rutka (2004) suggested that waterfowl were unable to forage profitably on waste rice densities $\leq$50 kg/ha. We desired to compare ECC estimates of actively and passively managed wetlands to this foraging threshold. However, because TME estimates (kcal/g) differ between moist-soil and agricultural seeds (Kaminski et al. 2003), we were uncertain of the applicability of a rice seed biomass threshold to nonagricultural wetlands. Foraging profitability of habitat patches is generally a function of instantaneous rate of energy intake and energetic costs of search and handling times (Stephens and Krebs 1986). We reasoned accordingly that a foraging threshold expressed in energetic (e.g., DED/ha) rather than biomass currencies could be more generically applied across habitat types, assuming negligible differences in search and handling times among habitats. We followed methods of Reinecke et al. (1989) and used 3.34 kcal/g as TME estimate for waste rice to convert 50 kg/ha (waste rice biomass foraging threshold) to its energetic equivalent of 572 DED/ha. Thus, we used 572 DED/ha as an energetic-based foraging threshold. We used PROC LOGISTIC in SAS Version 9.1 to model the effect of management regime on the probability that ECC of individual wetlands exceeded the foraging threshold prior to autumn and spring migration (SAS Institute 2004).

We estimated overwinter ECC depletion rates for individual wetlands by subtracting spring ECC from autumn ECC and dividing the difference by autumn ECC (i.e., [autumn ECC − spring ECC] / autumn ECC). We arcsin-transformed depletion rates to satisfy normality and equality of variance assumptions (Quinn and Keough 2002). We used PROC GLM in SAS Version 9.1 to test for differences in depletion rates between actively and passively managed wetlands for 2001–2002 and 2002–2003 (SAS Institute 2004). Because we sampled only passively managed wetlands during 2003–2004, comparisons to actively managed wetlands were not possible for that year. We were uncertain of the extent to which migrating ducks in our study areas depended upon submerged aquatic vegetation to satisfy energy demands. If submerged aquatic vegetation was a minor component of ducks' diet, then our inclusion of it could overestimate wetland ECC. We estimated ECC with and without submerged aquatic vegetation to assess the potential overestimation that could occur by including it in our analyses.

RESULTS

Sample sizes of studied wetlands varied among combinations of years, sampling periods (i.e., autumn, spring), and management regime (Table 2). These differences occurred because of limited availability of wetlands matching management regime criteria and greater logistical and time constraints associated with sampling during spring than autumn (i.e., brief time period between spring thaw and arrival of ducks prevented sampling of all wetlands during spring). However, we studied a subset of wetlands during multiple years (i.e., $n = 23$; 16 actively managed, 7 passively managed during 2001–2002 and 2002–2003) to satisfy objectives of a companion study (i.e., Steckel 2003). We included in analyses of spring ECC and overwinter depletion only wetlands for which we estimated spring ECC (n = 23 in 2001–2002 and 2002–2003; n = 15 in 2003–2004 [Table 2]).

Median size of actively managed wetlands was 4.3 ha (range = 0.6–44.7) during 2001–2002 and 4.1 ha (range = 0.6–44.7) during 2002–2003. Median size of passively managed wetlands was 0.5 ha (range = 0.2–3.0) during 2001–2002, 0.6 ha (range = 0.2–6.5) during 2002–2003, and 0.8 ha (range = 0.2–6.5) during 2003–2004. Estimated water levels of actively managed wetlands exceeded 80% of wetland capacity on 16 October 2001 and 2002. Water levels of passively managed wetlands were 78%, 46%, and 77% of wetland capacity on 16 October 2001, 2002, and 2003, respectively.

When we excluded submerged aquatic vegetation from analyses, ECC was reduced by 4–21%, with the greatest reductions occurring for passively managed wetlands during autumn 2001 and 2003. Thus, energetic value of submerged aquatic vegetation was a minor component of total ECC. Submerged aquatic vegetation accounted for a greater percentage of ECC in passively than actively managed wetlands (i.e., 21% vs. 6%) during autumn 2001, but accounted for similar percentages between actively and passively managed wetlands (i.e., 4% vs. 3%) during autumn 2002 (Fig. 2). Duck species most likely to consume submerged aquatic vegetation (i.e., American wigeon [*Anas americana*], Canvasback [*Aythya valisineria*], gadwall [*Anas strepera*], redhead [*Aythya americana*], and ring-necked duck [*Aythya collaris*]) annually accounted for 10% of total ducks counted during ODW aerial winter waterfowl surveys for years 1980–2000 (L. Miller, unpublished data). Because submerged aquatic vegetation is an important diet component for certain duck species, and potential overestimation of wetland ECC was small (i.e., $\leq$21%) for duck species not regularly consuming submerged aquatic vegetation, we report ECC estimates that include the energetic value of submerged aquatic vegetation.

Estimated autumn ECC was similar between actively and passively managed wetlands during 2001 (4,098 vs. 2,961

Table 2. Estimated means, standard errors, 95% lower (LCL) and upper (UCL) confidence limits, and coefficients of variation of autumn and spring energetic carrying capacity (duck energy-days/ha) of actively and passively managed wetlands in central and northwest Ohio, USA, 2001–2004.

					Energetic carrying capacity[b]				
Yr	Sampling period[a]	Management regime	*N* wetlands	*N* plots	$\bar{x}$	SE	LCL	UCL	CV (%)
2001–2002	Autumn	Active	16	238	4,098	1,175	1,595	6,602	29
		Passive	23	297	2,961	533	1,854	4,067	18
		Combined	39	535	4,025	1,092	1,814	6,237	27
	Spring	Active	16	238	66	21	21	111	32
		Passive	7	105	65	52	0	193	80
		Combined	23	343	66	20	24	108	31
2002–2003	Autumn	Active	22	312	2,769	1,463	0	5,812	53
		Passive	25	319	2,730	852	972	4,489	31
		Combined	47	631	2,766	1,335	77	5,455	48
	Spring	Active	16	240	113	43	22	204	38
		Passive	7	105	242	195	0	719	81
		Combined	23	345	120	41	35	206	34
2003–2004[c]	Autumn	Passive	50	599	1,722	339	1,040	2,404	20
	Spring	Passive	15	180	218	84	38	398	39

[a] Sampling dates: Autumn = 17 Aug–6 Oct; Spring = 1–21 Mar.
[b] Estimated with multistage sampling design with wetlands as primary sampling units, plots within wetlands as secondary sampling units, and wetlands stratified by management regime. Estimates accounted for metabolizable energy of moist-soil seeds, tubers, and submerged aquatic vegetation consumed commonly by waterfowl.
[c] Actively managed wetlands were not sampled during 2003–2004.

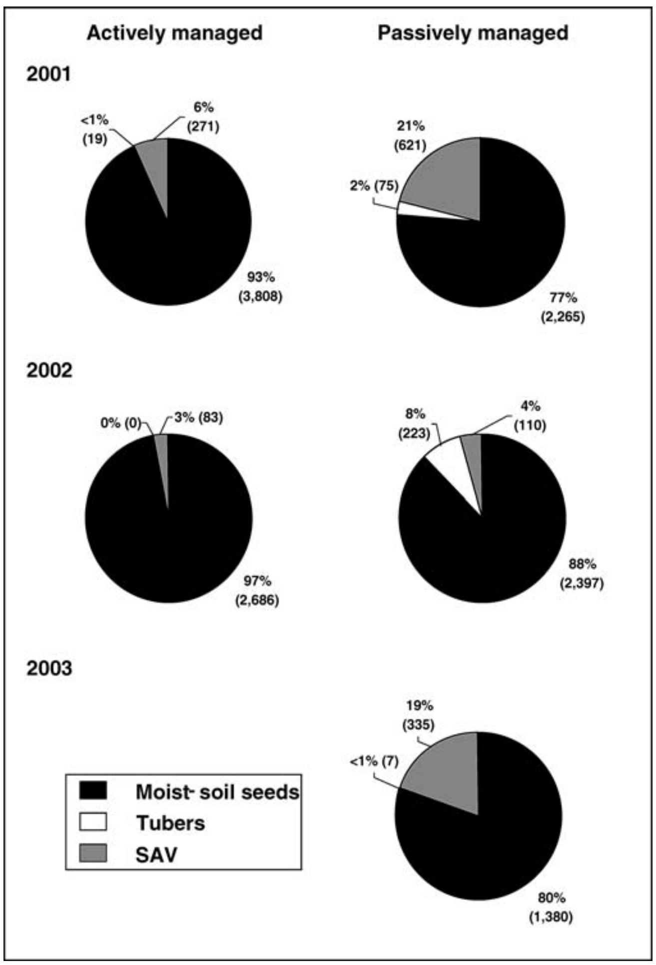

Figure 2. Contribution (%; duck energy-days/ha) of moist-soil seeds, tubers, and submerged aquatic vegetation (SAV) to total estimated autumn energetic carrying capacity of actively and passively managed wetlands in central and northwest Ohio, USA, 2001–2004.

DED/ha; $F_{1,\ 37} = 0.78$; $P = 0.384$) and 2002 (2,769 vs. 2,730 DED/ha; $F_{1,45} < 0.01$, $P = 0.982$; Table 2). Point estimates of autumn ECC for each year and management regime combination were 1.4–3.3 times (1,722–4,098 DED/ha) the UMR and GLRJV assumption of 1,236 DED/ha (Table 2). Combined across years, estimated ECC of actively and passively managed wetlands were 3,446 and 2,047 DED/ha, respectively. Actively and passively managed wetlands were equally likely to have autumn ECC estimates that exceeded the energetic foraging threshold (572 DED/ha) during 2001 (active: 13 of 16, 81%; passive: 17 of 23, 74%; Wald $\chi^2_1 = 0.28$, $P = 0.594$) and 2002 (active: 12 of 22, 55%; passive: 16 of 25, 64%; Wald $\chi^2_1 = 0.43$, $P = 0.511$). Sixty percent (30 of 50) of passively managed wetlands had autumn ECC greater than the energetic foraging threshold during 2003.

Estimated spring ECC was similar between actively and passively managed wetlands during 2002 (66 vs. 65 DED/ha, $F_{1,\ 21} < 0.01$, $P = 0.991$) and 2003 (113 vs. 242 DED/ha, $F_{1,21} = 0.42$, $P = 0.526$; Table 2). Combined across years, spring ECC of actively and passively managed wetlands was 89 and 207 DED/ha, respectively. Mean spring ECC estimates for all year and management regime combinations were less than the energetic foraging threshold of 572 DED/ha (Table 2). Combined across years and management regimes, only 3 of 136 (2%) wetlands had spring ECC that exceeded the foraging threshold. Mean ECC depletion rates were high and similar between actively and passively managed wetlands during 2001–2002 (95% vs. 99%; $F_{1,\ 21} = 0.98$, $P = 0.333$) and 2002–2003 (80% vs. 82%; $F_{1,21} = 0.08$, $P = 0.781$). Depletion rates were high (83%) for passively managed wetlands also during 2003–2004.

Moist-soil plant species accounted for the majority ($\geq$77%) of available food energy in actively and passively managed wetlands (Fig. 2). Barnyardgrass (*Echinochloa crusgalli*) was detected more frequently (>10%) than any other plant species in sample plots of actively and passively managed wetlands (Table 3). Japanese millet was encountered in only 4% of plots in actively managed wetlands, but produced a large quantity of seed and potential energy for foraging ducks (Table 3). Millet species (*Echinochloa* spp.) collectively accounted for 74% and 46% of total energy in actively and passively managed wetlands, respectively. Beggarticks (*Bidens* spp.), rice cutgrass (*Leersia oryzoides*), and panic grass (*Panicum* spp.) were more common and collectively accounted for a greater average percentage of energy in passively (33%) than actively (2%) managed wetlands (Table 3). Coontail (*Ceratophyllum demersum*) accounted for the greatest percentage (5%) of energy from submerged aquatic vegetation in actively managed wetlands. Pondweeds (*Najas* spp. and *Potamogeton* spp.) accounted for the greatest percentage (9%) of energy from submerged aquatic species in passively managed wetlands (Table 3).

Underground tubers of chufa and broad-leaved arrowhead contributed minimally ($\leq$8%) to ECC of actively and passively managed wetlands in our study (Fig. 2). Chufa is a valued foraging resource for waterfowl and may become locally abundant under ideal soil and moisture conditions (i.e., >10,600 DED/ha; Taylor and Smith 2003). Indeed, we observed large stands of chufa in several wetlands, but over all years detected chufa in <6% (2 of 38) and <7% (7 of 108) of actively and passively managed wetlands. We documented tuber production of broad-leaved arrowhead in only 2 wetlands across all years and management regimes.

DISCUSSION

Autumn ECC of actively and passively managed wetlands exceeded the UMR and GLRJV assumption of 1,236 DED per ha during each year, suggesting that duck foraging resources in these wetland habitats are abundant prior to autumn duck migration. Although the point estimate of autumn ECC for actively managed wetlands was 1.4 times that for passively managed wetlands during 2001, high inter-wetland variability prevented detection of real differences that may have existed. Mean estimates of autumn ECC exhibited a general decline over the 3 years of this study. Because our sample of wetlands differed among years, we were unable to determine if this decline was coincident with a similar trend across the landscape or an artifact of sampling different wetlands among years. Our estimates of autumn ECC in actively and passively managed wetlands were comparable to those reported in previous studies (Table 4). Variability in estimates among studies likely resulted from site-specific influences (e.g., soil fertility, weather, management intensity) or different sampling and estimation methods.

Overwinter reduction in wetland plant foods is caused primarily by granivory (e.g., waterfowl, passerines, rodents; Greer 2004, Stafford et al. 2005) and decomposition (Nelms and Twedt 1996). We are uncertain of exact causes of food depletion in our study and acknowledge that low estimates of spring ECC may have been influenced also by redistribution of seeds during winter. Nevertheless, our estimates of overwinter depletion were consistent with those of Greer (2004) for autumn-flooded moist-soil habitats in Missouri ($\bar{x} = 73\%$ and 87% during 2000 and 2001). High overwinter depletion rates resulted in few wetlands having spring ECC estimates that exceeded the energetic foraging threshold of 572 DED/ha, suggesting that waterfowl foraging resources in managed wetlands are more limiting during spring than autumn. Wetland conditions during late winter and spring have greater effects on mallard breeding productivity than those during autumn and early winter (Heitmeyer and Fredrickson 1981). Consequently, food limitation during spring may have greater consequences to duck productivity than food limitation during autumn.

Our estimates of autumn and spring energetic carrying capacity reflect only the extent to which foraging resources were present in wetlands. We did not quantify the extent to which foraging resources were available to ducks. Indeed, numerous factors influence waterfowl use of wetlands and availability of foraging resources within them, including human disturbance (Cox and Afton 1997), distance of foraging habitat from roost sites (Adair et al. 1996), and local wetland conditions (e.g., water depth; Riley and Bookhout 1993). We often observed the majority (i.e., >50%; M. Brasher, Ohio State University, personal observation) of moist-soil plants along the perimeter of wetland basins. Because wetland perimeters are the last areas to become flooded within a wetland basin, foraging resources along the perimeter may be functionally unavailable until water levels are near wetland capacity. Energetic carrying capacities based on foraging resource availability are likely different from and much less than those based on foraging resource abundance.

Invertebrates are a major component of the waterfowl diet during spring and summer as females prepare for egg formation and nesting (Krapu and Reinecke 1992). Our sampling of wetland food resources did not account for invertebrate availability. Additionally, we estimated seed abundance for only a limited number of wetland plant species (Table 1). Duck diets frequently contain minor amounts of seeds and foliage of wetland plant species other than those measured in this study (Farney 1975). Consequently, our results may slightly underestimate autumn and spring ECC of actively and passively managed wetlands. For example, Anderson and Smith (1999) estimated that invertebrates contributed an additional 300 and 265 DED/ha to carrying capacity of managed and unmanaged playas. We are unaware of the degree to which ducks relied on seeds versus invertebrates to satisfy energy demands during spring in our study. However, wetland plant seeds were identified as important dietary items for ducks during spring migration in Ohio (Farney 1975), Nebraska (Jorde et al. 1983), and Iowa (LaGrange and Dinsmore 1988). Depauperate seed resources during spring may constrain nutrient acquisition of ducks prior to breeding.

Few studies have documented wetland use patterns for

Table 3. Percent occurrence, mean biomass (kg/ha), and energetic carrying capacity (duck energy-days [DED]/ha) of moist-soil seeds, tubers, and submerged aquatic vegetation in plots sampled from actively and passively managed wetlands in central and northwest Ohio, USA, 2001–2004.

Food type	Management regime							
	Active				Passive			
Plant species	% occurrence	$\bar{x}$	SE	DED/ha	% occurrence	$\bar{x}$	SE	DED/ha
Moist-soil seeds								
Bidens spp.	2.0	10.7	7.1	20	5.4	56.7	11.5	107
Echinochloa colonum	0.2	0.1	0.1	1	0.3	0.7	0.4	6
E. crusgalli	12.2	75.7	15.6	685	10.9	79.8	11.3	721
E. crusgalli var. *frumentacea*	4.2	135.9	40.4	1,229	0.7	8.2	4.0	74
E. walteri	4.9	64.9	34.1	632	2.1	14.0	3.8	136
Fagopyrum esculentum	2.0	20.7	6.8	231	0.0	0.0	0.0	0
Leersia oryzoides	2.4	3.6	1.8	36	4.5	32.6	7.3	325
Panicum spp.	1.3	1.4	0.7	13	8.9	27.9	4.8	253
Polygonum lapathafolium	5.1	36.6	9.2	191	0.3	0.3	0.2	1
P. pensylvanicum	2.0	6.9	2.5	25	2.6	12.8	4.5	47
P. spp.	7.8	14.7	4.6	65	1.0	1.4	0.6	6
Setaria spp.	1.6	3.7	1.5	36	5.9	8.2	1.6	81
Tubers								
Cyperus esculentus	1.1	1.2	0.5	17	1.9	5.6	1.7	77
Sagittaria latifolia	0.0	0.0	0.0	0	0.2	0.1	0.1	1
Submerged aquatic vegetation								
Ceratophyllum demersum	2.0	99.7	52.2	167	1.7	18.9	5.4	32
Najas spp.	3..5	10.0	3.0	29	3.6	29.1	5.6	82
Potamogeton spp.	2.6	25.2	9.8	71	10.5	34.4	6.7	97

ducks during spring migration in the Midwestern United States. Consequently, we are unaware of the extent to which waterfowl rely on actively and passively managed wetlands as defined in this study to satisfy energy demands during spring. The timing of waterfowl migration generally coincides with periods of heavy rain and snow melt that lead to significant over-bank stream flooding and creation of ephemeral wetlands. These habitats are used heavily by waterfowl during late winter and spring migration (LaGrange and Dinsmore 1989, Heitmeyer 2006), but their energetic importance to migrating waterfowl is uncertain. Additional information is needed to understand the consequences to waterfowl populations of low energetic carrying capacity during spring of actively and passively managed wetlands similar to those in this study.

Seeds of moist-soil plants accounted for the majority of

Table 4. Published estimates of wetland plant food (i.e., moist-soil seeds, tubers, submerged aquatic vegetation [SAV]) biomass (kg/ha) and energetic carrying capacity (duck energy-days [DED]/ha) of actively and passively managed wetlands in various geographic study locations in the United States, 1982–2005.

Management regime[a]	Food types sampled	Study location	Biomass	DED/ha	Reference
Active	Moist-soil seeds	MS Alluvial Valley, MO	660	5,650[b]	Fredrickson and Taylor 1982
Active	Moist-soil seeds	Southern High Plains, TX	[c]	3,853	Haukos and Smith 1993
Active	Moist-soil seeds	Southern High Plains, TX	[c]	7,794	Anderson and Smith 1999
Passive	Moist-soil seeds	Southern High Plains, TX	[c]	1,806	Anderson and Smith 1999
Active	Moist-soil seeds	CA Central Valley	278[d]	2,371[b,d]	Naylor 2002
Active	Moist-soil seeds	MS Alluvial Valley; IL, MO	2,484	21,369[b]	Feddersen 2001
Active	Moist-soil seeds, tubers	Rio Grande Valley, NM	1,238[e]	15,353[b,e]	Taylor and Smith 2003
Active	Moist-soil seeds, tubers	MS Alluvial Valley; AR, LA, MS, MO	828[f]	6,988[f]	Penny 2003
Passive	Moist-soil seeds, tubers	MS Alluvial Valley; AR, LA, MS, MO	502	4,246	Penny 2003
Active	Moist-soil seeds	MO River Valley, MO	1,695[g]	14,512[b,g]	Greer 2004
Active	Moist-soil seeds	IL River Valley, IL	790	6,760	Bowyer et al. 2005
Active	Moist-soil seeds, tubers, SAV	Central and northwest OH	520[h]	3,502[h]	This study
Passive	Moist-soil seeds, tubers, SAV	Central and northwest OH	377[h]	2,320[h]	This study

[a] Management regime assigned based on our assessment of study descriptions and extent to which they matched our definitions of active and passive management.
[b] DED estimates not reported in referenced publication. Calculated for this table following methods of Reinecke et al. (1989) and using 2.5 kcal/g as $\bar{x}$ true metabolizable energy value for moist-soil seeds (Kaminski et al. 2003).
[c] Biomass estimates not reported in referenced publication.
[d] $\bar{x}$ of 2 study yr (2000, 2001).
[e] $\bar{x}$ of estimates reported for 3 management strategies (mowing, disking, sustained flood).
[f] $\bar{x}$ of estimates reported for 2 management regimes (intensive, active).
[g] $\bar{x}$ across study yr (2000, 2001) and treatments (autumn-flooded and spring-flooded).
[h] $\bar{x}$ across study yr (2001, 2002, 2003).

food energy in actively and passively managed wetlands, but species occurrence and seed biomass differed between actively and passively managed wetlands. Species composition of moist-soil plant communities is influenced by soil moisture, climatic conditions, abundance and diversity of propagules in seed bank, and successional stage of site (Fredrickson and Taylor 1982). Timing and duration of draw-down or natural drying of wetlands influence soil moisture conditions and subsequent moist-soil plant response (Fredrickson and Taylor 1982). Barnyardgrass, millets, and smartweeds are abundant following early and mid-season drawdowns of wetlands, whereas mid- and late-season drawdowns favor species such as rice cutgrass, panic grasses, barnyardgrass, and beggarticks (Fredrickson and Taylor 1982). Wetland managers conducted drawdowns of actively managed wetlands primarily during spring in this study. Natural drying of passively managed wetlands during summer simulated prolonged mid- or late-season drawdowns. We observed patterns of species colonization similar to that reported by Fredrickson and Taylor (1982) in response to timing and duration of drawdowns.

Wetland management strategies to enhance production of foraging resources for ducks typically consist of seasonal drawdowns with periodic soil and vegetation disturbances (e.g., disking, mowing) to promote growth of moist-soil plants (Fredrickson and Taylor 1982) or maintaining water at optimal depth and clarity to promote growth of submerged aquatic vegetation (Bookhout et al. 1989). We observed management strategies in this study that were limited to complete drawdowns with minimal soil disturbance, partial drawdowns to encourage hemi-marsh distribution of robust emergent vegetation (e.g., cattail [*Typha* spp.]; Kaminski and Prince 1981), and stabilized or elevated water levels to control growth of invasive plant species (e.g., purple loosestrife [*Lythrum salicaria*]). We believe this diversity of observed management practices was chiefly responsible for high inter-wetland variation in moist-soil seed and submerged aquatic vegetation biomass among actively managed wetlands. Restored wetlands may exhibit lower species richness and diversity than natural wetlands, with restored wetlands vegetated more frequently by facultative wetland species (e.g., moist-soil annuals; Seabloom and van der Valk 2003). Colonization of restored or created wetlands by moist-soil plants appears to provide an abundant forage base for ducks during autumn.

MANAGEMENT IMPLICATIONS

This study demonstrated that passively managed, restored, and created wetlands may contribute greatly to satisfying foraging demands of ducks during autumn. However, water levels in passively managed wetlands are largely dependent on precipitation, and water levels influence the availability of foraging resources (Riley and Bookhout 1993). If annually reliable foraging areas for waterfowl are desired, managers should promote wetland designs capable of increasing reliability of water levels in passively managed wetlands (e.g., adequate watershed area) and provide technical assistance to landowners for their consideration of greater management options (e.g., summer drawdowns [Kaminski 2005]). Conversely, because the variable hydroperiod of passively managed wetlands may encourage establishment of plant communities different from those in actively managed wetlands, managers of wetland complexes should consider passive management as a strategy to provide diverse foraging opportunities for waterfowl during autumn. Lastly, we encourage waterfowl managers and conservation planners in the UMR and GLRJV to reconsider assumed foraging values for managed wetlands and further investigate the impact of high overwinter food-depletion rates on habitat needs for ducks during spring migration.

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