




Research Article

The Influence of Water Depth on Energy Availability for Ducks

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ABSTRACT Habitat management and planning strategies for nonbreeding ducks are focused on providing enough energy to support a desired number of individuals. Therefore, regional estimates of energy availability for nonbreeding ducks are required to determine if sufficient habitat exists for them. I used core sampling to estimate food and energy density in 6 types of water bodies (i.e., actively and passively managed emergent wetlands, playas, small and large reservoirs, and sloughs) in northeastern Colorado, USA, during 3 sampling occasions throughout 2 nonbreeding seasons, 2015–2016 and 2016–2017. Also, I used precise depth measurements to estimate the percentage of each site that was shallow enough to facilitate feeding by dabbling ducks as a way to correct overall energy density to reflect availability to ducks. Emergent wetlands contained the greatest food and energy density, followed by playas and sloughs, and reservoirs contained little food or energy. Fall depletion of food was greatest in actively managed emergent wetlands and spring depletion was greatest in sloughs and passively managed emergent wetlands. Mean percentage of passively managed emergent wetlands, actively managed emergent wetlands, small reservoirs, large reservoirs, and sloughs shallower than 50 cm was 37%, 77%, 10%, 4%, and 83%, respectively. Incorporating these estimates into the energetic carrying capacity model developed by the Playa Lakes Joint Venture for eastern Colorado resulted in a 54% decrease in overall duck energy day estimates, which is below what is needed to support population goals. This research identifies the need for additional wetland restoration in eastern Colorado to meet energy requirements of nonbreeding ducks and provides information to conservation planners to make more informed decisions about the extent and location of wetland restoration activities. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

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Most habitat conservation planning, acquisition, and management to increase local duck populations during the nonbreeding season focus on providing abundant, energy-rich food (Playa Lakes Joint Venture [PLJV] Waterfowl Team 2005, Soulliere et al. 2007). Food availability can affect local duck abundance and distribution by attracting ducks to food-rich areas (Brasher 2010, O'Shaughnessy 2014, Hagy et al. 2017, Osborn et al. 2017) and influencing stopover duration during migration (O'Neal et al. 2012). Food availability can also affect how ducks use vigilance behavior to govern predation risk (Brown and Kotler 2007, Behney 2014). Furthermore, body condition is affected by food resources (Delnicki and Reinecke 1986), which can have cross-seasonal effects on productivity (Heitmeyer and Fredrickson 1981).

The North American Waterfowl Management Plan (U.S. Department of the Interior and Environment Canada

1986:14) tasked Joint Ventures (regional partnerships of government agencies, non-profit organizations, corporations, tribes, and individuals involved in habitat conservation) with “planning, funding and implementation of projects to preserve or enhance waterfowl habitat.” Currently, many Joint Ventures use bioenergetics approaches to guide habitat planning for nonbreeding waterfowl (Central Valley Joint Venture 2006, Soulliere et al. 2007, PLJV 2008, Intermountain West Joint Venture 2013, Rainwater Basin Joint Venture 2013). Energetic carrying capacity models predict the amount of habitat needed to support a desired number of individuals based on the energy requirements of the birds and energy availability in the environment (Williams et al. 2014).

Regardless of the complexity of energetic carrying capacity models, estimates of energy availability are necessary for the different types of water bodies in which ducks feed. Most dabbling and many diving ducks primarily consume benthic seeds during winter and migrations, but they also consume invertebrates, particularly during periods when protein requirements are high (e.g., prior to nesting, molting; Hitchcock 2009, Tidwell et al. 2013). In addition to energy density, estimates of energy availability should incorporate ducks' ability to exploit food. Water depth limits energy availability by restricting ducks to feeding where it is

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shallow enough for them to reach the substrate (Poysa 1983). Little information exists on the percent of food or energy that is actually available to be consumed by ducks. Ignoring availability or using assumed values may bias predictions from energetic carrying capacity models. The PLJV lists percent suitability for various types of water bodies, but this information is generally based on assumptions and information from other regions (PLJV Waterfowl Team 2005). The Upper Mississippi River and Great Lakes Region Joint Venture assumes 50% of food is unavailable to ducks (Soulliere et al. 2007). The Lower Mississippi Valley Joint Venture excluded water depth from their foraging models, citing a lack of data and need for more research (Edwards et al. 2012).

The lower South Platte River corridor in northeastern Colorado, USA, is considered a waterfowl conservation priority area for migrating and wintering ducks (Colorado Parks and Wildlife 2011) and a focus area for the United States Fish and Wildlife Service (USFWS) Partners for Fish and Wildlife Program (USFWS 2011). About 60% of Colorado duck hunters hunt along the Lower South Platte River and about half of the ducks harvested in Colorado are harvested in this area (Runge and Gammonley 2012). There are 26 State Wildlife Areas along the lower South Platte River offering opportunities for public hunting and numerous private duck hunting clubs. Therefore, the lower South Platte River corridor represents an important area for recreation opportunity and provides migratory stopover habitat. Despite the importance of the region to non-breeding ducks, I am unaware of any previous efforts to estimate energy density to determine if enough habitat exists to support the population goal. Currently, regional energetic carrying capacity models rely on many assumptions and estimates from other regions (PLJV Waterfowl Team 2005), which may bias model outputs.

My first objective was to estimate dabbling duck food and energy density in northeastern Colorado during 3 occasions throughout the nonbreeding season in 6 types of water bodies thought to provide foraging habitat for ducks. Sampling over multiple occasions facilitated estimating food depletion during each period, which may provide an index to intensity of duck use of sites (Hagy and Kaminski 2012b). Based on the attractiveness of moist-soil wetlands to ducks because of their structure and high food production (Kross et al. 2008, Osborn et al. 2017), I predicted that actively managed emergent wetlands (i.e., moist-soil impoundments) would produce the most energy and exhibit the greatest amount of energy depletion throughout the non-breeding period. My second objective was to estimate the average percentage of a wetland that was shallow enough to facilitate feeding by dabbling ducks, which represents a major component of how much food is actually available to be consumed. I predicted that emergent wetlands, sloughs, and playas would generally be shallow throughout, whereas reservoirs would contain little area shallow enough to facilitate dabbling duck feeding. Third, I tested the assumptions of the regional energetic carrying capacity model used by the PLJV by comparing estimates of food availability

from this study to those currently used, which are based on studies from other regions (PLJV Waterfowl Team 2005).

STUDY AREA

Study sites were in northeastern Colorado in Sedgwick, Washington, Logan, Morgan, Weld, and Larimer counties, encompassing 3,331,501 ha. All sites were within Bird Conservation Region 18 and the PLJV region. The area is generally classified as shortgrass prairie with intensive agriculture focusing on cattle production and row-crop farming. Upland prairie was generally dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*B. dactyloides*). The South Platte River flows through the region and the riparian areas were primarily plains cottonwood (*Populus deltoides*) forests with understory consisting of western snowberry (*Symphoricarpos occidentalis*), willow (*Salix* spp.), and mixed grasses, sedges, and forbs. Mean high temperatures in the summer ranged from 28°C to 30°C and lows in winter ranged from -10°C to -12°C. Mean annual rainfall for the approximate center of my study area (Brush, CO) from 2004–2018 was 40 cm (www.noaa.gov, accessed 1 May 2019). Annual rainfall during the 2 field seasons (Sep–May, 2015–2016 and 2016–2017) encompassing 3 calendar years in my study was 71 cm, 44 cm, and 33 cm in 2015, 2016, and 2017, respectively (www.noaa.gov, accessed 1 May 2019). Topography in the region is flat to gently undulating and elevation ranges approximately 1,100–1,585 m. Many duck species used the region during migration and winter until water bodies froze, although mallards (*Anas platyrhynchos*) were the most abundant (www.cpw.state.co.us/Documents/Hunting/Waterfowl/Statistics/Central_Flyaway_Waterfowl_Counts.pdf, accessed 12 Nov 2019).

I classified sites into 6 types based on hydrology, morphology, and classification used by previous research and monitoring efforts in the area (PLJV 2008, Lemly et al. 2015): actively managed emergent wetlands, passively managed emergent wetlands, sloughs, playas, small reservoirs, and large reservoirs. In actively managed emergent wetlands (i.e., moist soil wetlands), hydrology was actively managed to promote growth of duck food producing plants (Kross et al. 2008, Stafford et al. 2011), whereas in passively managed emergent wetlands, hydrology was not controlled or controlled for reasons other than producing duck food. There was no vegetation manipulation (e.g., disking or mowing) during the study. Sloughs were linear, creek-like features in the river basin. I classified reservoirs ≤ 200 ha as small and > 200 ha as large. More description of water body types are available online in Supporting Information (Table S1). These water body types represented a substantial proportion of the overall wetland area used in regional avian habitat planning models (PLJV 2008).

Most wetlands and reservoirs in the region, except playas, are associated with the South Platte River and are within the river floodplain. Therefore, to ensure a spatially balanced sample, I divided the South Platte River corridor (~10 km from river) into 4 quadrants (~70 river km/quadrant). Using wetland geographic information system data, I compiled a list of all potential sites within each quadrant for each water body type and randomly selected sites within each quadrant.

Playas are found farther from the South Platte River than other wetland types. Therefore, I selected study playas by creating a grid (7.5 × 7.5-min topographic map quadrangles) across northeastern Colorado. I randomly selected 2 grid cells that contained ≥5 playas that were >0.25 ha. I then randomly selected 3 playas within each grid cell to sample. During this study, playas were infrequently inundated, reducing my ability to sample repeatedly over multiple occasions and years.

METHODS

Food Sampling

Field and lab methods.—I refer to values with units kg/ha and kcal/ha as food biomass and energy density, respectively, and reserve the use of availability to where ducks' abilities to exploit food is incorporated. I used core sampling (Williams et al. 2014) during 3 sampling occasions to estimate food biomass for fall and spring migrants and assessed food depletion during fall and spring. The first occasion occurred in late September and early October (i.e., fall) 2015 and 2016 to estimate food biomass at the beginning of fall migration for most dabbling ducks. The second sampling occasion was in late winter, as soon as wetlands began thawing (Feb and Mar 2016 and 2017; winter) to estimate food biomass at the beginning of spring migration and assess depletion during fall. The third sampling occasion was in May (summer), when I observed a decrease in regional duck abundance, to assess food depletion during spring. Winter and summer sampling occasions occurred on a subsample of sites.

For sites <2 ha, I randomly distributed 7 core samples throughout the area that was shallower than 50 cm. For sloughs and reservoirs (≥2 ha), I randomly selected a 300-m stretch of the slough or reservoir shoreline and randomly distributed 7 core sample points along that stretch at random distances from the shoreline or slough bank ensuring depth at the sample point was <50 cm. I chose 50 cm as a cutoff because Behney (2014) reported that the majority of mallard feeding occurred at water depths <50 cm and mallards make up over 99% of the total duck population objective for the PLJV region of Colorado (PLJV Waterfowl Team 2005).

All core samples were 5 cm in diameter (Behney et al. 2014) and 5 cm deep (Evans-Peters 2010) and included the water column. If a random core sample location was deeper than 50 cm, I noted the conditions but did not collect a core sample because these are not conditions associated with feeding by dabbling ducks; I then selected a new random core location. I washed cores through a 500-μm sieve bucket in the field to wash away soil and placed the remaining material in a bag with 70% ethanol and transported it to a lab for processing.

In the lab, I washed core samples through a series of sieves (2,000 μm [number 10], 355 μm [number 45]) to separate different size particles. When the amount of material retained by the fine sieve was great, I subsampled this material by 25% (Williams et al. 2014). I visually searched through the material and picked out any seed, tuber, or invertebrate and identified items to the lowest taxonomic level possible, generally genus for plant matter and class or order for

invertebrates. I dried all material at 60°C to a constant mass (about 48 hr) and weighed it to the nearest 0.00001 g.

Statistical analysis.—I present estimates of food biomass (kg/ha) and energy density (kcal/ha) for seeds, invertebrates, molluscs (Phylum Mollusca), and total food for each water body type. Failing to account for non-food items recovered in samples can bias food biomass estimates (Hagy and Kaminski 2012b). I found many species of seeds and invertebrate taxa in samples that have not been documented in the diet of ducks; however, little research has been done on duck diet in northeastern Colorado and many items I recovered resemble or are closely related to documented food items. Therefore, for analyses, I included items closely related to those documented in ducks' diets (Tables S2, S3, available online in Supporting Information). I converted each individual core sample to an estimate of food biomass (kg/ha for seeds, invertebrates, molluscs, and total food) based on the mass of food items in the sample and the area of the sampler.

To convert estimates of food biomass to energy density, I assigned food items true metabolizable energy (TME) values from the literature at the lowest taxonomic level possible (Livolsi et al. 2015; Tables S2, S3). If multiple published estimates were available for the lowest taxonomic level, I used the average. For some taxa recovered in core samples, I could not find an associated published TME value. Therefore, I assigned these items the mean of other items' TMEs at the lowest taxonomic level possible. For example, I could not find a published TME value for seeds from the genus *Alopecurus*. Therefore, I assigned it the mean of TME values for other species in the family Poaceae. In the case where I could not find published values for any species in the same family, I used the mean of other species in the same order. If I could not find any published TME values for any species in the same order, I assigned it the mean of all published seed, tuber, or invertebrate values that I could find regardless of taxonomy (seeds = 1.82 kcal/g, tubers = 4.03 kcal/g, invertebrates = 0.70 kcal/g). I used 356.8 kcal/day as the daily energy requirement of mallards (Miller and Eadie 2006, Soulliere et al. 2007) for comparing duck energy days (DED) to other studies and conservation plans.

I modeled food biomass and energy density as lognormally distributed response variables (Y_i) in a Bayesian modeling framework. I added 0.1 to all observations to ensure there were no zeros in the data set, which are not supported by the log-normal distribution. I included fixed effects of year (β_q , $Q=2$), season (γ_m , $M=3$), water body type (δ_k , $K=6$), and an interaction between season m and type k (ε_{mk}). I included site as a group-level random effect (ζ_j). The model took the form:

$$\text{Log}(Y_{ijkmq}) \sim \text{Normal}(\mu_{ijkmq}, \sigma) \quad (1)$$

$$\mu_{ijkmq} = \alpha + \beta_q + \gamma_m + \delta_k + \varepsilon_{mk} + \zeta_j \quad (2)$$

$$\zeta_j \sim \text{Normal}(0, \sigma^2). \quad (3)$$

I assigned the intercept (α) and all fixed effect parameters (β_q , γ_m , δ_k , and ε_{mk}) vague normal (0, 0.001 [variance⁻¹])

priors and variance parameters (σ and σ^2) vague uniform (0, 5) priors. I calculated median food and energy density values for each water body type using the equation (Hobbs and Hooten 2015):

$$\text{median density} = \exp(\mu_{jkmq}). \quad (4)$$

I pooled predicted values across years and sites for presentation in tables and figures. I was not interested in trying to find the best predictors of food or energy density but simply presenting estimates for each water body type while incorporating the nested, dependent data structure. Therefore, I did not run multiple forms of the model and had no need for any model selection criteria.

I ran 3 chains for 50,000 Markov chain Monte Carlo (MCMC) iterations following 5,000 iterations for burn-in and 25,000 iterations for adaptation for optimal sampling. I fit models using Jags via the RJags package (Plummer 2016) in program R (R Core Team 2018). To assess convergence, I visually examined trace plots and calculated Gelman and Rubin's convergence diagnostic in the CODA package (Plummer et al. 2006) to ensure it was close to 1 (Gelman and Rubin 1992, Brooks and Gelman 1998, Gelman and Hill 2007). I ran models separately for seeds, Mollusca, other invertebrates, and total food. I found very few tubers ($n = 3$, 0.2% of samples) and, therefore, grouped them with seeds for modeling and presenting results.

I checked models using posterior predictive checks with Bayesian P -values based on means, standard deviations, and discrepancy (sums of squares) of the data and from simulated data from the fitted models (Gelman and Hill 2007, Hobbs and Hooten 2015). I calculated Bayesian P -values as the percentage of iterations for which the metric (i.e., \bar{x} , SD, discrepancy) from the observed data exceeded that of the simulated data, where extreme values (close to 0 or 1) indicate poor fit.

To assess food depletion at sites, I ran the same model described above on the subsample of sites visited during the occasions bracketing the period of interest (i.e., fall and winter to assess fall depletion and winter and summer to assess spring depletion). I ran the model separately for fall and spring depletion because the subsample of sites differed between periods. In the model, I included a derived quantity to estimate depletion by subtracting food or energy density in the second occasion from the first occasion. This method provides an estimate of depletion incorporating uncertainty associated with the food and energy density estimates. I pooled model estimates across years and sites for presentation.

Site Morphology

For sloughs, starting at a random point within the same randomly selected stretch used for food sampling, I distributed 9 or 10 transects at equal intervals, running across the slough, perpendicular to the bank (shortest distance to far bank) throughout each slough section. I placed a tape measure across the slough and noted the distance from the shore at which water depth reached 10, 20, 30, 40, 50, 75,

and 100 cm. I also measured the distance to these depths as the water got shallower toward the far shoreline and the total width, which allowed me to estimate the percentage of each transect shallower than each of the target depths.

For emergent wetlands (both actively and passively managed), I used a Trimble R1 global positioning system unit (Trimble, Sunnyvale, CA, USA) to map the extent of inundation (i.e., boundary of the water). I placed 10 transects running out into the wetland every 50 m around the edge of the wetland starting at a random point. At each transect, I measured the distance from the shore to where the water depth reached 10, 20, 30, 40, 50, 75, and 100 cm (Fig. S1, available online in Supporting Information). For each site, I calculated the average distance from the shore to each depth. In ArcMap (Esri, Redlands, CA, USA), I created a buffer inside the mapped outer boundary for the distance to each depth. I calculated the area encompassed by each buffer, which I used to calculate the percentage of the wetland less than each depth.

Large and some small reservoirs were too large to map the entire perimeter using a global positioning system handheld unit in the field. Therefore, I mapped an approximately 500-m stretch of the water line in the field. Similarly to emergent wetlands, I placed 10 transects running out into the reservoir spaced every 50 m around the edge starting at a random point. At each transect, I measured the distance from the shore to where the water depth reached 10, 20, 30, 40, 50, 75, and 100 cm. I overlaid the mapped water boundary line on aerial photographs for which the water line was similar to the line I mapped with the global positioning system handheld unit and digitized the rest of the reservoir in ArcMap using the water line in the aerial photograph as a guide. Again, I used the average distance to the various depths to create buffers inside the outer boundary and calculated the area encompassed by these buffers in relation to the total reservoir area to calculate the percentage of each reservoir less than each depth.

RESULTS

Food and Energy Density

I collected 1,265 core samples across 44 sites in northeastern Colorado (Table 1). Because of lack of precipitation, few playas were available for sampling after fall 2015. Trace plots indicated that the models converged for all parameters and Gelman and Rubin's convergence diagnostic was ≤ 1.01 for all parameters. Little evidence of lack of fit was revealed from posterior predictive checks; all Bayesian P -values were between 0.5 and 0.7.

Emergent wetlands contained the greatest biomass of waterfowl food during all 3 sampling occasions (Fig. 1; Tables S4, S5, available online in Supporting Information). This was primarily influenced by seed biomass. Excluding molluscs, I found relatively little invertebrate biomass. Mollusk biomass was highly variable and substantial at some sites. In most cases, variability among water body types appeared to be more substantial than variability among seasons within a site (Fig. 1). Energy density followed a

Table 1. Number of sites sampled during each sampling occasion for estimating food biomass for ducks in northeastern Colorado, USA, during fall, winter, and summer, 2015 to 2017.

Sampling occasion	Emergent passive	Emergent active	Playa	Reservoir small	Reservoir large	Slough
Fall 2015	6 ^a	8	5	5	6	8
Winter 2016	5	4	2	3	5	6
Summer 2016	5	2	1	3	5	6
Fall 2016	8	9	1	5	6	8
Winter 2017	8	4	0	3	6	9
Summer 2017	8	3	0	3	6	9

^a Only 5 samples collected at one of the sites.

similar pattern to food biomass (Fig. 2; Table S6, available online in Supporting Information). Smartweeds (*Polygonum* spp.) appeared in the top 5 taxa by mass and occurrence for each water body type (Table 2; Table S7, available online in Supporting Information). Docks (*Rumex* spp.) and lambs-quarters (*Chenopodium* spp.) also appeared in the top 5 taxa for all water body types except playas (Tables 2, S7). Other plant taxa appearing in the top 5 for percent mass or percent occurrence included bulrush (*Schoenoplectus* spp.), verbena

(*Verbena* spp.), and duckweed (*Lemna* spp.). For invertebrates, gastropods (Class Gastropoda) made up the greatest percent mass and were frequently encountered in emergent wetlands and sloughs. Dipterans (Order Diptera) also made up a relatively large percentage of the mass and frequently occurred in most water body types (Tables 2, S7).

I sampled fewer sites more than once to estimate depletion during fall and spring (Table 3). I excluded playas from the spring depletion analysis because there was only 1 site

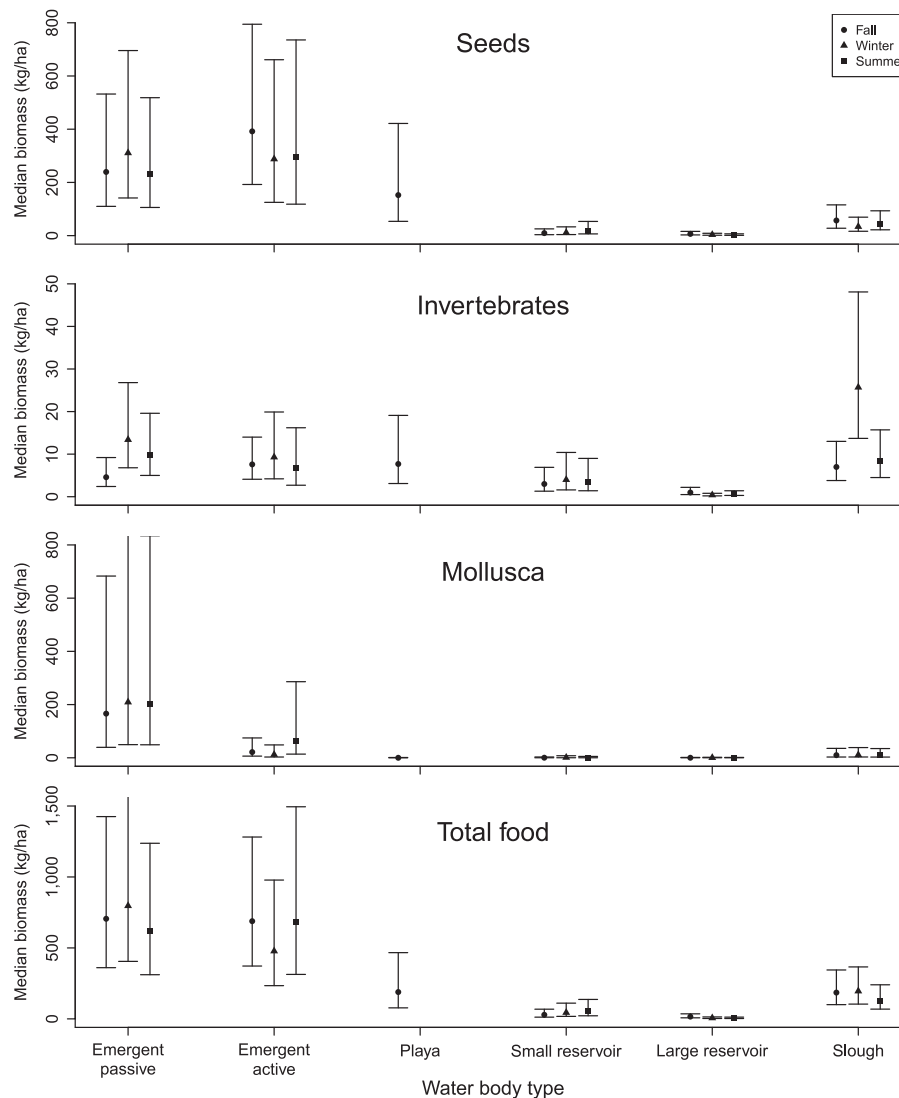


Figure 1. Model-predicted median biomass of seeds, invertebrates (excluding Mollusca), Mollusca, and total food for ducks at 3 sampling occasions and 6 water body types in northeastern Colorado, USA, 2015 to 2017. Error bars represent Bayesian 95% credible intervals.

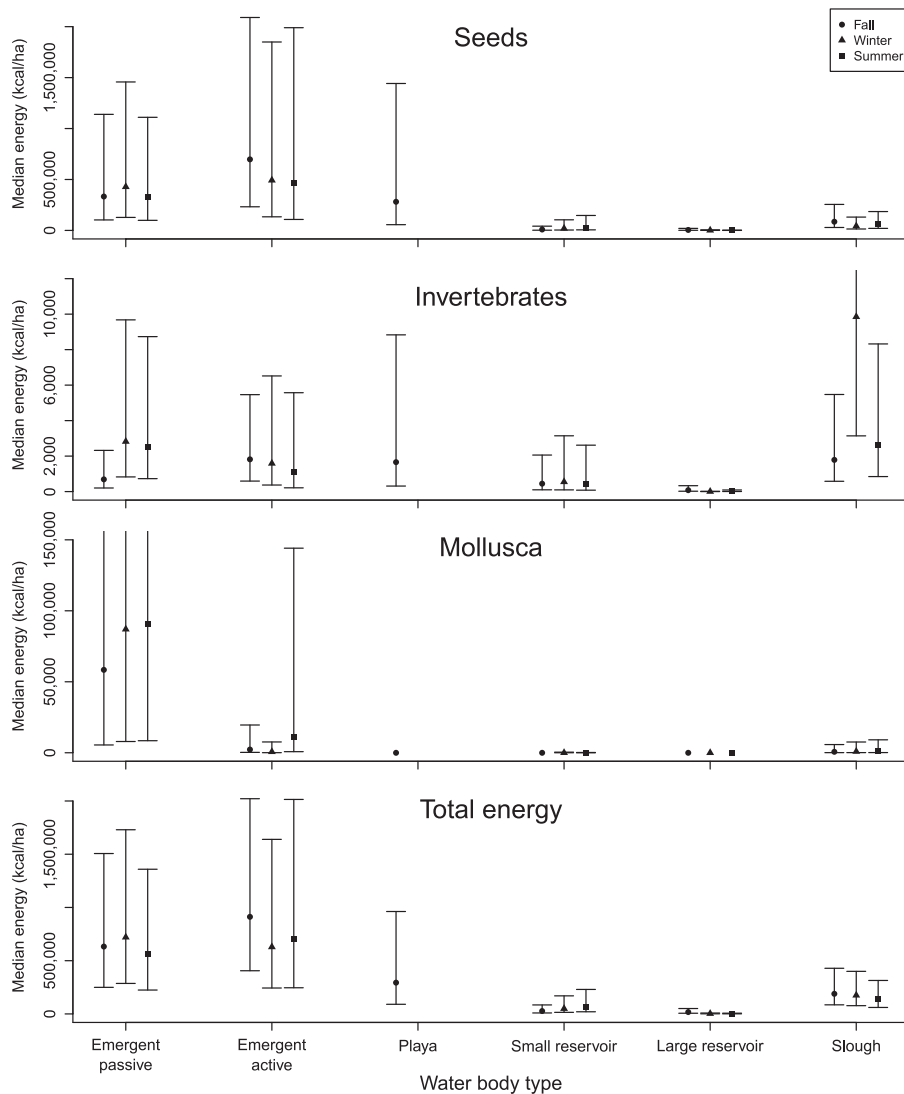


Figure 2. Model-predicted median energy (kcal/ha) of seeds, invertebrates (excluding Mollusca), Mollusca, and total food for ducks at 3 sampling occasions and 6 water body types in northeastern Colorado, USA, 2015 to 2017. Error bars represent Bayesian 95% credible intervals.

sampled during winter and summer. During fall, food depletion was greatest in actively managed emergent wetlands, which, along with large reservoirs, were the only water body type for which 95% credible intervals excluded zero (Fig. 3). During spring, depletion in sloughs was the only estimate for which credible intervals excluded zeros (Fig. 3); however, passively managed emergent wetlands also tended to show some depletion (Fig. 3). Depletion of energy tended to follow similar patterns to depletion of food biomass (Fig. 4).

Site Morphology

I collected morphology data on 5 passively managed emergent wetlands, 8 actively managed emergent wetlands, 3 small reservoirs, 5 large reservoirs, and 8 sloughs. Actively managed emergent wetlands and sloughs generally contained the greatest percentage of shallow water (Fig. 5). I estimated that the mean percentage of passively managed emergent wetlands, actively managed emergent wetlands,

small reservoirs, large reservoirs, and sloughs shallower than 50 cm was 37%, 77%, 10%, 4%, and 83%, respectively.

Comparison with Current Energetic Carrying Capacity Models

Estimates of energy availability currently used by the PLJV were generally greater than what I found (Table S8, available online in Supporting Information). In the most extreme case, reservoirs were assigned 10,435 DED/ha in the PLJV Conservation Strategy (PLJV Waterfowl Team 2005), whereas I found between 50 DED/ha and 77 DED/ha. Actively managed emergent wetlands (i.e., moist-soil units) were also assigned values substantially greater than what I found in this study (Table S8). Emergent marsh, moist-soil units, and sloughs were assumed to be 100% suitable (i.e., all energy is accessible), whereas I found only 37% of passively managed emergent marsh, 77% of actively managed emergent marsh, and 83% of sloughs were shallow enough for feeding by dabbling ducks. Using my energy density and feeding depth suitability values reduced estimated overall

Table 2. Mean percent mass for top 5 plant and invertebrate taxa recovered in duck food samples in each water body type in northeastern Colorado, USA, during fall, winter, and summer, 2015 to 2017.

Taxa	Emergent passive	Emergent active	Playa	Reservoir small	Reservoir large	Slough
Plants						
Schoenoplectus	20.0			11.6		9.7
Polygonum	18.7	15.3	11.6	11.3	15.0	9.8
Rumex	11.5	10.7		7.4	11.3	
Chenopodium	7.4	10.7		14.7	24.7	
Lemna	6.5				4.8	20.4
Cyperus						10.3
Zannichellia				7.1		
Echinochloa						11.8
Eleocharis		14.7				
Amaranthus			6.6		11.1	
Verbena			45.1			
Alopecurus		10.6				
Poa			4.3			
Hordeum			4.7			
Invertebrates						
Gastropoda	87.9	70.6	4.7	30.7	26.6	43.5
Diptera	6.5	15.4	67.0	31.2	41.7	24.1
Annelida	1.5	3.3	5.5	16.7	19.2	16.5
Odonata	1.5		4.4			
Coleoptera	1.2	6.9	14.4	9.3	3.3	
Cladocera					2.6	
Ephemeroptera		1.2				
Malacostraca						1.8
Bivalvia				4.3		9.3

Table 3. Number of sites used to estimate food depletion in northeastern Colorado, USA, during fall and spring, 2015 to 2017. To be used to estimate fall depletion, a site must have been sampled in both early fall and winter sampling occasions. To be used to estimate spring depletion, a site must have been sampled in both winter and early summer sampling occasions. Values in parenthesis indicate the number of sites that were included in both years of the project.

Water body type	Fall (both years)	Spring (both years)
Emergent passive	8 (5)	8 (5)
Emergent active	4 (4)	3 (2)
Playa	2 (0)	1 (0)
Reservoir small	3 (3)	3 (3)
Reservoir large	6 (5)	6 (5)
Slough	9 (5)	9 (6)

energy availability on the landscape to 21,950,047 DEDs (Table S8).

DISCUSSION

If bioenergetics strategies are to be used to guide habitat planning for nonbreeding ducks, local estimates of energy availability are imperative. I provide estimates of food and energy density for northeastern Colorado and for water body types that have not been previously studied. Furthermore, I provide estimates of the percentage of sites that are shallow enough to facilitate feeding by dabbling ducks.

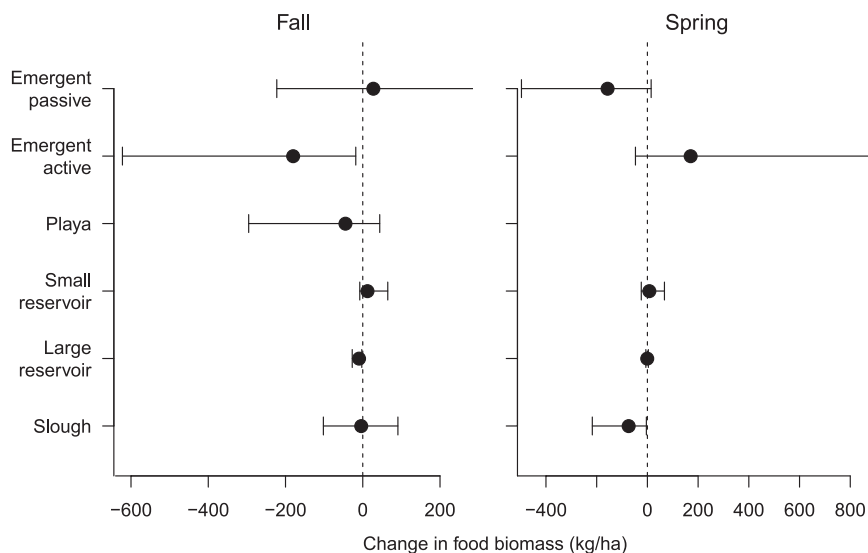


Figure 3. Model-predicted duck food (kg/ha) depletion during fall and spring periods for 6 water body types in Northeast Colorado, USA, 2015 to 2017. Error bars represent Bayesian 95% credible intervals.

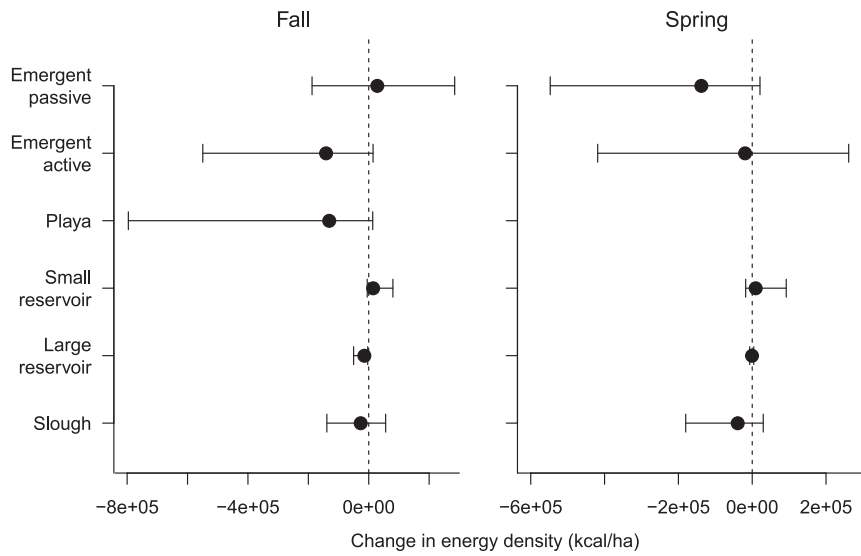


Figure 4. Model-predicted duck food-energy (kcal/ha) depletion during fall and spring periods for 6 water body types in Northeast Colorado, USA, 2015 to 2017. Error bars represent Bayesian 95% credible intervals.

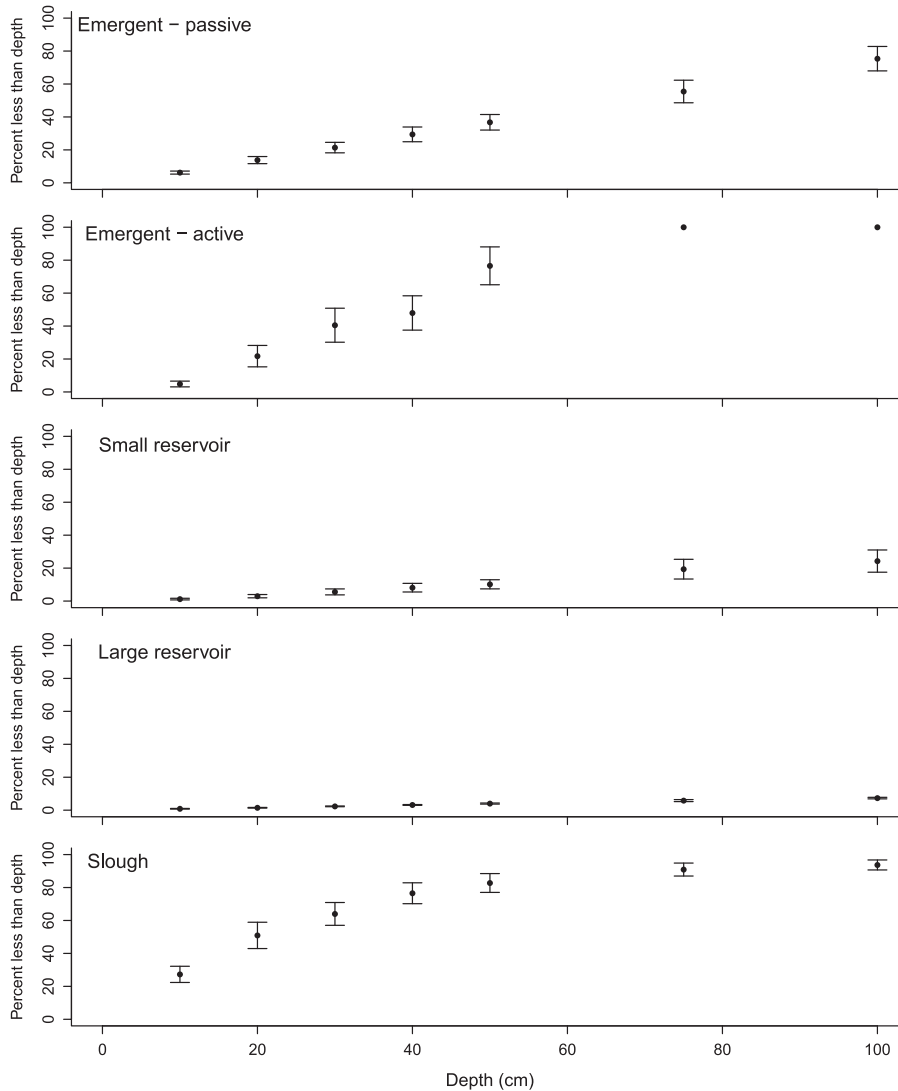


Figure 5. Mean (\pm SE) percentage of a site less than various depths in northeastern Colorado, USA, 2017. These estimates represent the percent of a site that is shallow enough to facilitate feeding by dabbling ducks.

Compared with my estimates of energy availability, the biological planning models used by the PLJV overestimate available energy. This is the result of using overestimates of energy density values and percent suitable foraging habitat. Many of the currently used values for energy availability were based on estimates from other regions (PLJV Waterfowl Team 2005), which I did not find to be representative of the Colorado PLJV region. Thus, this research highlights the need for local information in conservation planning models. Updating these energy values and feeding suitability values in the conservation strategy reduces the total energy available for ducks, potentially below levels necessary to support population goals.

Few estimates of food or energy availability are available in the region with which to compare my estimates. In the Rainwater Basin of Nebraska, USA, Drahota and Reichart (2015) reported overall wetland seed biomass in moist-soil plant communities prior to spring migration was 685 kg/ha, compared with my estimate of 291 kg/ha for actively managed emergent wetlands during winter sampling. In the Southern High Plains of Texas, USA, Anderson and Smith (1999) report playas with active hydrologic management produced 7,794 DED/ha of seeds, whereas unmanaged playas produced 414 DED/ha, compared with my estimate of 789 DED/ha of seeds in playas in the fall. Hydrology was not actively managed in any of the playas in my study. Most other research has been done on actively managed wetlands (i.e., moist-soil impoundments) in the Mississippi flyway. In the Mississippi Alluvial Valley, estimates of seed and tuber biomass in moist-soil wetlands generally range from 496 kg/ha to 750 kg/ha (Kross et al. 2008, Hagy and Kaminski 2012a, Olmstead et al. 2013). In riverine and backwater wetlands of the Illinois River Valley, seed and tuber biomass ranged from 20 kg/ha to 152 kg/ha (VonBank et al. 2016). In the Upper Mississippi River and Great Lakes Region, food biomass was 208 kg/ha in palustrine emergent, 87 kg/ha in palustrine forested, and 52 kg/ha in lacustrine-riverine wetlands (Straub et al. 2012).

One of the most challenging and overlooked aspects of estimating energetic carrying capacity is determining how much food is actually available to be consumed by ducks and what factors influence availability. Water depth is one obvious factor reducing ducks' abilities to feed on the substrate, which I have assessed by quantifying the percentage of sites that are shallow enough to facilitate feeding by dabbling ducks. As expected, reservoirs contained relatively low percentages of suitable depths for feeding. However, contrary to my predictions on average <50% of each passively managed emergent wetland was suitable for feeding by dabbling ducks. I make a number of assumptions in the depth sampling analyses; most importantly, I assumed the sampled area was representative of the larger site. For wetlands and some small reservoirs, I distributed sampling transects throughout the entire site, reducing the chance of bias. Some reservoirs were so large, I could not feasibly sample the entire perimeter and it is possible that the sampled area may deviate from other areas around the reservoir, although I randomly selected the sample locations to reduce bias.

Overall water levels different than during the sampling occasion may be associated with different slopes of the bank substrate and therefore different distances from the water line to the various depths and different percent inundation depth patterns. Hydrologic regimes for many actively managed sites included filling during late summer and maintaining a certain water level through winter. I focused my sampling during the period of relatively stable water levels after sites became inundated. The transition periods when wetlands were filling or draining could result in more or less area of suitable feeding depths than what I present here. These transition periods represent a substantially shorter time period than the more stable period when I sampled. Future research looking at how changing water levels affects energy density or the percentage of available shallow foraging habitat would be very beneficial for accounting for these changes in energetic carrying capacity models. Furthermore, additional research in other regions would provide insight into the general applicability of these results to other regions. My results of suitable feeding depths should be used cautiously outside of northeastern Colorado because wetland and reservoir structure may vary regionally.

My estimates of energy availability may slightly over- or underestimate energy availability because of the sampling methods I used; however, any biases are likely minimal with no effects on overall inference. First, although the core samplers I used captured the water column, they likely missed some nektonic invertebrates if the invertebrates were able to actively avoid the sampler as I placed it in the water (Cheal et al. 1993). Invertebrates, however, make up a small percentage of duck diet during the nonbreeding seasons, and specifically, nektonic invertebrates make up a very small percentage (Jorde et al. 1983, Combs and Fredrickson 1996) and generally represent a small portion of available energy for ducks (Hagy and Kaminski 2012a). Second, with regard to energy being available at various depths, it is possible that nektonic invertebrates or submersed aquatic vegetation could serve as an energy source to ducks in water that was deeper than 50 cm. By excluding energy found in deeper portions of wetlands, I may have omitted energy from these sources that was actually available to ducks. It has been repeatedly reported, however, that dabbling ducks focus their feeding in shallow portions of wetlands where they can reach the substrate (Johnson and Rohwer 2000, Hagy and Kaminski 2015) so any energy they gain from these sources in deeper water would be minimal. Furthermore, there was very little submersed aquatic vegetation in any of my study sites. Finally, many duck species are restricted to or prefer feeding in water that is shallower than 50 cm (Hagy and Kaminski 2015). For example, green-winged teal (*Anas crecca*) generally feed in water that is ≤ 29 cm deep (Euliss and Harris 1987, Johnson and Rohwer 2000) and Hagy and Kaminski (2015) report that dabbling ducks decreased feeding by 10% for each 10.7-cm increase in water depth. If ducks did not feed in areas as deep as 50 cm, my estimates may overestimate available energy. Mallards, however, are capable of feeding at 50-cm depths (Behney 2014) and most management actions

and energetic carrying capacity model parameters are for mallards. Furthermore, mallards make up 99% of the total duck population objective for the PLJV region of Colorado (PLJV Waterfowl Team 2005). Therefore, for this region, it made sense to present results most applicable to mallards. I provide the percentages of wetlands that are shallower than other depths (10, 20, 30, 40, 50, 75, 100 cm) for cases where smaller, shallower feeding ducks are of management importance.

Accounting for energy availability based on water depth in the range of water depths I observed, will generally only apply to dabbling ducks. Many diving ducks are found in northeastern Colorado during nonbreeding seasons and can feed at depths greater than the 50-cm cutoff I used (Torrence and Butler 2006). Diving duck population objectives, however, represent <1% of overall duck objectives for the PLJV area of Colorado (PLJV Waterfowl Team 2005). For areas where diving ducks make up a greater percentage of the overall duck population goal, guild-specific methods could be used in which water depth is accounted for when calculating dabbling duck habitat objectives but ignored or accounted for differently when calculating diving duck objectives.

Mistimed hydroperiods or lack of wetland inundation may also limit energy availability to ducks. This is especially true for playas (Cariveau et al. 2011, Johnson et al. 2011), which were infrequently inundated during my study. In the Texas High Plains, Johnson et al. (2011) reported the probability of a playa being inundated in January was 0.1 for playas in grassland systems. In the shortgrass prairie ecoregion, Bartuszevige et al. (2012) reported that playa inundation was affected by rainfall, playa area, slope of the surrounding area, and amount of Conservation Reserve Program land in the vicinity. Although playa condition (dry, wet, wet pit only) was accounted for in energetic carrying capacity models for the Playa Lakes Region, much of the information came from the southern extent of the region (e.g., TX). I recommend future research to quantify playa hydroperiods in other parts of the Playa Lakes Region so when they are dry, they can be excluded from energetic carrying capacity estimates.

An additional factor that can reduce the availability of food to foragers is the concept of foraging thresholds. Foragers generally do not consume all food in a patch and the amount remaining when they quit foraging is referred to as the giving up density (GUD; Brown and Kotler 2007). The giving up density results from food biomass being depleted to some threshold level that is influenced by predation (risky patches = greater GUD), energy (more energy required to forage = greater GUD), and missed opportunity (food rich environment = greater GUD) costs of foraging (Brown 1988). Similarly, the density at which foragers stop reducing food biomass because environmental factors limit availability is referred to as a food availability threshold (FAT; Hagy and Kaminski 2015). Because of the costs associated with consuming food at densities below the threshold value (GUD or FAT), this food biomass can be subtracted from energetic carrying capacity models (Central Valley Joint Venture 2006, Soulliere et al. 2007, Lower

Mississippi Valley Joint Venture 2015). It is clear that at some point food biomass gets too low to facilitate profitable exploitation; however, it is less clear how to account for foraging thresholds. The Lower Mississippi Valley Joint Venture subtracts 50 kg/ha from food biomass estimates to account for a foraging threshold (Lower Mississippi Valley Joint Venture 2015). The Upper Mississippi River and Great Lakes Joint Venture assumes 50% of food is unavailable (Soulliere et al. 2007) and the Central Valley Joint Venture subtracts 34 kg/ha from food biomass estimates to account for a foraging threshold (Central Valley Joint Venture 2006). Currently, forage thresholds are not incorporated in the PLJV energetic carrying capacity models (PLJV Waterfowl Team 2005). Applying Hagy and Kaminski's (2015) FAT estimate of 180 kg/ha for natural seeds and tubers from the Mississippi Alluvial Valley to the Playa Lakes region's models would substantially reduce the predicted number of ducks that can be supported. I am hesitant to derive a GUD or threshold estimate from this research in northeastern Colorado because it is a stopover area and ducks may not have the ability to deplete resources to a threshold before sites freeze, forcing them to continue migrating out of the region. I recommend further exploration of foraging thresholds in the region and how best to incorporate them into energetic carrying capacity models used by the PLJV.

During fall, I observed the greatest food depletion in actively managed emergent wetlands. Even though starting food densities were similar between actively and passively managed emergent wetlands in the fall, passively managed emergent wetlands experienced little to no depletion. Given similar food densities, it appears that something is preventing ducks from exploiting food in passively managed emergent wetlands. Perceived predation risk of ducks can be related to visual obstruction due to vegetation (Behney et al. 2018) and water depth (Poysa 1987, Guillemain et al. 2000). Furthermore, water depth can affect the energetic cost of foraging (deeper foraging takes more energy). Water was generally deeper in passively managed emergent wetlands (generally the center was >1 m vs. <1 m for actively managed wetlands) and had denser, taller vegetation than actively managed emergent wetlands (visual obstruction: active = $25 \pm 2\%$, passive = $42 \pm 4\%$ [SE], A. C. Behney, Colorado Parks and Wildlife, unpublished data). Depletion during spring tended to be greatest in passively managed emergent wetlands and sloughs, which may be a result of little depletion during fall so the ducks focused feeding in these types during spring. It is possible that the denser robust emergent vegetation may have contributed to less depletion on passively managed wetlands during fall by limiting ducks' abilities to actually maneuver on the water and feed. That depletion occurred during spring on passively managed wetlands seems counter to that idea.

Hagy and Kaminski (2012*b*) suggest that food items not known to be consumed by ducks in the region of interest should be excluded from carrying capacity models. Because few duck diet studies have occurred in northeastern Colorado, it was not surprising that many of the plant items

I found in core samples have not been documented in the diet of ducks. It seems reasonable to assume that a plant or animal item, closely related and similar in appearance to a known duck food, and found in areas in which ducks feed, should be included in estimates of food biomass and this is the best available approach until more diet studies are completed in this region. All of the top items (by mass and frequency) recovered in core samples from emergent wetlands, reservoirs, and sloughs are well known duck foods. Some of the top food items (e.g., verbena, poa grasses [*Poa* spp.], hordeum grasses [*Hordeum* spp.]) recovered from playas are generally more upland plants, which is probably an artifact of infrequent playa inundation in the study area allowing upland plants to encroach around or into playas.

Decomposition of seeds could account for some of the depletion I found. Hagy and Kaminski (2012b) estimated that Japanese millet (*Echinochloa frumentacea*) decomposed 8.9% every 2 weeks during winter in the Mississippi Alluvial Valley. In Texas, 3 species of moist-soil plant seeds lost about 33% biomass during the first 45 days of decomposition and between 50% and 80% by 120 days (Collins et al. 2015). Most decomposition information comes from farther south than this study area and, because decomposition may vary with latitude (Williams et al. 2014), seeds in this study area may decompose less than published estimates from elsewhere. If seeds in this study area were losing at least 50% of their mass by 120 days as in Collins et al. (2015), I would have observed substantially more depletion than what I observed. Depredation by non-ducks could also account for some of the depletion. All the water body types except actively managed emergent wetlands and playas generally supported fish that may have exploited seeds and invertebrates. Furthermore, shorebirds, which consume invertebrates, used the perimeters of many of the sites.

MANAGEMENT IMPLICATIONS

Energy availability estimates from this study can be directly incorporated into the energetic carrying capacity models used by the PLJV. Using my energy density and feeding depth suitability values reduced estimated energy availability to 21,950,047 DEDs (Table S8), which is below the goal for the region. Consequently, the amount of waterfowl foraging habitat that is necessary to support the population goal will increase. Furthermore, because actively managed emergent wetlands had greater availability of food due to water depth, they seem to represent the best choice to maximize food production and the ability of ducks to exploit food.

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