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From the Field

Implications of Uncertainty in True Metabolizable Energy Estimates for Estimating Wintering Waterfowl Carrying Capacities

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ABSTRACT Carrying capacity models for wintering waterfowl require estimates of energy availability based on food densities and true metabolizable energy (TME) of various food types. However, because TME values vary widely between studies, estimates of carrying capacity may be less precise than previously acknowledged. We explored how variation in TME values affected estimates of landscape-level energy availability for American black ducks (*Anas rubripes*), using 4 distinct approaches for assigning TME values to waterfowl food items collected over the winter period in 2011–2012 and 2012–2013: a "best practices" approach, which typically used average TMEs across species, a minimum and maximum reported values approaches, and a coarse-scale "order-average" approach. We found that all 4 approaches yielded significantly different estimates of energy availability across all saltmarsh habitat types. Additionally, we evaluated the potential management implications of variation in TME values by comparing energy supply on 1,223 ha of marsh in Prime Hook National Wildlife Refuge (DE, USA) using all 4 approaches for assigning TME values. We estimated carrying capacity and modeled depletion of energy on this refuge over a hypothetical wintering period. We found that even relatively small variations in TME values produced highly variable estimates of carrying capacity for the refuge. Thus, we recommend that researchers consider the inherent uncertainty in TME values of waterfowl foods, and explicitly include this variation in carrying capacity models.

KEY WORDS bioenergetics, core sample, food availability, invertebrate, marsh, moist-soil seed, TME, true metabolizable energy, waterfowl.

Because food availability is often considered to be a limiting factor for nonbreeding waterfowl, the Joint Ventures seeks to provide sufficient foraging habitat to meet population objectives set by the North American Waterfowl Management Plan (e.g., Atlantic Coast Joint Venture 2005, U.S. Fish and Wildlife Service 2012*a*). Joint venture scientists use bioenergetics modeling, accounting for energy supply and demand on the landscape, to estimate the amount of foraging habitat necessary to meet the needs of waterfowl at North American Waterfowl Management Plan population objectives.

To estimate available energy, researchers often collect soil core samples in the field, and calculate the biomass of waterfowl foods within those samples. The biomass of each food is then multiplied by the true metabolizable energy (TME) value for that food. True metabolizable energy values represent the amount of energy available to a bird from a given food, corrected for metabolic fecal and endogenous urinary (nonfood) energy spent (Sibbald 1976), and TME can vary considerably between different foods and between waterfowl species, which may metabolize them differently (Hoffman and Bookhout 1985, Fredrickson and Reid 1988, Sherfy 1999, Dugger et al. 2007, Coluccy et al. 2014). Relatively few studies have quantified TME values (and

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typically only for common foods), and then across only a small subset of waterfowl species. Because TME data are limited, researchers often rely on single TME values, which may lack replicated accuracy, or estimate unknown TME values for foods based on reported values from taxonomically related foods. Table 1 summarizes intra- and interspecific variation in TME values for common foods with multiple published TME estimates in the literature. For 32 additional foods, only one TME value was reported.

Although estimates of carrying capacity are based on either single or averaged estimates for TME values, there is inherent uncertainty in these values; the management implications of failing to account for this uncertainty have not been addressed. Additionally, if uncertainty has little impact, researchers may be better off using average values across broad taxonomic levels, thus reducing the need for further TME investigations and simplifying calculations of energetic carrying capacity. Using several values to represent uncertainty in TME multipliers, rather than a single number, acknowledges the inherent variation in TME estimates, and provides waterfowl managers with better information on the possible range of energy availability. Our goal was to compare landscape-level energy estimates by 4 methods of assigning TME values to foods, in an effort to assess the sensitivity of energy estimates to variation in TME values. We assigned TME values using 1) a "best practices" approach, wherein TME values for each food were averaged across the lowest taxonomic level to obtain the most accurate value possible; 2) a minimum reported TME approach, wherein the lowest reported TME value for any dabbling duck species was selected for each food; 3) a maximum reported TME approach, wherein the highest reported TME value for any dabbling duck species was selected; and 4) an order-average approach, wherein all foods within each taxonomic order were assigned a single average TME value for that order (Appendix S1). Additionally, we conducted a theoretical

Table 1. Intra- and interspecific variation in true metabolizable energy (TME, kcal/g) estimates for common dabbling waterfowl seed and animal foods collected along the Delaware Bayshore, 2011–2013, with multiple published TME values.[a] Four-letter species codes are interpreted as ABDU, American black duck; BWTE, blue-winged teal; MALL, mallard; NOPI, northern pintail. Superscripts denote references for TME values presented in the footnotes.

	Intraspecific variation						Interspecific variation		
Food	**Species**	$\bar{x}$	**SD**	**Range**	**CV (%)**	***N***	$\bar{x}$	**SD**	**CV (%)**
Plant foods									
Cyperus spp.	BWTE	1.96				1[5]	1.69	0.38	22.59
	NOPI	1.42				1[8]			
Digitaria spp.	MALL	3.10	0.00	3.09–3.10	0.23	2[7]			
Echinochloa spp.	MALL	2.67	0.17	2.54–2.86	6.30	3[1,4,7]			
	BWTE	2.67				1[6]	2.72	0.09	3.18
	NOPI	2.82				1[1]			
Eleocharis spp.	BWTE	−0.18				1[5]			
	MALL	0.50				1[9]	0.58	0.80	138.45
	NOPI	1.42				1[8]			
Leersia oryzoides	MALL	3.00				1[1]	2.91	0.13	4.37
	NOPI	2.82				1[1]			
Panicum spp.	BWTE	2.30	0.35	2.05–2.54	15.10	2[5]	2.52	0.32	12.75
	MALL	2.75				1[7]			
Polygonum spp.	NOPI	1.42	0.24	1.25–1.59	16.93	2[1,8]			
	MALL	1.30	0.31	1.08–1.52	23.93	2[1,7]	1.34	0.07	5.17
	BWTE	1.30				1[6]			
Ruppia maritima	ABDU	0.98				1[10]	1.20	0.31	25.93
	NOPI	1.42				1[8]			
Scirpus spp.	BWTE	0.57	0.10	0.50–0.64	17.37	2[5]			
	NOPI	1.39	0.76	0.85–1.93	54.94	2[1,8]	0.98	0.41	41.7
	MALL	0.99				1[1]			
Animal foods									
Gammarus spp.	ABDU	2.21	0.10	2.12–2.32	4.65	3[3]			
	BWTE	1.66	1.15	0.33–2.32	69.35	3[2,5]	2.07	0.37	17.83
	NOPI	2.36				1[8]			
Gastropoda	BWTE	−0.09				1[5]	0.26	0.49	191.33
	NOPI	0.60				1[8]			
Littorina spp.	ABDU	0.39	0.18	0.27–0.60	46.79	3[3]			
Mya arenaria	ABDU	0.52	0.36	0.26−0.93	69.10	3[3]			
Mytilus edulis	ABDU	0.76	0.41	0.44–1.23	54.24	3[3]			

[a] TME References: [1]Hoffman and Bookhout (1985), [2]Fredrickson and Reid (1988), [3]Jorde and Owen (1988), [4]Reinecke et al. (1989), [5]Sherfy (1999), [6]Sherfy et al. (2001), [7]Checkett et al. (2002), [8]Ballard et al. (2004), [9]Dugger et al. (2007), [10]Coluccy et al. (2014).

exercise to explore the impacts of uncertainty in TME values on American black duck (*Anas rubripes*) carrying capacity, because it is a species of particular conservation concern. We calculated black duck carrying capacities for a modeled refuge system (1,223 ha of marsh in the Prime Hook National Wildlife Refuge, DE, USA) using each of the above approaches to highlight the impacts of TME uncertainty for real-world management scenarios.

STUDY AREA

We collected soil core samples within an approximately 60-km span of the Delaware bayshore between Kent and Sussex counties, USA (39°17′N, 75°27′W to 38°48′N, 75°12′W) in October, January, and April of 2011–2012 and 2012–2013 to estimate black duck food availability. We selected 7 impounded marshes of varying salinities and management regimes, and 3 unmanaged, tidally regulated saltmarsh sites that were further divided into 5 habitat categories based on Cramer et al. (2012): subtidal, mudflat, low marsh, high marsh, and quasi-tidal pools. Subtidal habitats comprised irregularly exposed sites beneath the mean low-tide line. Mudflat habitats comprised regularly flooded and exposed sites typically lacking vegetation cover. Low marsh comprised regularly flooded sites between the mean high and low tide lines, dominated by saltmarsh cordgrass (*Spartina alterniflora*). High marsh comprised irregularly flooded sites above the mean high tide line, dominated largely by saltmeadow cordgrass (*S. patens*). Quasi-tidal pools comprised sites of relatively constant standing water subject to irregular tidal exchange, typically located within high marsh habitats.

METHODS

We collected 52 soil cores in each habitat type (impoundment, high marsh, low marsh, quasi-tidal pools, subtidal, and mudflat) using a custom polyvinyl chloride corer. Cores measured 5.1 cm in diameter × 12.7 cm in depth. We placed cores in plastic bags and transported them to the laboratory, where they were refrigerated for ≤3 days before being washed and fixed with a 10% formalin solution and Rose Bengal dye. We stored fixed cores in plastic cups until we could sort and process them to remove food items. Before sorting, we washed each core thoroughly through size-10 (2-mm mesh opening) and size-60 (0.251-mm opening) sieves to remove formalin and separate sample material by size. Material remaining in the size-10 sieve was categorized as "large" and material in the size-60 sieve as "small." We then sorted through each core under a 6× magnification dissecting microscope to remove seed and animal foods and identify them to the lowest possible taxonomic level (typically genus). We sorted through 100% of "large" material, and subsampled 25% and later 10% by mass of "small" material to reduce sorting time and costs (Livolsi et al. 2014). We then dried and weighed food items to 0.0001 g and multiplied biomass by 4 or 10 (respectively) to estimate total mass in the subsampled portion. We added "large" material biomass to estimated "small" material biomass to determine total biomass of each food within each sample. We excluded foods composing a very small proportion of total food biomass across all samples (<0.01 g in total) from our analysis.

To estimate energy available to black ducks, we used methods from Cramer (2009) to identify black duck foods within cores from each habitat type. We assigned each of these food items a TME value (kcal/g) based on values reported both in the literature and unpublished data. We used only TME values reported for dabbling ducks to reduce bias associated with TME values calculated for more distantly related species (such as geese). The majority of TME values were reported for black ducks, mallards (*A. platyrhynchos*), northern pintails (*A. acuta*), and blue-winged teal (*A. discors*; Table 1). To explore the sensitivity of landscape-level energy availability to different TME values, we estimated energy using 4 methods of assigning TME values to food items: A "best practices" approach (hereafter, BP), minimum TME (hereafter, MIN), maximum TME (hereafter, MAX), and order-average TME (hereafter, ORDER; SI Appendix 1).

Best Practices Approach

The BP approach was intended to represent a realistic method investigators might use to assign TME values (e.g., used in Cramer 2009). Thus, it incorporates multiple TME values for each food when available, and probably yields the most accurate energy estimates given available information. For the BP approach, we assigned each food a value at the lowest possible taxonomic level at which a TME value was reported. For foods with multiple TME values reported, we averaged values from lower taxonomic levels to determine a TME value (i.e., foods from the "species" level were averaged to obtain a "genus" level average value). If values were reported for black ducks or mallards, we preferentially selected these values and excluded values for other species, assuming values determined for these species to be most accurate because of similarities in gut morphology. If no TME values were reported for a food, we averaged values reported for closely related foods. For one seed, *Humulus japonicus*, no closely related values were reported; we averaged values for all other seed orders and assigned this average as a BP TME value (although this food type had little impact in our analysis because we found only small amounts of this seed across all of our core samples).

Minimum and Maximum Approaches

In the MIN and MAX approaches, we assigned the smallest and largest reported values (respectively) for foods with multiple reported TME values, rather than an average value. For many foods, only one TME value was reported. Therefore, to avoid assigning a single value to the BP, MIN, and MAX approaches, we attempted to estimate the hypothetical MIN and MAX for foods with only one reported TME value. To accomplish this, we examined all foods with multiple reported TME values, and calculated the percent deviation of the MIN and MAX values from the BP value. We then averaged these percent deviations to determine a mean percent deviation for MIN and MAX values (MIN: −45%, MAX: +65%). We applied this mean percent deviation to all foods with only one reported value to determine hypothetical MIN and MAX values for analysis. We did not preferentially select TME values for black ducks or mallards in these approaches in order to investigate the impacts of a wider range of variation in TME values.

Order-Average Approach

In addition to the BP, MIN, and MAX approaches, which were intended as a sensitivity analysis, we assigned TME values at the order level. We included the ORDER approach to assess whether sorting and identifying foods to order (as opposed to identifying at the lowest taxonomic level, typically genus or species) has a significant impact on energy estimates. This is relevant from a methodological perspective, because coarse sorting of foods to the order level could save researchers time and money (Livolsi et al. 2014), and if order-level TME values are sufficient it may reduce the need for further TME research. For the ORDER approach, we assigned each food the average TME value for foods in that order. To determine the average TME for each order, we "averaged up the ladder"; that is, we averaged all values reported at the species level for each food to determine a mean species-level TME value, and then averaged these mean species-level values within each genus to determine a mean genus-level value, etc., until we obtained a mean order-level value for each order present in our samples.

Energy Comparisons

For each approach, we multiplied the biomass of each food in a core by its respective TME value, and summed all food energy within a core to estimate total available energy per core using each approach. We then extrapolated each core energy value to the hectare level. We pooled all cores for analysis ($n = 312$) to capture variability between habitat types. To test for differences in estimated energy per ha between the BP, MIN, MAX, and ORDER approaches, we $\log_{10}$-transformed energy values (kcal/ha) to achieve a normal distribution and conducted a repeated-measures analysis of variance (ANOVA; Greenhouse–Geiser- corrected for violations in sphericity) because of autocorrelation in data sets (SPSS, Version 22; IBM Corporation, Armonk, NY). If the 4 approaches were significantly different (at an alpha level of 0.05), we conducted a within-subjects pairwise comparison to determine which approaches were different from each other.

Implications of TME Uncertainty to Estimates of Carrying Capacity

To outline potential management implications of variability in TME estimates, we modeled depletion of food energy by black ducks using Prime Hook National Wildlife Refuge (Milton, DE) management units I, II, and III as an example landscape. The area of each habitat type at Prime Hook was estimated using Delaware State Wetlands Mapping Project land-cover data (Delaware Department of Natural Resources and Environmental Control 2007). In total, we estimated 1,223 ha of marsh in the Prime Hook study units; of that, 660 ha were considered impoundment, 252 ha were low marsh, 230 ha were high marsh, 28 ha were quasi-tidal pools, 47 ha were subtidal, and 6 ha were mudflat. To estimate initial available energy using the BP, MIN, MAX, and ORDER approaches, we estimated mean kcal/ha for each habitat type separately using each approach, multiplied by the number of ha of each habitat, and summed across habitats. We assumed that Prime Hook holds up to approximately 40% of Delaware's black duck population, based on numbers reported by the refuge for October 2005 (U.S. Fish and Wildlife Service 2012*b*); although this value is approximate, we felt it represented a reasonable conservation goal for the refuge. Therefore, based on a mean midwinter survey population estimate of 8,071 black ducks for the state of Delaware (10-yr mean, 2003–2013, Delaware Division of Fish and Wildlife 2014), we assumed black duck numbers on the refuge peak at 3,230 ducks. We modeled a steady influx and outflow of black ducks over a hypothetical 212-day migration and wintering period based on black duck migration patterns in the mid-Atlantic region from 1 October to 30 April (Bellrose 1980). Starting at zero, 53 black ducks were added to the refuge each day until day 61. We maintained maximum black duck numbers on the refuge from days 62 to 151. After day 151, 53 black ducks were removed each day until zero remained at day 212. We multiplied black duck numbers by 291 kcal/day/bird to determine total daily energy requirement for each day (Jones et al. 2014). We then subtracted daily energy requirement from available energy each day to model energy depletion over time. We ignored foraging thresholds in our energy model, assuming that 100% of the food estimated on the landscape was available to ducks, and that ducks will forage until resources are entirely depleted. We acknowledge there are several sources of imprecision in this model (e.g., migration curves, foraging thresholds, competition), but we believe this does not detract from our goal of highlighting the impact of uncertainty in TME values on carrying capacity estimates. Although Prime Hook has not shown evidence of energy depletion (K. M. Ringelman, unpublished data), we explicitly modeled depletion to broaden the applicability of our analysis to other systems and to provide insight for managers concerned with black duck carrying capacity. We compared estimates of carrying capacity for each approach in terms of available duck use-days (DUDs) at the start and end of the 212-day wintering period following Reinecke et al. (1989):

$$\text{DUDs} = \frac{\text{Energy Supply (kcal)}}{\text{Daily Energy Requirement (kcal/bird/day)}}$$

RESULTS

Energy Differences Between Approaches

Across all habitat types, the MAX approach to assigning TME values yielded energy estimates ($\bar{x} = 239{,}089 \pm$ SE 26,083 kcal/ha) more than double those calculated for the MIN approach ($105{,}375 \pm$ SE 14,241 kcal/ha). The BP approach yielded $158{,}584 \pm$ SE 18,965 kcal/ha, and the ORDER approach yielded $204{,}486 \pm$ SE 25,874 kcal/ha, on average. Repeated-measures ANOVA revealed a significant difference in estimated $\log_{10}$ [kcal/ha] values ($F_{1.69,\ 526.14} = 57.25$, $P < 0.001$) and pairwise comparisons

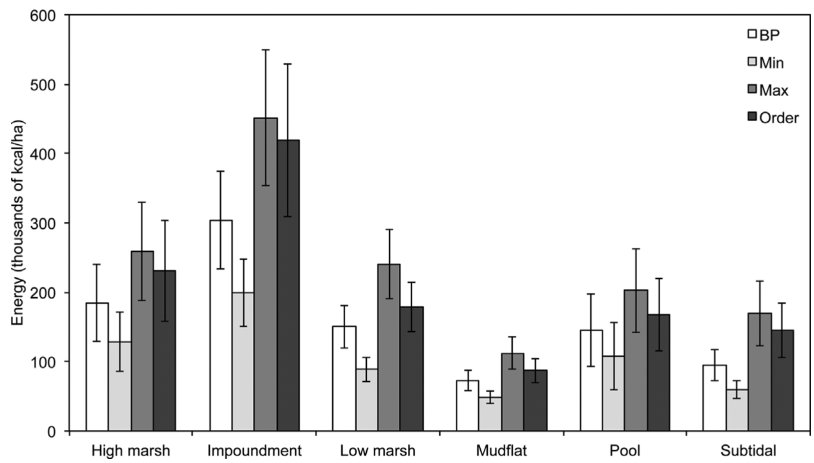

Figure 1. Mean energy (kcal/ha) in 6 habitat types along the Delaware bayshore (USA) estimated using 4 approaches ("best practices": BP, "minimum reported": Min, "maximum reported": Max, "order-average": Order) for assigning true metabolizable energy (TME) values to American black duck foods, October–April, 2011–2013.

between all approaches were significantly different from each other ($P < 0.001$).

Carrying Capacity Estimates

We found that when separated by habitat type, impoundments tended to contain the highest mean energy estimates, and mudflats tended to contain the lowest (Fig. 1). We estimated between 189,000,000 and 433,000,000 kcal initially available to black ducks in our hypothetical refuge depending on the approach used to assign TME values, with the MIN and MAX approaches yielding the lowest and highest energy estimates, respectively. At the start of the wintering period, before black ducks arrived, we estimated 997,000 DUDs available using the BP approach, 651,000 DUDs using the MIN approach, 1,490,000 DUDs using the MAX approach, and 1,330,000 DUDs using the ORDER approach. We estimated that cumulative energy depletion over the winter period was 488,000 DUDs. Therefore, at the end of the wintering period, we estimated that there were 509,000 DUDs remaining using the BP approach, 163,000 DUDs using the MIN approach, 999,000 DUDs using the MAX approach, and 841,000 DUDs using the ORDER approach (Fig. 2). Our modeling exercise revealed that if energy is calculated using the BP approach, 48.92% of DUDs initially available are depleted over the winter period. However, if the MIN approach is used, 74.96% of DUDs are depleted, and if the MAX approach is used, 32.75% of DUDs are depleted.

DISCUSSION

A great deal of effort has been devoted to estimating waterfowl carrying capacity, with a focus on estimating energetic demand and food availability. However, studies quantifying and corroborating true metabolizable energy (TME) values for common waterfowl foods are scarce. Our results indicate that energy estimates differ significantly depending on the method by which foods are assigned TME values and therefore represent a potentially significant, and understudied source of variation in carrying capacity estimates. Current bioenergetics models and management strategies often fail to account for variation in TME estimates, which leads to hidden uncertainty and imprecision. Thus, it is clear that variation in TME estimates holds significant implications for bioenergetics modeling, and management strategies should be designed with this uncertainty in mind.

Typically, investigators opt to assign TME values at the lowest taxonomic level possible, similar to our "best practices" approach (Brasher et al. 2007, Cramer 2009). We advocate continued use of this approach, because it likely yields the most accurate estimates of available energy. That said, because many waterfowl foods only have a single published TME value, the best practices approach ignores unobserved variation in these estimates. Therefore, minimum TME and maximum TME approaches may be useful in providing a potential range of energy availability that incorporates uncertainty in TME values. Additionally, our results suggest that there is a significant difference in estimated energy between the order-average TME and best practices methods; thus, to avoid possible overestimation of available energy (and carrying capacity), we conclude that researchers should continue to sort and identify foods to the lowest possible taxonomic level, despite the significant effort involved in processing core samples with such detail.

We suggest that investigators consider the variability associated with current TME values when managing for specific waterfowl population goals. Based on our results, even seemingly small fluctuations in TME values may result in significantly different estimates of available energy. Such fluctuations are not unlikely given that TME estimates vary by 32% on average within duck species and 46% between species, with differences up to 200% between studies in some cases (Fredrickson and Reid 1988, Sherfy 1999, Table 1). Additionally, because we selected TME values for both black ducks and mallards in our analysis, the number of reported values was relatively high compared with that of other waterfowl species. Thus, variability in TME values is likely even higher for other waterfowl, and investigators may be

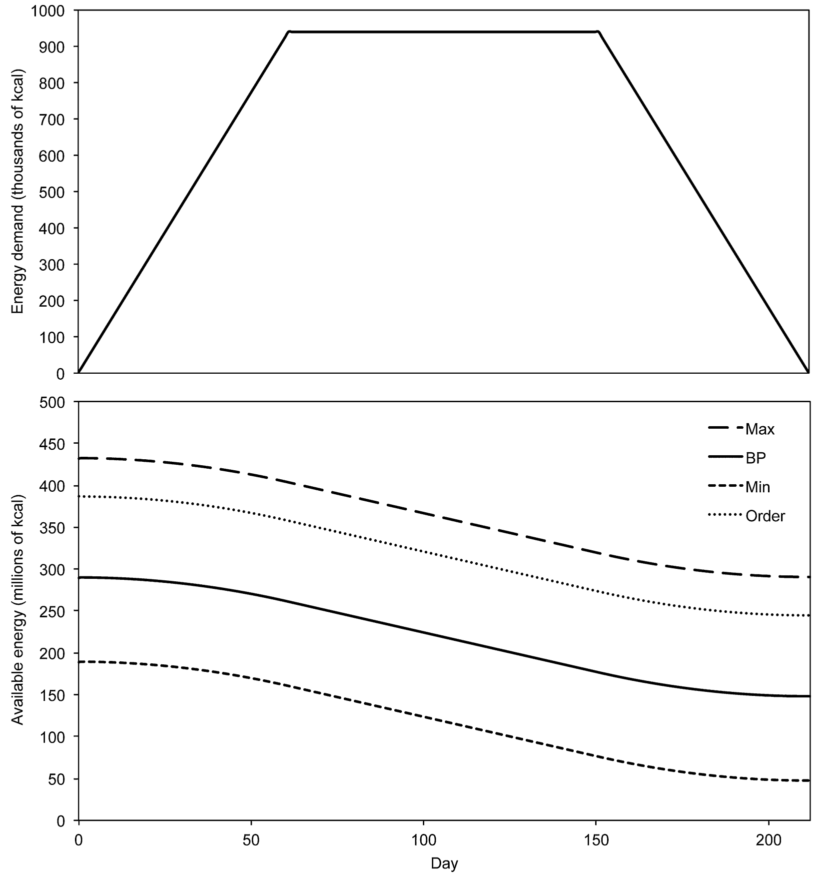

Figure 2. Energy demand and depletion of available American black duck food energy on Prime Hook National Wildlife Refuge (Milton, DE, USA) over a hypothetical 212-day wintering period, calculated using 4 approaches ("best practices": BP, "minimum reported": Min, "maximum reported": Max, "order-average": Order) for assigning true metabolizable energy values to American black duck foods.

forced to either work with fewer TME values or accept the potential bias associated with using TME values reported for nonfocal species. To correct these biases, gaps in TME data must ultimately be filled by additional studies quantifying TME for a variety of foods and waterfowl species.

Our sensitivity analysis illustrates the impact that uncertainty in TME values could have for real-world management scenarios. If true TME values deviate from best practices values on the order of magnitude observed between reported values, estimates of black duck carrying capacity could vary significantly. Though our results suggest that black ducks are not at carrying capacity in this simplified model, several other waterfowl species likely compete with black ducks for similar food resources, and energy demands associated with these species do not appear in our model. Thus, if true TME values are closer to minimum TME estimates of carrying capacity, black ducks may approach or exceed carrying capacity at Prime Hook. If true TME values are closer to maximum TME estimates of carrying capacity, the landscape may be able to support significantly more black ducks (and other waterfowl). Clearly, the choice of which TME values to use can have dramatic effects on measurements of carrying capacity: the difference in initial energy availability between minimum TME and maximum TME is nearly twice the total amount of energy estimated to be consumed during the entire wintering period. Managers using bioenergetics models to set management guidelines may be basing their strategies on models that do not account for this range of variation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix 1. Appendix 1 contains the food item energy values (true metabolizable energy [TME]) we used for the 4 methods (a "best practices" approach [BP], minimum TME [MIN], maximum TME [MAX], and order-average TME [ORDER]).