Articles

Estimating Waterfowl Carrying Capacity at Local Scales: A Case Study From Edwin B. Forsythe National Wildlife Refuge, New Jersey[1]

Kevin M. Ringelman,* Christopher K. Williams, Paul M. Castelli, Mason L. Sieges, Rebecca A. Longenecker, Theodore C. Nichols, Stephen D. Earsom

K.M. Ringelman
School of Renewable Natural Resources, Louisiana State University AgCenter, Baton Rouge, Louisiana 70803

C.K. Williams
Department of Entomology and Wildlife Ecology, University of Delaware, Newark, Delaware 19716

P.M. Castelli, M.L. Sieges, R.A. Longenecker
U.S. Fish and Wildlife Service, Edwin B. Forsythe National Wildlife Refuge, Galloway, New Jersey 08205; *P.M. Castelli*, retired
Present address of M.L. Sieges: Great Plains Regional Office, Ducks Unlimited, Bismarck, North Dakota 58503
Present address of R.A. Longenecker: U.S. Fish and Wildlife Service Northeast Regional Office, Hadley, Massachusetts 01035

T.C. Nichols
New Jersey Division of Fish and Wildlife, 2201 County Route 631, Woodbine, New Jersey 08270

S.D. Earsom
U.S. Fish and Wildlife Service, Division of Migratory Bird Management, 11510 American Holly Drive, Laurel, Maryland 20708

Abstract

The management of wintering North American waterfowl is based on the premise that the amount of foraging habitat can limit populations. To estimate carrying capacity of winter habitats, managers use bioenergetic models to quantify energy (food) availability and energy demand, and use results as planning tools to meet regional conservation objectives. Regional models provide only coarse estimates of carrying capacity because habitat area, habitat energy values, and temporal trends in population-level demand are difficult to quantify precisely at large scales. We took advantage of detailed data previously collected on wintering waterfowl at Edwin B. Forsythe National Wildlife Refuge and surrounding marsh, New Jersey, and created a well-constrained local model of carrying capacity. We used 1,223 core samples collected between 2006 and 2015 to estimate food availability. We used species-specific 24-h time–activity data collected between 2011 and 2013 to estimate daily energy expenditure, morphometrically corrected for site- and day-specific thermoregulatory costs. To estimate population-level energy demand, we used standardized monthly ground surveys (2005–2014) to create a migration curve, and proportionally scaled that to fit aerial survey data (2005–2014). Crucially, we also explicitly incorporated estimates of variance in all of these parameters and conducted a sensitivity analysis to diagnose the most important sources of variation in the model. Our results from an outlier-removed, a strict depletion model indicated that at estimated mean levels of supply (923 million kcal) and cumulative demand (3.4 billion kcal), refuge food resources were depleted before November. However, a constant-supply model that represented tidal replenishment of resources indicated that just enough energy was present to sustain peak winter populations. Variation in model output appeared to be driven primarily by uncertainty in population abundance during peak periods of use, emphasizing a new management focus on studying migration chronologies of waterfowl. This model allows for relative assessment of biases and uncertainties in carrying-capacity modeling, and serves as a framework identifying critical science needs to improve local and regional waterfowl management planning.

* Corresponding author: kringelman@agcenter.lsu.edu

Introduction

Management of North American waterfowl is often touted as a premier example of a successful wildlife conservation program (Williams and Castelli 2012). The North American Waterfowl Management Plan (and its revisions) provides an overarching framework for waterfowl conservation, establishes regional population goals, and tasks interagency Migratory Bird Joint Ventures (partnerships established under the North American Waterfowl Management Plan to help conserve the continent's waterfowl populations and habitats; hereafter, JVs) with meeting these goals (U.S. Fish and Wildlife Service 2012). During the nonbreeding period, these policy frameworks typically assume that food is the limiting factor for populations. Therefore, wintering JVs focus on meeting population objectives by providing enough foraging habitat. To estimate how many ducks the habitat can support, some JVs have built bioenergetic models that incorporate population goals, waterfowl energetic demand, and foraging values of different habitat types (e.g., Gulf Coast Joint Venture [Esslinger and Wilson 2001] and Central Valley Joint Venture 2006).

Within the boundaries of any particular JV, State and National Wildlife Refuges ("refuges") provide a substantial amount of wintering habitat and can support regionally and continentally significant proportions of waterfowl populations. Managers of large public refuges are interested in the same questions that are being addressed at regional scales by JVs: 1) how many ducks are using the habitat and 2) how many ducks can the refuge theoretically support? As a step-down approach, these questions may actually be easier to answer at local (refuge) scales, where population abundances and habitat areas can be estimated more precisely. Building robust, refuge-specific carrying-capacity models helps inform management of those areas, which can comprise a large percentage of JV habitat and population goals. Additionally, well-constrained local models can identify sources of bias and uncertainty to help improve stepped-up regional models of carrying capacity.

One refuge ideally suited for building such a model is the Edwin B. Forsythe National Wildlife Refuge (hereafter, "Forsythe"), located in coastal New Jersey, which provides a core wintering site for Atlantic Flyway waterfowl populations. Greater than 20,000 ha in size, most of the Forsythe refuge is comprised of salt marsh with several freshwater impoundments created to provide moist-soil seeds for wintering waterfowl. The most abundant dabbling duck wintering at Forsythe is the American black duck *Anas rubripes*, a species of conservation concern since their population began a steady decline in the 1950s (Rusch et al. 1989, Conroy et al. 2002, Sauer et al. 2014). There has been a great deal of waterfowl research conducted at Forsythe over the past decade, much of which has sought to address information gaps in black duck ecology. These include detailed behavioral studies of waterfowl movements (Ringelman et al. 2015b), energy expenditure (Cramer 2009, Jones 2012), and food availability (Cramer et al. 2012, Ringelman et al. 2015a, Goldstein et al. 2016, Fino et al. 2017). In addition, several different population surveys are available for Forsythe, including the annual Mid-winter Waterfowl Survey (MWS), standardized ground surveys from 2005 to 2014, and aerial transect surveys for black ducks from 2011 to 2014.

In short, this accumulation of refuge-specific data afforded us a unique opportunity to build a well-parameterized waterfowl carrying-capacity model for Forsythe. We explicitly addressed various sources of sampling error stemming from model assumptions, estimates of food supply, and estimates of energetic demand. We explicitly modeled the variation in parameter estimates and used a sensitivity analysis to diagnose how each contributed to overall model uncertainty to help waterfowl biologists identify the most important avenues for future research and planning at both local and regional scales.

Study site

Forsythe spans 77 km of the Atlantic Coast of southern New Jersey (39°27′N, 74°24′W). For the purposes of this study, we considered the study area to be portions of
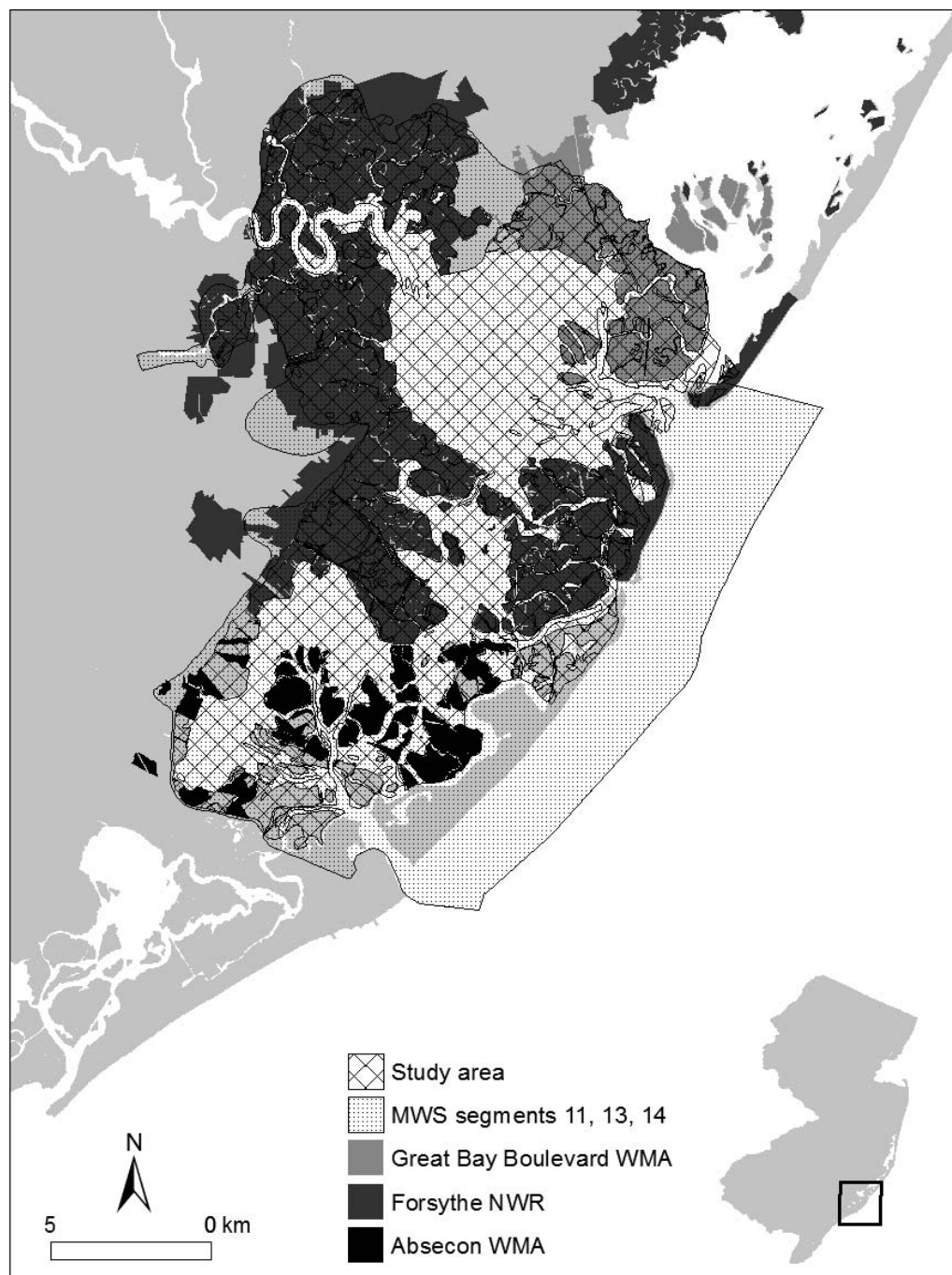
Figure 1. Location of waterfowl carrying-capacity research in coastal New Jersey, 2004–2015.

MWS segments 11, 13, and 14, which span the lower third of Forsythe as well as Absecon and Great Bay Boulevard Wildlife Management Areas (22,091 ha; Figure 1). For simplicity, in this manuscript we refer to our study area as "Forsythe," although the area boundaries extend beyond the refuge. This study area exactly corresponded to that used by Jones (2012) and Goldstein et al. (2016) to estimate black duck energy demand and supply, respectively. Within Forsythe, there was a range of foraging habitats available to black ducks, including managed freshwater marshes, forested wetlands, salt marsh that is regularly (low marsh) or irregularly (high marsh) flooded by the tide, mudflats, and shallow subtidal habitats.

Methods

To build a waterfowl carrying-capacity model, at a minimum, researchers must estimate both the energy supply on the landscape available to waterfowl and energetic demand of the birds. To estimate supply, this requires quantifying: 1) the amount of each type of

Table 1. Energy values (kcal/ha) derived from benthic cores taken between 2010 and 2014 from specific habitat types at Edwin B. Forsythe National Wildlife Refuge and surrounding marsh, New Jersey. General salt marsh values are the simple averages of high marsh, low marsh, mudflat, and subtidal habitats. We assumed that sand and deep open water had no foraging value for dabbling ducks.

Habitat type	n	Seed energy/ha	Animal energy/ha	Total energy/ha	Hectares
High marsh					11,329
All data	347	25,684 ± 4,532	155,512 ± 66,429	181,196 ± 66,530	
Outliers removed	323	25,872 ± 4,808	18,631 ± 2,457	44,504 ± 5,358	
Low marsh					181
All data	202	26,188 ± 6,531	146,887 ± 34,588	173,074 ± 35,206	
Outliers removed	186	25,933 ± 6,995	30,355 ± 4,700	56,287 ± 8,269	
Mudflat					13
All data	207	7,920 ± 1,194	541,664 ± 264,318	549,584 ± 264,256	
Outliers removed	191	7,985 ± 1,259	30,346 ± 4,264	38,331 ± 4,351	
Subtidal					9,889
All data	196	19,853 ± 7,440	1,057,605 ± 639,720	1,077,457 ± 640,538	
Outliers removed	175	14,884 ± 5,322	15,674 ± 1,812	30,558 ± 5,545	
Freshwater					360
All data	233	241,692 ± 36,359	8,880 ± 2,142	250,572 ± 36,376	
Outliers removed	230	244,489 ± 36,798	5,787 ± 668	250,276 ± 36,831	
Forested wetlands					87
All data	38	152,707 ± 46,978	6,289 ± 1,898	158,995 ± 46,845	
Outliers removed	38	152,707 ± 469,78	6,289 ± 1,898	158,995 ± 46,845	
General salt marsh					55
All data	0	19,911 ± 4,924	475,417 ± 251,264	495,328 ± 251,633	
Outliers removed	0	18,669 ± 4,596	23,752 ± 3,308	42,420 ± 5,881	
Sand	—	—	—	—	94
Deep open water	—	—	—	—	83

habitat available and 2) energy value of those habitat types. Estimating waterfowl energetic demand requires quantifying: 1) the daily energy requirement of each species and 2) how many individuals of each species are present each day during the time period in question. We address each of these points in turn. We performed all analyses in R (R Core Team 2013) and present means ± standard error (SE) unless otherwise noted.

Quantifying energy supply

We used the U.S. Fish and Wildlife Service National Wetlands Inventory layer in ArcMap (Esri 2012) to identify habitats available to foraging dabbling ducks *Anas, Mareca, and Spatula* spp. The Black Duck JV scientists slightly modified this layer to split (where tractable) unclassified salt marsh into high marsh, low marsh, and mudflat. We also included freshwater impoundments, subtidal habitats shallower than 1 m (identified by the National Oceanic and Atmospheric Administration bathymetry data), and forested wetlands in our analysis (see Ringelman et al. 2015b for additional information). We assumed that sand and open water consistently deeper than 1 m had no foraging value for dabbling ducks. To quantify the amount of each habitat type present, we clipped the National Wetlands Inventory layer with the outside perimeter used by Jones (2012) and calculated the total number of hectares of each habitat type (Table 1).

We used data from Cramer et al. (2012), Goldstein et al. (2016), Fino et al. (2017), and newer unpublished data to evaluate foraging resources in high marsh, low marsh, mudflats, subtidal habitats, forested wetlands, and

freshwater impoundments within our study area. We used an average value for salt marsh habitats to estimate energy availability in unclassified salt marsh. These data sets excluded foods not known to be eaten by black ducks, as well as ribbed mussels *Geukensia demissa* and killifish *Fundulus* spp. deemed too large (>21.4 mm) to be consumed by black ducks (Cramer et al. 2012). Despite this, outlier data points clearly remained in the core sampling data. These remaining outliers could be the result of naturally variable densities of food items or the result of inadequate removal of biological outliers. Therefore, we took a conservative approach and also used the statistical removal of food items following Ringelman et al. (2015a), hereafter referred to as outlier-removed data. Rather than statistically removing outliers from each habitat in each study, we again took a conservative approach and pooled all data and then removed outliers from each habitat type (n = 80 outliers removed in total; Table 1). For most of our analyses, we used the outlier-removed data to estimate available energy (Tables S1, S2), but present outlier-included data for comparison. Ringelman et al. (2015a) counterintuitively found no evidence for food depletion in any habitat at Forsythe; however, because potential replenishment or redistribution of coastal marsh foods remains an active research question, we developed both constant-supply and monthly depletion models.

Quantifying demand

Daily energy expenditure. Existing carrying-capacity models use rough approximations for daily energy

Table 2. Population estimates for American black ducks *Anas rubripes* at Edwin B. Forsythe National Wildlife Refuge and surrounding marsh, New Jersey, derived from 2011–2013 Mid-winter Survey (MWS) data (segments 11, 13, and 14) and aerial transect survey data.

Year	Population size (N_{circ})		Mean per transect	SE	95% CI
	MWS	Transect surveys			
2011	17,380	28,430.37	261.78	1,411.11	25,664.58–31,196.15
2012	29,250	31,300.35	288.03	1,763.95	27,843.02–34,757.69
2013	31,220	38,033.86	350.20	2,322.55	33,481.66–42,586.06

expenditure (DEE). Some use single-species estimates of metabolic rate and linearly scale that value to other species on the basis of body size (Gulf Coast Joint Venture; e.g., Esslinger and Wilson 2001), whereas others use allometric equations (Miller and Eadie 2006) and loosely estimate the average body size across all species to obtain a single value (Central Valley Joint Venture 2006). For our analysis, we used DEE values from Jones (2012), who used 24-h behavioral observations, species-specific allometric estimates of resting metabolic rate (Miller and Eadie 2006), and metabolic multipliers (Wooley and Owen 1978) to estimate baseline DEE. Following McKinney and McWilliams (2005) and Livolsi (2015), we used morphometric measurements and site- and day-specific weather data to correct these baseline values to account for the cost of thermoregulation. Below is the complete DEE equation we used from Livolsi (2015), where a_i is the activity-specific multiplier of resting metabolic rate, CT is the cost of thermoregulation (kcal/bird h^{-1}), and T_i is the amount of time engaged in a given activity:

$$\text{DEE} = \sum_{h=1}^{n} \sum_{i=1}^{n} \left(\left[\left\{ \left(457 \times \text{Mass}^{0.77} \right) \times a_i \right\} + \text{CT} \right] \times T_i \right). \tag{1}$$

Population estimates. The MWS has been performed annually in the United States since the 1930s to track population trends for wintering ducks, but has been criticized for lack of sampling design and estimates of variance (Eggeman and Johnson 1989; Reinecke et al. 1992). However, the MWS is well suited to the Atlantic Coast, where black ducks are widely distributed and easily counted from the air (Conroy et al. 1988). Indeed, Conroy et al. (1988) used 4 y of Atlantic Flyway aerial transect data to confirm that the MWS fell within the 95% confidence interval (CI) of their transect estimate for all 4 y. To verify that the MWS was appropriate at our smaller scale, we established nine aerial transects (1.3–22.2 km long) spaced 2 km apart over our study area. Transects were flown at an elevation of 45 m, a speed of 90 knots, and observers surveyed a 152-m-wide area on each side of the plane. The same crew and aircraft that conducted the MWS flew transects three times per year during early January 2011–2013. We calculated the mean number of black ducks per transect for each year, and estimated the population size using a combined-ratio estimator (Cochran 1977; Conroy et al. 1988). We compared these estimates to MWS totals from segments

11, 13, and 14 in each year. Midwinter survey estimates for black ducks fell within the 95% CI of the black duck transect survey in all but 1 y, indicating that the MWS is a reasonable index of black duck abundance (Table 2). In our analyses, we used MWS estimates because the transect survey only counted black ducks (not other species) and also to take advantage of the longer-term MWS data set to build a more robust migration chronology.

Migration chronology. A major challenge in quantifying energy demand is estimating how many birds are using a refuge during each day of the wintering season. Here, we used standardized diurnal ground-count surveys (2005–2014) conducted at Forsythe to estimate waterfowl migration chronologies. Three to four times per month throughout the year, trained observers counted waterfowl along a 12.9-km unpaved road that affords viewing access to both salt marsh and freshwater impoundments. We used the average monthly count from this survey to construct an approximate migration index for waterfowl during the nonbreeding season (August–March; e.g., black ducks; Figure 2). Because ground observers can only see a portion of the ducks present on the refuge, we then converted raw ground counts to proportions of peak abundance. We used the January population estimates from the MWS as an anchor point, and scaled our ground-count migration chronology to a population-level chronology using proportions (Figure 2, Table S3).

Carrying-capacity modeling

Commensurate with our migration chronology, we modeled depletion of resources on a monthly timescale with the following equations (specific to habitats and species):

$$\text{Supply} = \text{kcal}_{\text{habitat}} \times \text{ha}_{\text{habitat}} - \text{monthly demand.} \tag{2}$$

$$\text{Monthly demand} = \text{DEE}_{\text{species}}$$
$$\times \text{monthly midpoint population}_{\text{species}} \times {}^{\text{days}}/_{\text{month}}. \tag{3}$$

To estimate variance in supply and demand, we ran the above equations using values of the mean ± 1 SE for $\text{kcal}_{\text{habitat}}$, $\text{DEE}_{\text{species}}$, and monthly midpoint population$_{\text{species}}$. We also created a model with no depletion, where supply was held constant. Our model assumed omniscient foragers, no interference competition, complete utilization of the resources, and no other sources of depletion.
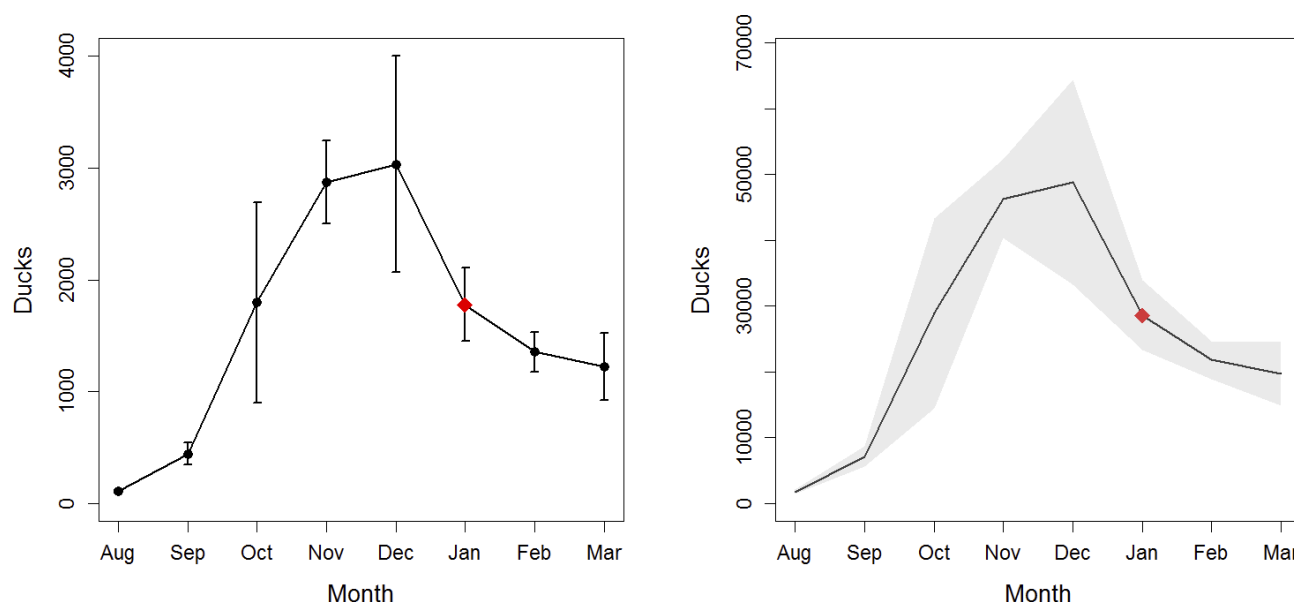
Figure 2. Average ± standard error monthly counts of American black ducks *Anas rubripes* from standardized ground surveys (2005–2014) at Edwin B. Forsythe National Wildlife Refuge, New Jersey (left panel), scaled to match January population estimates from the Mid-winter Waterfowl Survey (2011–2013; right panel).

Sensitivity analysis

To determine the extent to which uncertainty in each parameter contributes to the model outcome (time until resource depletion), we conducted a sensitivity analysis. We randomly drew parameters for species-specific DEE, species-specific abundance in each month, and habitat-specific energy totals. We drew parameters from a normal distribution with empirically derived mean and variance, but we discarded parameter draws outside ±1 SE to be comparable with our bounding conditions in our other analyses. We calculated the total depletion over the wintering period following the equations above, and ran 100,000 simulations. We then used linear regression to model total depletion as a function of every input variable, and used standardized regression coefficients to evaluate the strength of each in determining the response variable (Miller et al. 2014).

Results

Energy supply

Our study area was 22,091 ha, primarily comprised of high marsh (51%) and subtidal habitats shallower than 1 m (45%; Table 1). Freshwater habitats rich with moist-soil seeds had a high energy value (~250,000 kcal/ha), but comprised only 1.6% of the habitats at Forsythe (Table 1). Animal food outliers in the data resulted in estimates of food availability that were one to two orders of magnitude greater in saline habitats (Table 1). After removing outliers, the total energy potentially available to foraging waterfowl was 923 ± 135 million kcal, most of which was derived from high marsh (55%). Managed freshwater impoundments comprised less than 10% of the available energy for wintering waterfowl. When the

80 core-sampling outliers were included, landscape-level estimates of food availability increased by more than an order of magnitude to 12.88 ± 7.12 billion kcal.

Energy demand

Black ducks were the most abundant waterfowl that we observed during ground surveys, followed by mallard *Anas platyrhynchos*, northern pintail *Anas acuta*, and green-winged teal *Anas crecca*. We observed American wigeon *Mareca americana*, gadwall *Mareca strepera*, and northern shoveler *Spatula clypeata* in low numbers throughout the nonbreeding season. Black duck abundance peaked in December (Figure 3) as birds migrated through to points farther south for the winter. As expected, northern pintail and green-winged teal migrated through Forsythe earlier (in October) than mallards (in November), and few teal remained at Forsythe for the duration of the winter (Figure 3).

We used a DEE of 440.49 ± 4.46 kcal/bird d^{-1} for American black ducks, 395.88 ± 13.21 for mallards, 353.49 ± 16.07 for northern pintail, 176.61 ± 17.21 for green-winged teal, and 221.36 ± 17.78 for northern shoveler. We observed too few American wigeon and gadwall at Forsythe to compute DEE values, so we used values estimated by Livolsi (2015) from ducks observed in Delaware for these species (272.59 ± 40.42 for American wigeon and 232.99 ± 18.96 for gadwall). After scaling migration chronologies up to estimate populations and daily energetic demand, black ducks comprised the majority of energetic demand at Forsythe (Figure 3).

Carrying capacity

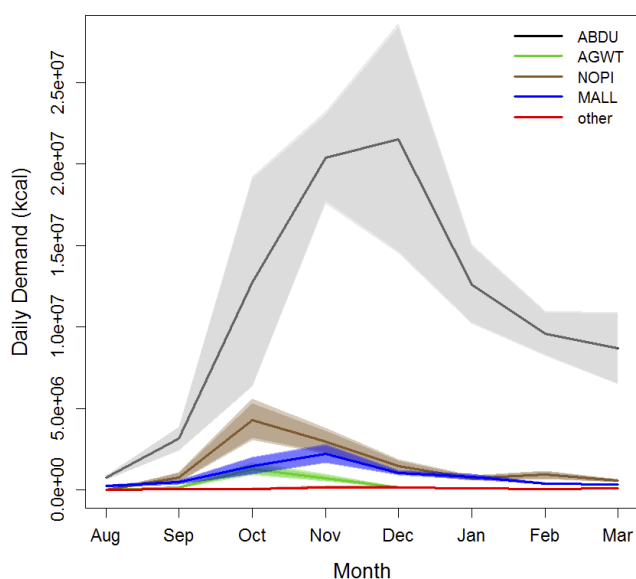We summed daily energy expenditure for all species for each month and modeled food energy depletion over

Figure 3. Daily energy demand (kcal) for populations of dabbling ducks wintering at Edwin B. Forsythe National Wildlife Refuge, New Jersey. We derived the model from data collected 2004–2015. Interior shading represents 1 standard error (SE) in population estimates. The lighter shading represents 1 SE in species-specific estimates of daily energy expenditure. Species codes refer to American black ducks *Anas rubripes* (ABDU), green-winged teal *Anas crecca* (AGWT), northern pintail *Anas acuta* (NOPI), and mallard *Anas platyrhynchos* (MALL). The "other" line represents summed demand from gadwall *Mareca strepera*, American wigeon *Mareca americana*, and northern shoveler *Spatula clypeata*.

the nonbreeding season. For comparison, we also modeled resources that were not depleted (sensu Ringelman et al. 2015a; Figure 4). In the depletion model, at average values for food abundance and energetic demand, the model indicated that refuge food resources were fully depleted by late October (Figure 4). Even at high (+1 SE) estimates of food supply and low estimates (−1 SE) of demand, resources were fully depleted by the middle of November (Figure 4). The nondepletion model could represent potential redistribution of resources in a tidal system; here, overlapping estimates of variance in supply and demand suggest that Forsythe is close to carrying capacity during peak periods of use (Figure 4). Finally, we also ran the depletion model on the basis of the full set of core samples, including outliers (Figure 5). This model showed that between 1.4 and 17.5 billion kcal remained on the landscape at the end of the nonbreeding season.

Sensitivity analysis

At the coarsest scale, we modeled total energy depletion as a function of species-specific DEEs, total populations over the wintering season, and total food availability. This analysis confirmed initial results (Figure 4): food depletion at Forsythe was driven primarily by waterfowl abundance ($\beta = -0.962$), as opposed to food availability ($\beta = 0.248$) or species-specific DEEs (all $\beta <$
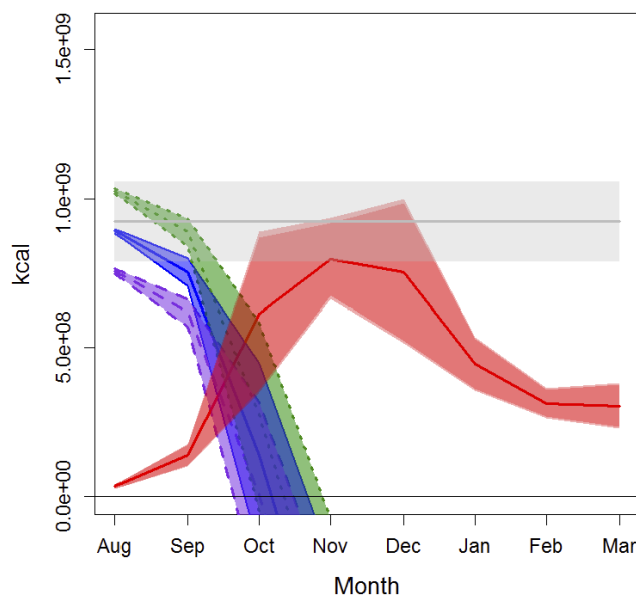

Figure 4. Waterfowl carrying-capacity model of the Edwin B. Forsythe National Wildlife Refuge and surrounding marsh, New Jersey. We derived the model from data collected 2004–2015. Tick marks are at monthly midpoints. The red line shows mean monthly demand; inside shading indicates ±1 standard error (SE) in populations, outside shading indicates ±1 SE in daily energy expenditure (DEE). Food resources are estimated using core sampling data with outliers removed, and are either not depleted (gray line ±1 SE) or are depleted (colored lines). Green, blue, and purple lines show depletion from high, average, and low food supply; bands represent maximum (+1 SE in DEE and populations) and minimum (−1 SE in DEE and populations) demand.

$|-0.083|$). Our fully parsed model showed that waterfowl abundance during periods of peak use (October–December) was more sensitive than measures of food abundance; species-specific DEEs did not have a large influence on energy depletion (Table 3).

Discussion

Carrying-capacity models are ubiquitous tools for managing nonbreeding waterfowl, and used by JVs to prioritize regional habitat delivery goals. Of necessity, such large-scale models are typically built using simplified or approximate parameter estimates for both supply (habitat quantity and quality) and demand (populations, migration chronologies, and DEE estimates). Because of the inherent error associated with these approximations, existing models are unable to explicitly incorporate statistical error in parameter estimates; thus, model results (and downstream management actions) are based only on mean values. It is well known that these regional models are plagued by uncertainty, but we lack the biological information at the appropriate scale to satisfactorily diagnose sources of error. Simply put, we are unable to estimate how much we do not know.
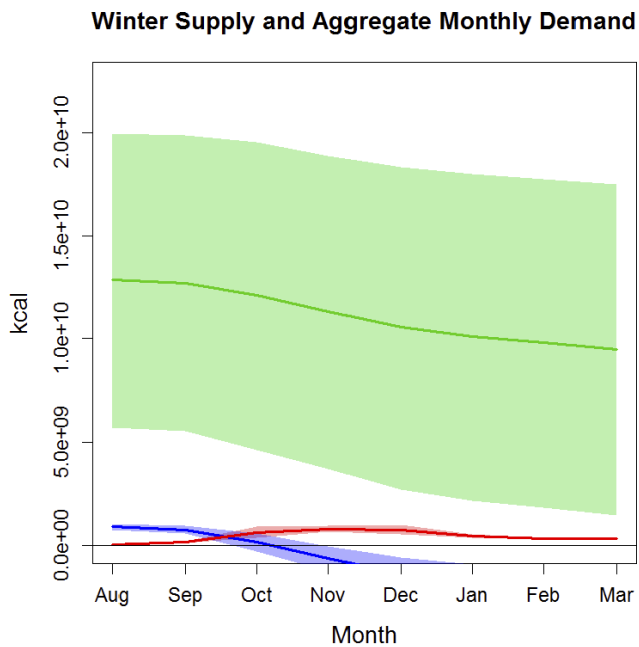
Winter Supply and Aggregate Monthly Demand

Figure 5. Waterfowl carrying-capacity depletion model of the Edwin B. Forsythe National Wildlife Refuge and surrounding marsh, New Jersey. We derived the model from data collected 2004–2015. Tick marks are at monthly midpoints. The red line shows mean monthly demand; shading indicates minimum and maximum demand based on variation in population abundance and daily energy expenditure (DEE). The green supply curve shows estimated food supply when outliers are left in the core sampling data, and the blue curve shows supply when outliers are removed. Shading on supply curves represents maximum (+1 SE in DEE and populations) and minimum (−1 SE in DEE and populations) demand.

Table 3. Standardized coefficients from a linear regression in a carrying-capacity sensitivity analysis for Edwin B. Forsythe National Wildlife Refuge and surrounding marsh, New Jersey, for which we modeled total energy depletion as a function of listed parameters. We derived the model from data collected 2004–2015.

Parameter	Standardized regression coefficient (β)
Daily energy expenditure	
American black duck	−0.0822
Green-winged teal	−0.0228
American wigeon	−0.0019
Gadwall	−0.0029
Mallard	−0.0212
Northern pintail	−0.0480
Northern shoveler	−0.0015
Total population	
August	−0.0143
September	−0.0677
October	−0.5962
November	−0.2462
December	−0.6358
January	−0.2161
February	−0.1093
March	−0.1976
Habitat Energy Value	
Forested wetlands	0.0122
Freshwater marsh	0.0396
High marsh	0.1813
Low marsh	0.0044
Mudflat	0.0005
Subtidal	0.1641
General salt marsh	0.0007

Our goal was to constrain and explicitly model sources of uncertainty by building a carrying-capacity model with supply-and-demand data of unprecedented resolution, and provide rigorous estimates of carrying capacity for an important wintering area in the Atlantic Flyway. On the supply side, we used the best available refuge-specific geographic information system layers to estimate the amount of each habitat type, and estimated food density using more than 1,200 core samples. Ringelman et al. (2015a) recommended removing core sample outliers that lack biological outlier removal criteria, especially those with large animal foods from the data. In our case, removal of outliers likely resulted in conservative estimates of black duck food supply, but also reduced variance, which allowed more precision and predictive ability in model results. Certainly, the identification and treatment of outliers in core sampling data are of paramount importance in estimating landscape-level energy availability, but continue to receive little attention from waterfowl biologists and managers.

On the demand side of the equation, we used species-specific 24-h time–activity budgets corrected for the cost of thermoregulation to estimate DEE. This represents a substantial improvement over existing models that use either a single value for all species (Central Valley Joint Venture 2006) or linearly scaled estimates based on

mallards (e.g., Esslinger and Wilson 2001). Our sensitivity analysis indicated that estimates of DEE were not important determinants of carrying capacity at Forsythe. However, it is important to note that we only explored the parameter space associated with measurement error in DEE (which was well constrained). Additionally, there are lingering concerns regarding the validity of metabolic multipliers (Miller et al. 2014), and further refinements to these are in progress (Williams, unpublished data).

We used ground counts to estimate migration chronologies and then scaled that to population estimates from the MWS. This represents an advancement over linear migration chronologies (Central Valley Joint Venture 2006), and may be a broadly useful method if obtaining frequent population-level estimates (e.g., from aerial transects; Esslinger and Wilson 2001) is cost prohibitive. We conducted our counts in sanctuary habitat, and we had no way to estimate if and to what extent individual sampling counts were influenced by hunting in surrounding marshes. However, we believe that by averaging weekly ground counts by month over 9 y, our chronology is robust to these perturbations. Model outcomes were the most sensitive to waterfowl abundance during peak periods; refining these estimates should be a high priority for waterfowl managers. Indeed, as waterfowl distributions and migration chro-

nologies continue to shift with changes in landscape use and climate (Ringelman et al., in press), tracking the dynamics of waterfowl abundance will become increasingly critical. This is especially true in areas where waterfowl habitat availability depends on well-timed flooding of moist-soil and agricultural fields.

At first glance, our depletion model of carrying capacity shows a worrying scenario for waterfowl at Forsythe, with available energy being completely consumed sometime between October and the middle of November. However, on the basis of observed duck use at Forsythe, this demonstrably must not be true. This suggests that either 1) strict depletion models are inappropriate for tidal systems or 2) the outliers-included data set is a more reasonable approximation of the food available to nonbreeding waterfowl. The best available habitat data from East Coast salt marshes support the idea that depletion does not occur in these habitats (Cramer et al. 2012, Goldstein et al. 2016, Ringelman et al. 2015a), and indeed, our model of peak energetic demand overlaps estimates of (constant) supply as one might expect in a nondepletion scenario. In addition, we acknowledge that patchily distributed, large, high-calorie animal foods ("outliers") may be important in sustaining waterfowl populations at Forsythe, but means and variance are poorly estimated by the expansion factors associated with core sampling methods.

Several factors influencing supply and depletion were not included in this model. For example, black ducks are known to eat snails on marsh grass and killifish in the water column, which are poorly sampled with coring; therefore, our estimates of food supply were likely biased low. We did not model uncertainty in the energy content of waterfowl foods, which could increase variation in energy supply by at least 10% and likely closer to 30–40% (Livolsi et al. 2015). We did not account for niche differentiation in habitat use, nor species-specific dietary preferences, but focused on habitat and food types selected by black ducks (Cramer et al. 2012); this probably had a minimal influence on the outcome of the model given that black ducks comprise the majority of energetic demand at Forsythe. We also did not model depletion through degradation or consumption by nontarget species such as shorebirds or include foraging effectiveness or thresholds (Central Valley Joint Venture 2006; Miller et al. 2014; Hagy and Kaminski 2015). Given substantial variation in observed foraging thresholds (10–459 kg/ha; Hagy and Kaminski 2015), the fact that these thresholds have never been studied in coastal systems and most recent evidence shows no depletion in our system, we were reluctant to include these in our model (Ringelman et al. 2015a). Nevertheless, as a post hoc analysis, we were interested in how food availability in our salt marsh system compared with foraging thresholds observed in inland wetlands. We used an average true metabolizable energy content for waterfowl foods of 1.55 kcal/g (Livolsi et al. 2015) to back-calculate an average kilogram per hectare over our entire study site (outliers-removed data). Our high (mean + 1 SE) estimate of food availability roughly equates to 31 kg/ha, which is below the observed foraging threshold in many other

systems (Naylor 2002 [30–164 kg/ha]; Greer et al. 2009 [49 kg/ha]; Hagy and Kaminski 2012 [260 kg/ha]). Simply stated, the threshold at which ducks cannot (or will not) forage (profitably) could appear as a horizontal line anywhere on Figure 4. Clearly, landscape-level resource dynamics that emerge from the foraging ecology of waterfowl deserve closer scrutiny in coastal systems.

The most useful aspect of our modeling exercise was in explicitly incorporating uncertainty in parameter estimates, which has been largely ignored in carrying-capacity modeling. We believe there is value in understanding this variation and its underlying sources for several reasons: 1) it helps managers understand and plan for a range of scenarios; 2) it identifies critical knowledge gaps to help direct funding agencies and applied researchers; and 3) transparency about model uncertainty builds trust with regulatory agencies and the general public. For example, at Forsythe our model was clearly more sensitive to energetic demand than energetic supply. Although we acknowledge the continuing problem of dealing with outliers in core sampling data, if managers believe the results of our model, which used well-constrained estimates of food availability based on outlier-removed data, focus should turn to understanding migration chronologies and periods of peak use. Of all species considered here, refining estimates of peak black duck populations will have the greatest impact in reducing uncertainty in bioenergetic models at Forsythe. Managers should continue pairing frequent, inexpensive ground surveys with occasional aerial surveys to measure waterfowl abundance.

Quantitative biologists from JVs whose task it is to step down continental population objectives to regional levels may view our results with a sense of dismay: if the uncertainty surrounding outliers and migration chronologies is so great even in a well-known, well-constrained system, what hope is there of developing reliable regional models? We believe the value of carrying-capacity models is best viewed in relative terms. One strategy used by wintering JVs to increase carrying capacity is to provide more hectares of the habitats that on average (or range) provide more energy per hectare, and the currency used in judging the value of these investments is often "duck-use days." Our model suggests that we are far from accurately estimating duck-use days, but the relative value of habitat management or restoration actions as they affect energy supply may still be evaluated in this currency. Meanwhile, other potential metrics such as the number of ducks present during a given interval, body condition, overwinter survival, or hunter days afield may provide alternative or complementary measures of the success of waterfowl management actions, and merit further consideration.

Supplemental Material

Table S1. Habitat-specific core sampling data collected from 2010 to 2014 at Edwin B. Forsythe National Wildlife Refuge, New Jersey.

Acknowledgments

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