



Note

Carrying Capacity of Wintering American Black Ducks in Forested Wetlands

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ABSTRACT Wintering populations of American black ducks (*Anas rubripes*) have declined throughout their range since the 1950s. Conservation for wintering black ducks is based largely on bioenergetic models of carrying capacity, and managers seek to provide wetlands with sufficient food energy to support target populations. Although the significance of salt marsh to wintering black ducks along the Atlantic Coast is well documented, forested wetlands are also used by wintering black ducks, and yet their foraging value and energetic potential is unknown. Therefore, quantifying the energetic value of forested wetlands is important for accurately estimating the carrying capacity of black ducks. We collected soil core samples from forested wetlands on Prime Hook National Wildlife Refuge, Milton, Delaware in 2014 ($n = 46$) and Edwin B. Forsythe National Wildlife Refuge, Galloway, New Jersey, USA in 2015 ($n = 41$) to estimate food biomass and quantify the energetic capacity of forested wetlands representative of the mid-Atlantic region. We estimated the mean energetic value of forested wetlands as $84,667 \pm 21,822$ kcal/ha. Considering all forested wetlands that are potentially available to black ducks along the mid-Atlantic Coast, we estimated that forested wetlands within a 24.1-km distance from the coast provide between 103,696,524–192,678,224 duck-use days supporting 489,135–908,860 black ducks over the 212 days of winter. Forested wetlands may be an important foraging resource for wintering black ducks, and our estimates of energetic value will help to refine bioenergetic models for black ducks in the Atlantic Flyway. © 2017 The Wildlife Society.

KEY WORDS *Anas rubripes*, Atlantic Flyway, bioenergetics, biomass, core sampling, true metabolizable energy, waterfowl.

Wintering populations of American black ducks (*Anas rubripes*) have declined by approximately 350,000 individuals during the last 60 years (U.S. Fish and Wildlife Service [USFWS] 2015). There are several explanations for this decline, including loss in the quantity and quality of breeding habitat, overharvest, interactions (e.g., competition, hybridization) with mallards (*Anas platyrhynchos*) during breeding and wintering periods, and loss in the quantity and quality of wintering habitats (Anderson et al. 1987, Conroy et al. 2002). The historical loss of coastal wetlands in the eastern United States between 1998 and 2004 is estimated to be

146,092 ha (Stedman and Dahl 2008) and approximately 6% in the mid-Atlantic region from approximately 1955–1979 (Tiner 1987). The continued degradation of coastal wetlands (Tiner 1987; Dahl 2000, 2006; Stedman and Dahl 2008; Dahl and Stedman 2013) may limit the ability of the eastern survey area to support wintering black duck populations at conservation goals (i.e., 628,000 individuals; Morton et al. 1989, North American Waterfowl Management Plan [NAWMP] 2014).

The Black Duck and Atlantic Coast Joint Ventures use a bioenergetics modeling approach to determine how much habitat is needed to achieve black duck population goals (NAWMP 2014). To inform regional habitat acquisition and management, the Joint Ventures prioritized energetic carrying capacity research throughout the wintering range of black duck (Black Duck Joint Venture Management Board

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2008). Determining the carrying capacity of any landscape requires knowledge of the types and amounts of different foods available (Miller and Newton 1999, Ballard et al. 2004).

Estuarine marsh systems and salt marsh are the most commonly used wetlands by wintering black ducks along the mid-Atlantic (Longcore and Gibbs 1988, Morton et al. 1989, Ringelman et al. 2015b) and previous studies have quantified food availability for salt marsh and freshwater impoundments along the Atlantic Coast (Plattner et al. 2010, Cramer et al. 2012, Livolsi 2015, Ringelman et al. 2015a). However, recent telemetry research has reported that black ducks also use forested wetlands adjacent to coastal marshes in the mid-Atlantic. Ringelman et al. (2015b) reported that 9.2% ($n = 1,609$) of all black duck locations recorded occurred in forested wetlands, and ducks increased use of forested wetlands during cold weather. Although migrating black ducks have been previously observed in the inland forested wetlands of the Mississippi Flyway (Morton et al. 1989, Byrd 1991, Chipley 1995, Davis and Afton 2010), their presence in forested wetlands in the Atlantic Flyway has yet to be thoroughly investigated. Forested wetlands, which have not been previously considered when studying wintering habitat, may provide thermal refuges and cover from severe weather but also contain food resources that provide energetic and survival advantages for black ducks.

To provide a more accurate estimate of energetic capacity and priority conservation areas, managers need estimates of the energy available in forested wetlands (Reinecke et al. 1989, Petrie et al. 2011, Williams et al. 2014). Our objective was to estimate food resource availability and energetic carrying capacity of forested wetlands for wintering black ducks in Delaware and southern New Jersey, USA. Specifically, we determined the abundance of black duck foods (seeds and invertebrates) found in the soil of forested wetlands, and used these estimates to extrapolate to other forested wetlands throughout the Atlantic Flyway. Determining the energetic value of forested wetlands will improve the accuracy of current estimates of carrying capacity for black ducks (Coluccy et al. 2013) and improve habitat planning and delivery along the Atlantic Coast.

STUDY AREA

We conducted our research at Prime Hook National Wildlife Refuge (PHNWR) in Milton, Delaware at 38.8478 N, 75.2669 W and Edwin B. Forsythe National Wildlife Refuge (EBFNWR), which spans 77 km of the Atlantic Coast of southern New Jersey, USA centered on 39.6963 N, 74.1827 W between 2014–2015. Both refuges contain salt marsh, freshwater marsh, ponds and impoundments, wooded swamps, upland grasslands, and forests. Forested wetlands were identified using the USFWS classification of wetlands and deepwater habitats of the United States (Cowardin et al. 1979). Forested wetlands on both study areas are dominated by seasonally flooded open to closed forests with a canopy of red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*), green ash (*Fraxinus*

pennsylvanica), and sweetgum (*Liquidambar styraciflua*), with an occasional American holly (*Ilex opaca*), sassafras (*Sassafras albidum*), sweetbay (*Magnolia virginiana*), tulip-tree (*Liriodendron tulipifera*), or willow oak (*Quercus phellos*). They can also contain a variable shrub layer including highbush blueberry (*Vaccinium cyanococcus*), coastal sweet pepperbush (*Clethra alnifolia*), swamp azalea (*Rhododendron viscosum*), swamp doghobble (*Eubotrys racemosa*), and common winterberry (*Ilex verticillata*), and a sparse herbaceous layer transitioning to a graminoid and fern-dominated layer in the sedge swamp community (USFWS 2013, 2014).

METHODS

Sample Collection and Analysis

To estimate food availability in forested wetlands in the mid-Atlantic region, we used a geographic information system (GIS) to generate 50 random points (≥ 10 m apart) in areas classified as forested wetlands within PHNWR and EBFNWR. Forty to 50 points are required to reduce bioenergetics variance in core samples (Ringelman et al. 2015a). Within the time and man-power constraints, we were able to collect 46 soil core samples at PHNWR on 18 April, 25 April, and 2 May 2014, and 41 core soil samples at EBFNWR on 2 December 2014 and 2 April 2015. We made the assumption our sampling was representative of the winter period, but foraging depletion and degradation likely mean that our estimates of food density in forested wetlands are conservative. The core samples were 51 mm in diameter by 120 mm in length. We placed individual core samples in 946-ml plastic bags and transported them to a laboratory for processing. In the laboratory, we refrigerated samples for ≤ 3 days before sieving them with water through 500- μ m (no. 35) and 2-mm (no. 10) screens. We placed sieved material in a 150-ml specimen storage cup, fixed it with 10% formalin buffer solution, and stained it with rose bengal dye for ≥ 7 days to facilitate identification of invertebrates.

Prior to sorting the stained material, we washed samples twice with water and separated the sample based on size and density of its substrates using a 2-mm (no. 10) and 0.251-mm (no. 60) screen. We then separated each core into large material (material too large to pass through the no. 10 sieve) and small material (material too large to pass through the no. 60 sieve). To reduce time in sorting, we used subsampling methods described by Livolsi et al. (2014), where we sorted through 100% of the large material and 10% of the small material to remove seed and invertebrate foods.

We identified seeds to genus or species, and invertebrates to the lowest taxonomic level possible. We dried seeds and invertebrates in an oven at 50–58 °C for 48 hours, and then weighed each sample to the nearest 0.0001 g. We included in our analysis only samples of taxa that we identified as foods used by black ducks wintering in mid-Atlantic marsh habitats (Cramer 2009, Livolsi 2015) because including non-food items in models of carrying capacity may overestimate energy density by as much as 30% (Hagy and Kaminski 2012). We multiplied biomass of foods in the 10% subsample

by 10 to estimate the biomass in the small material portion, and added it to the biomass in the large portion to estimate total biomass for each food item in the soil core (Livolsi et al. 2014). To increase the utility of our estimates for bioenergetics modeling, we summarized energetic resource availability (kcal/ha) by multiplying the biomass of seed and invertebrate items by true metabolizable energy values (TME; kcal/g [dry]) taken from the literature (Table 1). Following these past studies, we used black duck-specific values whenever possible, and averages in instances where multiple published values existed (Livolsi et al. 2015a). When TME values were lacking, we used the values for the closest related taxon (e.g., mallard, blue-winged teal [*Anas discors*]) so that all potential food items were included in the summation of energy estimates (Cramer 2009, Livolsi 2015). We tested the null hypothesis that biomass and energy of animal and seed foods did not differ between EBFNWR and PHNWR. Examination of the data showed the distribution was right skewed. Therefore, we conducted non-parametric Mann-Whitney U tests to assess any possible differences.

Extrapolating Landscape Energy and Estimating Carrying Capacity

We estimated the energy per hectare of forested wetland. To estimate landscape-scale carrying capacity along the Atlantic Coast, we combined 5 classifications of forested wetlands from the National Wetlands Inventory GIS layer including estuarine forested (E2FO), estuarine shrub-scrub (E2SS), forested freshwater wetland (PFO), and freshwater scrub-scrub wetland (PSS). Following recommendations from the Black Duck Joint Venture, we considered habitats within 24.1 km of the coast to be available to black ducks wintering in salt marshes, commensurate with previous studies (Ringelman et al. 2015b).

For wintering waterfowl, carrying capacity is often represented by duck use-days (DUD), or the number of individuals that can be supported on the landscape for a single day based on energy availability and expenditure (Reinecke et al. 1989). We used a daily energy expenditure (DEE) value of 338.92 ± 15.61 kcal/day based on time-energy budgets over the 24-hour period in Delaware

Table 1. Preferred American black duck food items identified in the core samples from Prime Hook National Wildlife Refuge (PHNWR, Delaware, USA; collected 18 Apr, 25 Apr, and 2 May 2014) and Edwin B. Forsythe National Wildlife Refuge (EBFNWR, New Jersey, USA; collected 2 Dec 2014 and 2 Apr 2015) with their respective true metabolizable energy (TME) values (summarized from Cramer 2009, Livolsi 2015).

Food item (seed [S] or invertebrate animal [A]) ^a	TME (kcal/g)	Derivation and source of TME	PHNWR	EBHNWR
<i>Aster</i> spp. (S)	0.55	Sherfy (1999)	*	*
<i>Brassica</i> spp., Mustard (S)	1.31	Value for <i>Lepidium latifolium</i> from Dugger et al. (2007)	*	*
<i>Carex</i> spp., sedge (S)	1.00	\bar{x} of Cyperaceae genera values in Stewart (1962)	*	*
<i>Eleocharis parvula</i> , dwarf hairgrass (S)	0.50	\bar{x} of McGilvrey (1966), Jorde et al. (1983), and Gruenhagen and Fredrickson (1990)	*	
Fabaceae, legumes (S)	1.74	\bar{x} of all seed orders from Muztar et al. (1977), Reinecke et al. (1989), and Petrie et al. (1998)	*	
American holly (S)	1.96	Anderson (1959)		*
<i>Juncus</i> spp., rushes (S)	1.21	Value for <i>Juncus canadensis</i> from Anderson (1959) and Stewart (1962)	*	*
<i>Panicum</i> spp., panic grass (S)	2.75	Value for <i>Panicum dichotomiflorum</i> from Stewart (1962) and Jorde et al. (1983)	*	
<i>Polygonum</i> spp., e.g., smartweed (S)	1.30	\bar{x} of Anderson (1959), Stewart (1962), McGilvrey (1966), Jorde et al. (1983), Gruenhagen and Fredrickson (1990)	*	
<i>Phytolacca Americana</i> , American pokeweed (S)	2.49	\bar{x} of Caryophyllales family values from Livolsi et al. (2015a)		*
<i>Salicornia</i> spp., e.g., glassworts (S)	2.97	Value for <i>Amaranthus</i> spp. from Livolsi et al. (2015a)		*
<i>Schoenoplectus</i> spp., sedges (S)	0.82	\bar{x} from Stewart (1962) and Gruenhagen and Fredrickson (1990)	*	*
<i>Spartina alterniflora</i> , saltmarsh cordgrass (S)	1.39	Coluccy et al. (2015)		*
Diptera, flies (A)	0.27	\bar{x} of Diptera and Hemiptera from Anderson (1959) and Jorde et al. (1983)	*	*
Isopoda, crustaceans (A)	0.08	\bar{x} from Anderson (1959), Stewart (1962), Jorde et al. (1983), and Combs and Fredrickson (1996)		*
<i>Gammarus</i> spp., amphipod crustacean (A)	2.21	\bar{x} of <i>Gammarus</i> spp. from Anderson (1959) and Stewart (1962)	*	*
<i>Uca</i> , fiddler crabs (A)	1.57	Coluccy et al. (2015)		*

^a Some non-preferred food items included *Acer saccharum* (sugar maple), *Anemone* spp., *Arabis canadensis* (sicklepod), Arachnida, *Arctostaphylos uva-ursi* (bearberry), *Bidens comosa* (three-lobed beggartick), *Ceanothus americanus* (New Jersey tea), *Centrosema virginianum* (spurred butterfly pea), *Collembola* (springtails), *Commelina communis* (Asiatic dayflower), *Commelina crispa*, *Cornus paniculata* (American shrub dogwood), *Crataegus* (hawthorn), *Cyclopoida* (crustacean), *Cyperus* spp. (sedges), Diplopoda (millipedes), *Distichlis spicata* (seashore saltgrass), *Dulichium arundinaceum* (three-way sedge), *Echinochloa* spp., Foraminifera, Formicidae, *Hibiscus* spp., *Iva* spp. (marsh elder), *Leersia oryzoides* (rice cutgrass), *Leptochloa fascicularis* (bearded sprangletop), *Linaria vulgaris* (yellow toadflax), *Liquidambar styraciflua* (American sweetgum), *Madia sativa* (Chilean tarweed), *Magnolia grandiflora* (southern magnolia), mite, *Myriophyllum spicatum* (Eurasian watermilfoil), nematode spp., *Nyssa biflora* (swamp tupelo), *Nyssa sylvatica* (black tupelo), Oligochaeta, Ostracod, *Ostrea virginiana* (American hop hornbeam), *Paspalum setaceum* (slender beadgrass), *Passiflora incarnate* (maypop), *Pinus rigida* (pitch pine), *Physalis* spp., *Potamogeton crispus* (curled pondweed), *Rhus glabra* (smooth sumac), *Rhus typhina* (staghorn sumac), *Robinia pseudoacacia* (black locust), *Rubia* spp., *Rubus* spp., Rumex, *Sagittaria latifolia* (broadleaf arrowhead), *Sassafras albidum* (Sassafras tree), *Scleria triglomerata* (whip nutrush), *Scutellaria* spp., *Strophostyles umbellata* (pink fuzzybean), *Smilax glauca* (greenbrier), *Verbesina occidentalis* (yellow crownbeard), *Viburnum dentatum* (southern arrowwood), and *Vitis aestivalis* (grape).

(Livolsi 2015), which account for increased costs of thermoregulation (Livolsi et al. 2015b). We calculated the winter carrying capacity (no. black ducks that can be supported in terms of energy by forested wetlands) using the number of days in the non-breeding season based on black duck migration chronology (1 Sep–31 Mar, 212 days), which was based on presence of black ducks in monthly winter counts at EBFNWR (P. M. Castelli, U.S. Fish and Wildlife Service, unpublished data).

RESULTS

For PHNWR, out of the 42 seed and invertebrate taxa identified, 11 (26%) food items had been previously described as food for black ducks (Table 1). There was 26.18 ± 7.34 kg/ha of food items, of which 25.65 ± 7.36 kg/ha (98%) were seed food items and 0.54 ± 0.50 kg/ha (2%) were invertebrate items (Table 2). We estimated landscape-level energy at $28,512 \pm 7,061$ kcal/ha, of which $28,077 \pm 7,413$ kcal/ha (98%) were seed food items and 435 ± 136 kcal/ha (2%) were invertebrate food items (Table 2).

For EBFNWR, out of the 49 seed and invertebrate taxa identified, 13 (27%) food items had been previously described as food for black ducks (Table 1). There were 94.42 ± 23.43 kg/ha of food items, of which 82.74 ± 23.37 kg/ha (88%) were seed food items and 11.68 ± 2.98 kg/ha (12%) were invertebrate food items (Table 2). We estimated landscape-level energy at $147,670 \pm 43,840$ kcal/ha, of which $141,888 \pm 43,922$ kcal/ha (96%) were seed items and $5,782 \pm 1,747$ kcal/ha (4%) were invertebrate food items. Non-parametric comparison (Mann-Whitney U test) of biomass and energy values between refuges showed EBFNWR had significantly higher invertebrate, seed, and total biomass and energy than PHNWR ($U \geq 1.999$, $P < 0.046$).

Within a 24.1-km distance from the coast, there were 584,988 ha of forested wetland in the mid-Atlantic region (Fig. 1). Although refuge-specific biomass and energy differed, for the sake of landscape-scale extrapolation, we assumed grand average values. Across refuges, there were 57.69 ± 12.16 kg/ha of preferred food items, of which 51.86 ± 11.97 kg/ha were seed food items and 5.83 ± 1.54 kg/ha were invertebrate food items (Table 2). This produced a landscape-level energy estimate of $84,667 \pm 21,822$ kcal/ha resulting in $49,529,178,996 \pm 12,765,608,136$ kcal of energy in mid-Atlantic forested

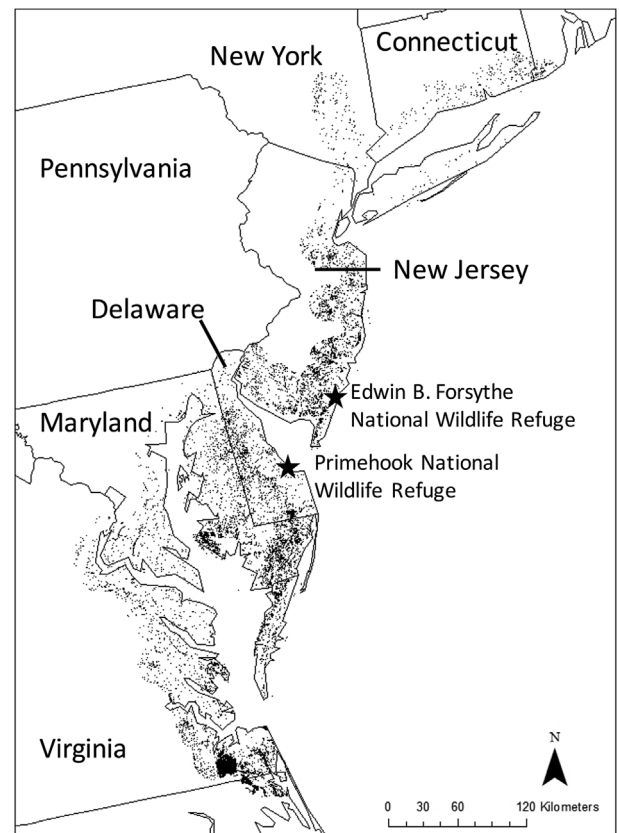


Figure 1. Forested wetlands, in black, within a 24.1-km distance from the coast ranging from Rhode Island to northern North Carolina, USA, 2014–2015, used to determine black duck food energy at a landscape level. Prime Hook National Wildlife Refuge (PHNWR), Delaware and Edwin B. Forsythe National Wildlife Refuge (EBFNWR), New Jersey, USA, where we obtained core samples to measure black duck food availability, are noted by black stars.

wetlands. We estimated 103,696,524–192,678,224 DUD and therefore 489,135–908,860 individuals over the winter season.

DISCUSSION

Salt marshes along the Atlantic Coast tend to contain large amounts of energy (e.g., $123,831 \pm 16,968$ kcal/ha for high marsh and $214,223 \pm 22,638$ kcal/ha for freshwater impoundments; Ringelman et al. 2015a) and thus help to support robust wintering waterfowl populations. We documented that neighboring forested wetlands within

Table 2. Estimates of resource availability and variability for wintering black duck forested wetland habitat in Prime Hook National Wildlife Refuge (PHNWR), Delaware and Edwin B. Forsythe National Wildlife Refuge (EBFNWR), New Jersey, USA, 2014–2015 in terms of biomass (kg/ha) and energy (kcal/ha; Cramer et al. 2012, Livolsi 2015). We used non-parametric Mann-Whitney U tests to compare mass and energy between study areas.

	PHNWR		EBFNWR		<i>U</i> (<i>n</i> = 87)	<i>P</i>	PHNWR and EBFNWR	
	\bar{x}	SE	\bar{x}	SE			\bar{x}	SE
Black duck food biomass	26.18	7.34	94.42	23.43	3.231	0.001	57.69	12.16
Invertebrate	0.54	0.50	11.68	2.98	4.640	<0.001	5.83	1.54
Seed	25.65	7.36	82.74	23.37	1.999	0.046	51.86	11.97
Black duck food energy	28,511.84	7,060.89	147,670.55	43,839.69	2.888	0.004	84,667.11	21,822.08
Invertebrate	435.03	135.59	5,782.18	1,747.10	4.545	<0.001	2,954.95	880.05
Seed	28,076.80	7,412.89	141,888.31	43,922.34	2.118	0.034	81,712.12	21,778.65

24.1 km of the Atlantic Coast, have an average 84,667.11 kcal/ha of black duck food. We acknowledge that because the data is right skewed, it is possible the arithmetic mean may overestimate the forage available in most forested wetlands. To discuss the implications of this possible over-inflation, we examined the medians of our data. We found estimated landscape-level energy was 1,500 kcal/ha at PHNWR and 29,557 kcal/ha at EBFNWR thus producing landscape-level energy estimate of 10,769 kcal/ha (6,299,735,772 kcal across the landscape). Certainly, these median values provide greatly reduced results from the mean values and thus we encourage future researchers to examine more closely the effects of right-skewed bioenergetic estimates on landscape energy.

Although food energy estimates for forested wetlands (57.69 kg/ha) are substantially below those of salt or fresh water marsh, they are well above the 10 kg/ha theoretical foraging threshold for hardwood forested wetland (Anderson and Davis 2013, Gray et al. 2013) and thus provide a potentially significant additional source of energy for wintering black ducks. Granted, the 10 kg/ha estimates were based on only hard mast, so the inclusion of invertebrates and small seeds and tubers increase the foraging threshold estimate. Assuming a liberal 50 kg/ha foraging threshold that applies to a combination of all seed and invertebrate species (Hagy and Kaminski 2015), our food estimates of 57.69 ± 12.16 kg/ha would be reduced to 7.69 kg/ha of food available to black ducks after the foraging threshold is removed. However, extrapolating from food thresholds to energy availability is difficult because it is unknown if ducks uniformly ignore 50 kg/ha across all taxa or they prefer or ignore some taxa with a higher or lower energetic values. Nevertheless, if we assume that 86.67% of the total food resources are below the foraging threshold (50 kg/ha), black ducks will still have $11,286.13 \pm 2,908.88$ kcal/ha available.

Because we conducted our study in the spring, our samples may have represented a foraging landscape that was depleted by black ducks (and other species) and decomposition over the course of the winter. Indeed, energetic carrying capacity and mean seed mass decreased between the autumn and spring in actively and passively managed freshwater wetlands because of consumption, depletion, and decomposition of food resources over time (Greer et al. 2009, Brasher et al. 2010). Hagy and Kaminski (2015) estimated a reduction in seed and tuber availability between 5–71% in early winter. Although these studies occurred in freshwater coastal wetlands, we feel that this may explain the significant differences between the lower values of PHNWR (collected in the spring) and the higher values of EBFNWR (collected throughout winter and spring), and an underestimation of available food resources. Future research involving the energetic value of mid-Atlantic forested wetlands during fall (before potential depletion) will also provide a more accurate DUD value, contribute to more accurate estimates of overall winter carrying capacity, and refine bioenergetic models. Future investigation of foraging thresholds (Hagy

and Kaminski 2015) in forested wetlands may help improve bioenergetic models.

There was large variation in biomass between sites and years (26.18–94.42 kg/ha); however, this variation was consistent with the variation reported in Straub et al. (2012) across multiple mid-western sites and the ranges in coefficient of variation in Hagy et al. (2014) for seed and tuber density (9–77% within wetlands and 32–115% across years). Although food densities were highly variable and foraging thresholds unknown in this system, forested wetlands appear to provide a substantial food energy that may contribute to the wintering black duck carrying capacity. Therefore, we recommend that food biomass from forested wetlands should be incorporated into ongoing bioenergetics modeling efforts to refine landscape carrying capacity estimates.

Although a recent meta-analysis of black duck telemetry documented black duck use of forested wetlands (Ringelman et al. 2015b), it is unknown if it is a preferred feeding habitat or if it serves another ecological role (Osborn 2015). Although there is evidence that black ducks prefer forested wetlands for breeding and brood-rearing because they promote reproductive success by providing warmth, effective protective cover from predators and harsh weather, and access to adequate food resources (Ringelman et al. 1982a,b; Ringelman and Longcore 1982; Diefenbach and Owen 1989; Reinecke et al. 1989), it is not as well known if winter use of forested wetlands is for energy consumption or if it is also for isolation, security, thermal cover, or avoiding disturbance (Straub et al. 2012, Newcomb 2014).

Forested wetlands provide food resources that meet the nutritional and thermoregulatory needs of black ducks that are either unavailable in other habitats or are only accessible at greater risk (Newcomb 2014). Additionally, similar to salt marsh wetlands (Fredrickson and Heitmeyer 1985, Chipley 1995, Stafford et al. 2007), some studies reported that forested wetlands may provide inherent niche separation and a barrier to interspecific competition for resources with mallards (Reinecke et al. 1989). Particular freshwater areas, including forested wetlands, may not freeze over during prolonged periods of cold weather because they are spring-fed pools or running streams, thus allowing for smaller core ranges in areas of higher energy densities when compared to salt marshes (Ringelman et al. 2015b). Other studies reported strong support that the use of forested wetlands significantly increased on days when the temperature remained below freezing (Ringelman et al. 2015b) and in late winter (Chipley 1995, Clark 1996). Wintering waterfowl often use the shrub layer of forested wetlands because of the low and thick vegetation that retains heat (Nelms et al. 2007).

If not for isolation, security, or thermal cover, perhaps black duck presence in forested wetlands is due to the continued loss and fragmentation of coastal habitats, or increased human disturbance in these areas (Conroy et al. 2002). Sea level rise has risen about 0.19 m since 1901 and is projected to rise another 0.26–0.98 m by 2100 (Church et al. 2013), leading to direct loss of coastal marsh. With coastal wetlands

being lost because of sea level rise and human development, forested wetlands may increase in value as landscape change persists. In the face of continued coastal habitat loss and fragmentation, forested wetlands may become an increasingly important resource for wintering black ducks. Using the mean and standard error, we estimated that forested wetlands in the mid-Atlantic region can provide winter food resources to 489,135–908,860 individual black ducks (although note this does not account for any foraging threshold). Combined with telemetry data (Ringelman et al. 2015b) that black ducks were using forested wetlands during cold snaps, this suggests that the value of these habitats for wintering black ducks has been underestimated, and that forested wetlands should be included in Joint Venture habitat acquisition and management plans. However, we suggest extrapolating to a smaller subset of forested wetlands in future landscape-level analyses to reduce variance.

There are several potential biases in our data. First, the abundance or quality of black duck foods may change with the fluctuations of annual flooding (Fredrickson and Heitmeyer 1985), although seeds in forested wetlands are more resilient to decomposition than those in other land cover types (Davis and Afton 2010). Similarly, the consumption of food items by other wildlife species may potentially reduce black duck carrying capacity (Turner and Trexler 1997, Straub et al. 2012). Our study was limited spatially and temporally, and so we suggest future studies sample over many years in different locations. We also feel that using core sampling may have underestimated our invertebrate abundance estimates because it would only include species in the benthic column (Ringelman et al. 2015a). Several invertebrate species exist outside of the benthic column, with their populations increasing as winter progresses (Davis and Afton 2010). Our methodology may have prevented detection of a high invertebrate abundance in the winter. Turner and Trexler (1997) suggest using funnel traps, sweep nets, and stovepipes in addition to benthic corers to sample invertebrates.

Another potential bias in our dataset was the correct identification of preferred black duck foods. We identified preferred food items from black ducks scientifically harvested in primarily coastal marsh and freshwater or brackish impounded areas, and so our methods may not have included forested wetland seeds that are actually preferred by black ducks. For example, Rawls (1978) published the diet of hunter-collected (and therefore potentially biased [Sheeley and Smith 1989, Heitmeyer et al. 1993]) waterfowl in the Chesapeake and reported black ducks consumed some additional fruits and seed species that could have been found around forested wetlands. Therefore, we recommend a scientifically collected diet study of black ducks in forested wetlands to refine and confirm preferred foods.

A final bias in our data was the simple extrapolation to the potential carrying capacity of mid-Atlantic forested wetlands. We used a simple presence-absence estimate of black ducks occurring on the wintering grounds ($n = 212$ days) because a detailed migration chronology of numbers of ducks

over the winter season does not exist for the mid-Atlantic. We encourage future researchers to build more detailed chronologies to improve carrying capacity estimates. Additionally, we acknowledge our results are based on mean values and will tend to be artificially high because of the right-skewed nature of the data; however, because past bioenergetics studies have presented averages, we used them in our analysis for the sake of biological comparison. We suggest using medians may provide a more accurate representation of food resource availability.

MANAGEMENT IMPLICATIONS

Managers require estimates of energetic carrying capacity for areas used by black ducks to build landscape-level bioenergetic models. Our food energy estimates for forested wetlands can be used to refine such models that are being developed by the Atlantic Coast and Black Duck Joint Ventures. Although it is unclear why black ducks use forested wetlands, our results suggest that they provide an additional foraging resource. Therefore, we recommend that researchers evaluate black duck occupancy and use of forested wetlands during the non-breeding period along the Atlantic Coast to determine their ecological value to wintering waterfowl.

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