Habitat selection and foraging strategy of American Black Ducks *Anas rubripes* wintering in Tennessee, USA

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Abstract

American Black Duck *Anas rubripes* populations in North America have declined over the last 20 years, especially in the Mississippi Flyway. The Tennessee River Valley of west-central Tennessee historically has been an important winter terminus for Black Ducks in the Mississippi Flyway, but there is limited information on habitat resource selection during winter to guide management for this species. Available habitat resources and Black Duck behaviour were studied at the Tennessee and Cross Creeks National Wildlife Refuges during December–February in winters 2011/12–2012/13, and the Black Ducks' activities were compared to a broader community of dabbling ducks *Anatini* sp. wintering in the same area. Black Ducks used wooded wetlands and flooded agriculture at a greater relative frequency than other available wetland types throughout winter, but foraged more in moist-soil and mudflats than in other wetland types. They selected foraging patches independent of measured food densities, but the density of food at selected foraging sites did not decline throughout winter in line with resources available in the larger landscape, indicating that the ducks may have selected foraging patches at densities above critical food densities rather than distributing optimally according to total food densities. Factors other than absolute food abundance likely influence resource selection by Black Ducks and, despite some use of flooded agricultural fields, their behaviour and use of resources indicate that they are not likely food-limited during winter at these refuges. Management for Black Ducks in western Tennessee should include a complex of natural wetland types, including forested and moist-soil wetlands, within sanctuaries where disturbance is limited.

Key words: activity budgets, Anatini, Tennessee, waterfowl, wetland management.

North American dabbling ducks are a diverse group of birds, of which 13 species regularly breed, migrate and winter throughout the continent (Baldassarre 2014). Given great variability in morphology and physiology of many North American ducks, co-occurring species often enhance niche partitioning through dietary preferences, physiological specialisations and by using fine-scale habitat attributes (*e.g.* water depth; Gurd 2006; Estevo *et al.* 2017). Dabbling ducks *Anatini* sp. are typically gregarious during autumn migration and winter and often occur as larger mixed-species communities of individuals occupying available niche spaces where they vie for food, mates and other resources (DuBowy 1988; Raveling 2004). Given the diverse morphologies and behaviours among dabbling ducks, competitive exclusion (Volterra 1926; Gause 1934) is thought to be rather minimal, at least at broad spatial-temporal scales (but see Schummer *et al.* 2020). Resource or niche partitioning relates to like species occupying the same environment but accessing resources (*e.g.* food) differently, in accordance with their unique morphological or behavioural characteristics (Ricklefs & Travis 1980; Pöysä 1983; Gurd 2008). Under the competitive exclusion principle (Hardin 1960), no two species that have identical foraging and spatial needs should co-exist if resources are limiting. For example, Mallards *Anas platyrhynchos* and American Black Ducks *A. rubripes* (hereon Black Duck) are species of similar body mass, foraging strategies and daily energy needs, but large-scale geographic and local habitat resource partitioning has not been explored with a view to targeting management for these species in the interior USA, including at national wildlife refuges (Ringelman *et al.* 2015a; Osborn *et al.* 2017; Monroe *et al.* 2021). Traditional conservation planning and management activities focus on maximising food resource availability (USFWS 2010, 2014), but if Black Ducks are not limited by food densities, do not forage optimally with respect to mean food availability across management areas, or are affected by social or physiological factors more than food densities, these traditional management actions may not be appropriate for this species.

Effects of habitat loss and degradation are often more pronounced in habitat specialists, particularly when the availability of resources is severely limited or fragmented (Hannon & Schmiegelow 2002; Schmiegelow & Monkkonen 2002; Gurd 2008). Black Ducks may exemplify a species experiencing potential negative consequences of forested wetland loss (Morton *et al.* 1989; Davis & Afton 2010; Ringelman *et al.* 2015a). The area of forested wetlands decreased by

> 40% in the United States over the period 1950–2009 (Dahl 2011), and Tennessee has lost > 60% of its wetlands (Dahl 2011), largely because of river channelisation, agricultural expansion, and urban sprawl. West Tennessee borders the eastern edge of the Lower Mississippi River Alluvial Valley, a region of extensive deforestation and conversion of land to other uses (Sternitzke 1976; Haynes & Egan 2004). It is suspected that loss of forest and associated wetlands, and their transition to agricultural and other land uses, has reduced the Black Ducks' wintering area because the birds historically utilised these habitat resources (USFWS 2014). Habitat segregation and potential competitive interactions between the two species have been documented largely on breeding grounds (Merendino *et al.* 1993; Merendino & Ankney 1994; Petrie *et al.* 2012), for instance Petrie *et al.* (2012) found that Black Ducks frequented wetlands with > 75% forest cover to a greater extent than Mallards in important Black Duck breeding areas in western New Brunswick, Canada. If competitive interactions occur in wintering areas where the species are sympatric, it could be that Mallards outcompete or displace Black Ducks to lesser quality habitat resources (Hanson *et al.* 1990; Mank *et al.* 2004; Bleau 2018). In the Finger Lakes Region (FLR) of New York, Mallards' use of agricultural land was five times greater than by Black Ducks, whereas the percentage of time foraging when in forested wetlands was eight times greater for Black Ducks in comparison with Mallards (Bleau 2018). A better understanding of resource partitioning between closely related Black Ducks and Mallards therefore is needed, particularly in historical shared wintering regions such as western Tennessee.

The Tennessee River Valley of west-central Tennessee historically represented one of the principal southern termini for Black Ducks wintering in the midcontinent (Baldassarre 2014; Lavretsky *et al.* 2014). According to the midwinter waterfowl survey, from the 1970s to the mid-1990s, > 40% of the Black Ducks in the Mississippi Flyway were observed in west-central Tennessee, with 75% of those occurring on either the Tennessee or the Cross Creeks National Wildlife Refuges (NWR) (Sanders 1995; USFWS 2010). Despite this historical significance, the number of Black Ducks at Tennessee NWR declined by 98%, from 35,200 to 807 birds, between 1990 and 2019 (USFWS 2020; Monroe *et al.* 2021; R. Wheat unpubl. data). Causes for a noticeable decline of a species in a particular area or region can sometimes be explained by coarser-scale mechanisms such as climate change (Meehan *et al.* 2021), density-dependent mechanisms operating at various scales (Nudds & Wickett 1994), intolerance to hunting or other disturbances (Fox & Madsen 1997), changes in local habitat resource availability (Rosenberg *et al.* 2019; Uher-Koch *et al.* 2021), or changing breeding populations (Zimpfer & Conroy 2006; Ashley *et al.* 2010; Lavretsky *et al.* 2014; USFWS 2019). For species like Black Ducks that have undergone long-term population declines and have fallen below their North American Waterfowl Management Plan (NAWMP) population objective, understanding the resource requirements of birds wintering in the Mississippi Flyway is necessary to determine whether the food supply is inadequate, or if other causes are contributing to the decline (United States Fish and Wildlife Service 2019; Monroe *et al.* 2021). Data are also needed to develop bioenergetics models for the species, which can be used to evaluate wetland habitat quality and establish step-down conservation goals and habitat objectives, if these prove to be appropriate planning measures (Soulliere *et al.* 2007).

These information needs prompted us to initiate a study of a community of dabbling ducks (*sensu* DuBowy 1988; Gurd 2008) in the Tennessee River Valley of west-central Tennessee, in relation to the habitat resources available at two national wildlife refuges (NWR) managed by the US Fish and Wildlife Service. Companion studies included Newcomb *et al.* (2016) and Monroe *et al.* (2021), who documented survival and resource use by radio-marked Black Ducks to determine their second order (home range) habitat selection. Moreover, Osborn *et al.* (2017) examined food availability and the birds' activities for a range of species in the dabbling duck guild at these NWRs. Here, we focus on the resource exploitation and social behaviour of Black Ducks, a focal species for management at the two NWRs and more widely in the region (USFWS 2010, 2014). We predicted that, without interference competition with Mallards, Black Ducks would subscribe to the marginal value theorem, which suggests that predator (*e.g.* foraging ducks) abundance should increase in proportion to food availability where other factors do not limit use of resources within the birds' habitat (Anderson & Ohmart 1988; Hagy & Kaminski 2015; Hagy *et al.* 2017). Optimal foraging behaviour considers the perceived risk of predation, whereby feeding locations may be selected based on a trade-off between foraging efficiency and the need to minimise predation risk (Abramsky *et al.* 2002; Quinn *et al.* 2012; Bonter *et al.* 2013). Specifically, the objectives of the study were to: 1) identify habitat resource use and selection (*sensu* Krausman & Morrison 2016), 2) estimate food density at mobile foraging patches compared to fixed sites, to identify whether food biomass was a primary driver of habitat selection (*sensu* Johnson 1980) and 3) develop activity budgets to determine functional resource use by Black Ducks during winter in the Tennessee River Valley of west-central Tennessee. Based on previous research (Osborn *et al.* 2017; Monroe *et al.* 2021), we predicted that forested wetlands, moist-soil wetlands and mudflats would provide substantial food resources for, and would be selected by, Black Ducks during winter.

Methods

Study area

Black Ducks were studied at the Duck River Unit of the Tennessee NWR (35°57.5'N 87°57.0'W; 10,820 ha) and the Cross Creeks NWR (36°29.6'N 87°47.7'W; 3,586 ha) in and adjacent to the Tennessee River Valley of west-central Tennessee, USA, during November–February in winters 2011/12–2012/13 (Fig. 1). The NWRs are within the floodplains of the Cumberland and Duck Rivers, at or near 107 m above sea level. The Lower Cumberland Tennessee Ecosystem climate typically experiences warm, humid summers (temperature of > 20°C), mild

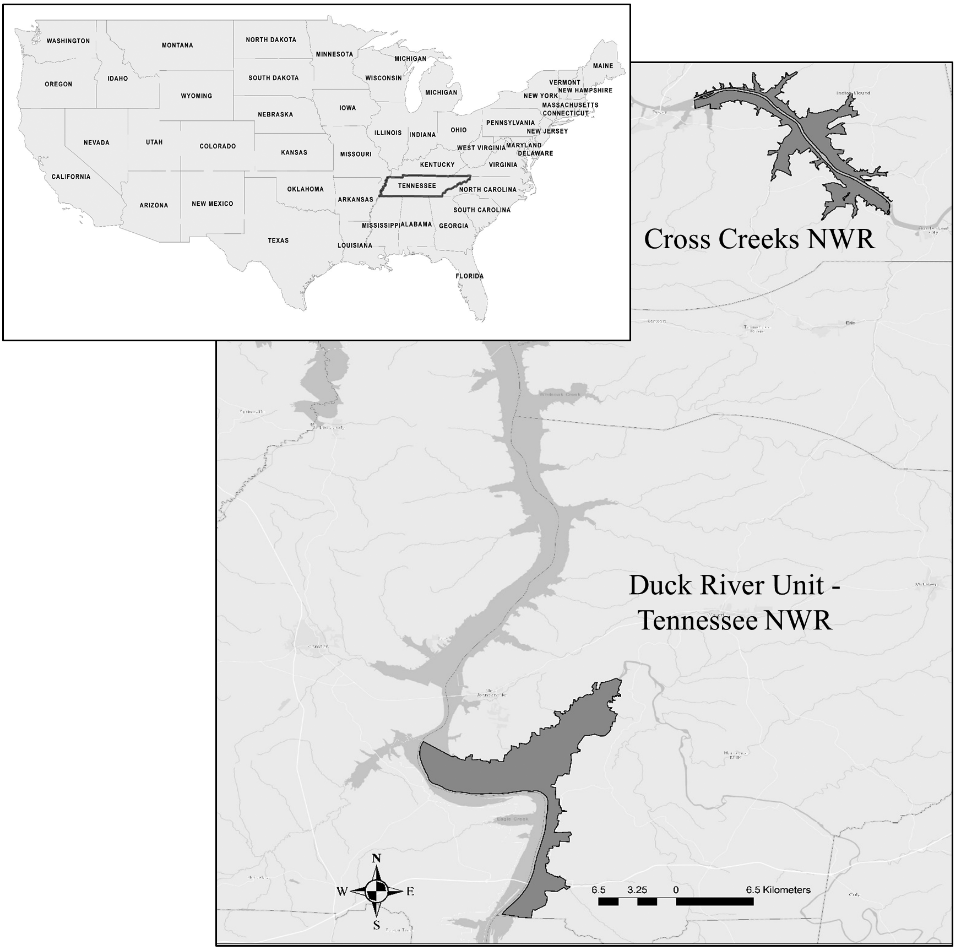

Figure 1. Geographic locations of the Duck River Unit of Tennessee National Wildlife Refuge (NWR) and Cross Creeks NWR within the Tennessee and Cumberland River watersheds, Tennessee, USA.

winters (temperature > 1°C), and rainfall (annual precipitation = 1,346 mm; USFWS 2014) that is well-distributed seasonally. In combination, the NWRs encompass > 14,000 ha and provide > 2,000 ha of seasonal wetlands, which are inundated gradually in autumn and winter to provide habitat for migrating and wintering waterfowl. The two NWRs typically support *c.* 150,000 migrating and wintering waterfowl each year (Hagy 2020), including Black Ducks which is a priority species for habitat management (USFWS 2010, 2014). Waterfowl hunting is prohibited on these NWRs during late autumn and winter (November–February) and most of the refuges are managed as waterfowl sanctuaries with no or extremely limited public use. Wetland management at the refuges provided a complex of resources (USFWS 2014), including palustrine forested and scrub-shrub (hereafter, wooded wetlands); palustrine emergent with primarily annual, herbaceous vegetation (hereafter, moist-soil); aquatic bed with submersed aquatic vegetation (SAV [aquatic bed]); deep (> 45 cm), open water devoid of vegetation (*i.e.* open water); exposed and shallowly flooded mudflats (mudflat; Cowardin *et al.* 1979); and harvested and unharvested agricultural crops (*e.g.* Corn *Zea mays*) flooded for waterfowl (Osborn *et al.* 2017). Wooded wetlands were typically narrow (≤ 100 m width) areas of open water and stream channels, bounded by scrub-shrub and forest vegetation. Moist-soil communities, or those primarily composed of annual, hydrophytic plants occurred within managed impoundments (Fredrickson & Taylor 1982). Aquatic bed and open water wetlands occurred within impoundments and portions of the Duck, Tennessee and Cumberland Rivers, and mudflats occurred along those rivers where hydrology was highly variable but unfavourable for emergent vegetation. Unharvested, flooded corn occurred within a small number of impoundments and adjacent upland crop fields, and standing corn was pushed over with machinery to a height of *c.* 75 cm during December or January to promote easy access to grain by waterfowl.

Habitat and resource selection

Prior to waterfowl arriving in November, four sites were established at each refuge for each of the six wetland types described above (*i.e.* moist-soil, forested, agricultural, mudflat, SAV and open water). Sites were separated by > 200 m to reduce spatial dependence and prevent double-counting birds within a single survey period. Wetland types naturally varied in size, but we believed all sites were of sufficient size (*i.e.* ≥ 0.5 ha) to identify resource selection by waterfowl species (Johnson 1980). Flooding schedules and logistical considerations associated with accessing sites for bird surveys precluded random selection of survey sites, so we selected sites with a broad distribution that we believed represented wetland types available to Black Ducks within the NWR and the adjacent region (*cf.* Newcomb *et al.* 2016).

Dabbling ducks were counted to species level ≥ 1 times/week each winter (December–February) from camouflaged tree stands or concealed vantage points at all sites (hereafter fixed sites; n = 24 sites/NWR; see Osborn *et al.* 2017). Blinds and vantage points were positioned where observers could enter and exit without disturbing the birds. Surveys were conducted between sunrise and 5 h thereafter (from *c.* 07:00–12:00 h), along pre-determined daily routes which were rotated weekly among observers. Generally, 2–4 observers conducted a total of 8–10 fixed site surveys/day, with the survey at each site taking *c.* 2.5 h, including time to enter and exit the blind, count the birds, and travel between survey points. In addition to the fixed sites, we identified and sampled other areas used by Black Ducks during autumn and winter from field observations, locations of radio-marked birds from a concurrent study (Newcomb *et al.* 2016; Monroe *et al.* 2021), aerial surveys, or incidental encounters (hereafter, mobile sites). At mobile sites, food density and bird activities were estimated monthly (*n* = 3 sites/wetland type/month). Locations of mobile sites often differed between months and were used to document potential shifts in resource use and selection of sites by Black Ducks during winter relative to the fixed sites, which provided our comparison reference data. We considered the fixed sites to be representative of the region, and by comparing food densities there with those at locations used by birds observed from the mobile sites, we could infer third-order selection by Black Ducks in our study area (Johnson 1980).

Evening or nocturnal sampling surveys were not completed for various logistical and technical reasons, and we assumed that daytime use was representative of general habitat use and selection within waterfowl sanctuaries, consistent with previous research (Hagy & Kaminski 2012a). Monroe *et al.* (2021) observed similar patterns of wetland use by Black Ducks on the Tennessee NWR across diurnal and nocturnal periods. White polyvinyl chloride markers were placed at 100 m intervals from observation blinds nearby each fixed site to aid in distance estimation during waterfowl surveys (Buckland *et al.* 2001). In open water and other sites where we could not place distance markers, we estimated the distance of fixed objects using a high-precision laser rangefinder (Buckland *et al.* 2001; Bolduc & Afton 2004). When fixed sites were ≥ 60% inundated and representative of each plot at each site, we measured water depth systematically at 10 locations along two random transects within each site, and erected a fixed depth gauge to record average depth during surveys without disturbing the waterfowl (Hagy & Kaminski 2012a). Water gauges could not be erected in open water and mudflats because of deep or fluctuating water levels in riverine areas (Osborn *et al.* 2017).

If the birds flushed, or were displaced from a fixed site immediately before or during a survey, we abandoned the survey and returned later. If a minor disturbance occurred (*i.e.* birds were alert or flushed to different parts of an impoundment but did not leave), we waited for *c.* 5 min to allow waterfowl to resume normal activities before initiating a count. Average water depths were recorded and we ocularly estimated the percentage of horizontal emergent vegetation cover (± 5%) within fixed sites during each survey. At fixed sites, we made a single 180° scan of the site with binoculars or a spotting scope, using a digital voice recorder to record the number, species, distances and activities of dabbling ducks ≤ 200 m from the blind (Kaminski & Prince 1981; Smith *et al.* 2004; Beck *et al.* 2013).

Food availability

Food density was estimated monthly, using a standard core-sampler (10 cm diameter and depth; Manley *et al.* 2004; Stafford *et al.* 2006) in all shallow emergent (≤ 45 cm) and mudflat sites, whereas a modified Gerking box sampler was used in open water, aquatic bed, and deeply flooded emergent sites (> 45 cm; Sychra & Adamek 2010). Five samples were collected systematically along a randomly-oriented transect within each site, at regular intervals according to the size of the site. These were washed through a 500 m aperture sieve bucket whilst in the field, then placed into polyethylene bags for transport and storage. Core, sweep and box samples were preserved in 70% ethyl alcohol and stored at –10°C (Salonen & Sarvala 1985). At the mobile sites, we sampled food resources ≤ 1 day post-surveys, also by collecting five core samples systematically along a transect, spanning the approximate area used by the Black Ducks (*i.e.* at *c.* 5–15 m intervals; Greer *et al.* 2007). Mobile-site samples were washed, preserved and stored the same way as in the fixed-site samples.

The number of core or other samples needed to obtain precise estimates of the energetic carrying capacity of wetland habitats can be numerous and vary greatly, but Ringelman *et al.* (2015b) recommended that 40 cores per wetland type reduced variance sufficiently, to acceptable levels, in different wetlands along the Atlantic coast. In this study, our objectives were to understand habitat selection by Black Ducks and to index food abundances in small wetland units, rather than making a rigorous estimate of the energetic carrying capacity of the region, similar to several previous studies (Hagy & Kaminski 2012a; Osborn *et al.* 2017). Our samples could be combined across refuges and sites within each sampling period, however, to achieve recommended sample sizes and estimate the regional carrying capacity level.

In the laboratory, we thawed food samples, stained them with 1% rose Bengal solution, washed combined sets of five samples through graduated sieves (mesh sizes: no. 4 = 4.75 mm, no. 14 = 1.40 mm, and no. 50 = 300 µm), and removed with forceps all aquatic macroinvertebrates and SAV typically consumed by dabbling ducks (Hagy & Kaminski 2012b). We identified and enumerated macroinvertebrates to Order, dried them for 24 h at 60°C, and weighed them to the nearest 0.1 mg (Murkin *et al.* 1994). We identified SAV to genus and dried and weighed the vegetation as previously described for macroinvertebrates. Following removal of macroinvertebrates and SAV, we air dried remaining material for 24–48 h, extracted all seeds and tubers known to be consumed by dabbling ducks from no. 4 and no. 14 sieves, identified seeds and tubers to genus or species and dried them for 24 h at 60°C, and weighed foods to the nearest 0.1 mg (Hagy & Kaminski 2012b).

To account for materials in the no. 50 sieve which were too numerous and laborious to extract using previously described methods, we randomly subsampled small-sieve contents from three sites for each wetland type, refuge and year to create correction factors for small seeds. Seeds were extracted from a 25% portion by mass and identified, dried and weighed, using previously described protocols (Reinecke & Hartke 2005; Hagy *et al.* 2011; Livolsi *et al.* 2014). Each biomass estimate was adjusted by the appropriate correction factor for the contents of the small sieve, estimates were corrected for processing bias (Hagy *et al.* 2011) and the final dry weight biomass (dry kg ha^{-1}) measures for seeds, tubers, SAV, and invertebrates were converted to duck energy days (DED ha^{-1}; Reinecke *et al.* 1989; Gray *et al.* 2013) using published, taxon-specific true metabolisable energy values (TME; Sherfy 1999; Checkett *et al.* 2002; Kaminski *et al.* 2003; Ballard *et al.* 2004). Mean (± s.e., 95% CI) monthly densities of plant foods (combined seed, tubers and SAV) and invertebrates are presented.

Waterfowl activity

At least five activity budgets of Black Ducks were recorded weekly at each fixed site (n = 24 sites/NWR). Black Ducks were the focus of this study, as previously described in a report on the larger community of dabbling ducks wintering at these refuges (Osborn *et al.* 2017). Observers selected individuals for study at random, by placing the spotting scope or binoculars at the midpoint of the survey area, then scanning from left to right, and recording activities for the first five Black Ducks encountered, for one continuous minute each. In mudflat and open water sites, we surveyed to the distance at which we could no longer identify birds reliably (Smith *et al.* 2004), which did not exceed 800 m. Distance to individuals and groups of birds were estimated to the nearest 10 m to aid in density estimation in Distance 6.0 (Buckland *et al.* 2001). Black Duck activities were classified as foraging (surface feeding or tipping up), resting (sleeping, loafing or inactivity), locomotion (walking or swimming), aggression (chasing, biting or fighting), courtship (displaying or copulation), alert (inactive with head erect), and maintenance (preening, bathing or stretching; Kaminski & Prince 1981; Paulus 1983, 1988). Birds seen in flight during the surveys were not included (Buckland *et al.* 2001), and we did not sample waterfowl in dense fog or if winds exceeded 30 km h^{-1} (Hagy & Kaminski 2012a).

Within 7 days of the end of each month, Black Duck activities and habitat characteristics were also recorded at mobile sites throughout the Tennessee NWR and the Cross Creeks NWR. Mobile sites were small, foraging patches which occurred within and outside of fixed-sites. Activity budgets of birds at the mobile sites were also recorded at 1 min intervals, from permanent elevated and ground blinds, automobiles, levees, or other accessible locations that permitted inconspicuous observers an unobstructed view without disturbing the ducks. Individuals or groups separated by ≥ 200 m were considered to be spatially independent and assigned to different mobile sites. As for the fixed sites, we classified mobile sites according to six main wetland categories.

Statistical analyses

Habitat selection. Black Ducks were classed as being present (1) or absent (0), to calculate odds of their presence and determine the greatest likelihood of habitat use among wetland types and across months (Zar 2009). Logistical regression was applied because of the absence of Black Ducks during most surveys of fixed sites (79%) and resulting violation of assumptions of normality (PROC LOGISTIC; Keating & Cherry 2004; SAS Institute Inc. 2008). Wooded wetlands and December were used as reference variables for wetland type and month, respectively. Model fit was assessed using the Hosmer Lemeshow test (Hosmer & Lemeshow 1989), with the percentage of emergent vegetation cover (0–25%, 30–50%, 55–75%, 80–100%) and mean water depth (3–9 cm, 10–25 cm, 26–45 cm and > 45 cm) as categorical covariates, and we examined simple correlations to prevent issues of collinearity (Isola *et al.* 2000; Moon & Haukos 2008; Zar 2009).

To infer resource selection, GIS shapefiles (available for both refuges), elevation contours, aerial imagery (2012 National Agricultural Imagery Program, with 1 m resolution), refuge water gauge and wetland site gauge data, and field delineated maps were used to estimate the extent of refuge-wide flooded areas (ha) each month for each wetland type in ArcMap 10.1. Mean proportions of Black Ducks (and other dabbling ducks) were calculated in relation to total Black Duck and dabbling duck estimates from weekly surveys conducted by USWFS Refuge biologists (USFWS unpubl. data). Details of resource selection by dabbling ducks other than Black Ducks were reported in Osborn *et al.* (2017). Total flooded area (ha) among wetland types, across refuges and years, was also estimated. We ranked proportions of flooded wetland availability and waterfowl densities (PROC RANK) and then compared them, to make inferences on possible selectivity among wetland types (Johnson 1980).

Food availability. We tested for the effects of wetland type on: 1) plant biomass (*i.e.* the sum of seeds, tubers and SAV biomass), and 2) invertebrate biomass (dry weight kg ha^{-1}) for Black Duck mobile plots at the Tennessee NWR and Cross Creeks NWR, using separate linear mixed models (PROC MIXED; Littell *et al.* 2006; SAS Institute, Inc. 2008). The combined biomass from plants and invertebrates was highly-correlated with mass of seeds and tubers ($r = 0.99$, $n = 187$, $P < 0.001$), indicating that invertebrate biomass represented a very small portion of the food biomass available, so we did not test for the effect of wetland type on total food biomass in an additional analysis (Hagy & Kaminski 2012b). Wetland type was given as a fixed effect, year as a random effect, and month as a repeated measure in the model. Only seeds and tubers reported as potential food for dabbling ducks were included in analyses (Hagy & Kaminski 2012b), but we included all aquatic invertebrate taxa because there is little information available on invertebrates in waterfowl diets (Callicutt *et al.* 2011; Hagy & Kaminski 2012b). We also used linear mixed models (PROC MIXED; Littell *et al.* 2006, SAS Institute, Inc. 2008) to test for differences in dry weight food density (kg ha^{-1}) between fixed and mobile sites among months and wetland types, again designating wetland type as a fixed effect, year as a random effect, and month as a repeated measure.

Waterfowl activity. Activity budget data recorded in both years were combined to provide sufficient sample sizes, for comparing the proportion of time that Black Ducks spent on different activities among wetland types and months. Proportional data potentially violate assumptions of independence due to the unit-sum constraint (Aitchison 1986). Lack of independence can be overcome via compositional analysis (Aebischer *et al.* 1993), but activity data contained many zeros causing compositional procedures to inflate Type I error rates (Bingham & Brennan 2004). Thus, in our investigation of potential differences in Black Duck activities among wetland types and months, we applied multi-variate analysis of variance because it is applicable when zero-sum constraint can bias other types of analyses (MANOVA; PROC GLM; Crook *et al.* 2009; Mason *et al.* 2013). Observations of aggression, courtship, maintenance and alert behaviours were relatively uncommon

(≤ 10% of collective Black Duck activities) and were excluded from final analyses. We selected the proportion of time that the birds spent on each of four activities (foraging, inactive, locomotion, maintenance) as dependent variables, cover type and month as fixed effects, and refuge (the NWR) as a random effect. We arcsine-square root transformed the proportion of time spent in maintenance to overcome violations of multivariate-normal distribution (Zuur *et al.* 2010). We measured but did not include mean water depth, nor the percent of emergent vegetation cover, because these variables were highly correlated ($r = 0.93$) and decreased model fit when included individually. Surveys were assumed to be independent and we did not consider month as a repeated measure because mobile site surveys among months were separated temporally by 4–7 weeks and sampling areas often varied among months. Statistical significance of MANOVA was included in analyses using Wilks' lambda.

For all analyses, we examined boxplots and histograms of variables, variances of independent variables, and plots of residuals to ensure that data and distributions met assumptions of the analyses (Zuur *et al.* 2010). Recommended transformations were used when appropriate (Zar 2009). All plant and invertebrate biomass estimates are reported as dry masses, with means and standard errors (s.e.) given as untransformed data. We estimated degrees of freedom (d.f.) via Kenward-Rogers in analyses involving mixed models and compared AICc scores to select covariance structures and random effects (Zuur *et al.* 2010). We designated $\alpha = 0.05$ *a priori* and performed Tukey's pairwise multiple comparisons tests of means when categorical effects differed significantly (Zar 2009; Zuur *et al.* 2010).

Results

Habitat selection

Across all wetland types, open water was the most available during our study (mean ± s.e. = 6,602.5 ± 48.3 ha month^{-1}), followed by moist-soil vegetation (1,031.7 ± 67.6 ha month^{-1}), wooded wetlands (546.9 ha month^{-1} ± 10.1), mudflats (444.6 ha month^{-1} ± 56.7), aquatic bed (387.0 ha month^{-1} ± 30.1), and flooded corn (32.7 ha month^{-1} ± 2.8; Table 1). Black Ducks were observed in 186 (20.4%) of 910 fixed plot surveys made at the Tennessee NWR and the Cross Creeks NWR during the study, occurring most frequently in wooded plots (33.9%), followed by aquatic bed (23.2%), flooded corn (22.2%), moist-soil vegetation (19.6%), mudflat (15.5%) and open water (11.2%) fixed plots (Table 1). The proportional occurrence of Black Ducks at the observation points during the 910 surveys was greatest during December (27.1%), declining to 19.0% in January and 18.1% in February.

The final logistic regression model included wetland type and month as predictors of Black Duck presence (AICc = 882.3, $\chi_1^2 = 37.4$, $P < 0.001$), and there was no evidence for a lack of fit in the data ($\chi_1^2 = 6.42$, $P = 0.599$, n.s.). Relationships between wetland type (Wald $\chi^2 = 33.6$, $P < 0.001$) and month (Wald $\chi^2 = 5.9$, $P = 0.032$) with the presence of Black Ducks were detected. Likelihood of use was greater for wooded wetlands than for open water (4.3×), mudflats (2.9×), moist-soil

Table 1. Estimates and ranks of habitat use[a] (proportional abundance) by American Black Ducks and habitat availability[b] from November–February in winters 2011/12 and 2012/13 at the Tennessee National Wildlife Refuge and Cross Creeks National Wildlife Refuge, Tennessee, USA.

Wetland type	Proportional abundance[a]	Ranked abundance	Availability[b]	Proportional availability[c]	Ranked availability
Wooded wetlands	33.9	1	546.9	6.0	3
Aquatic bed	23.2	2	387.0	4.3	5
Unharvested flooded corn	22.2	3	32.7	0.4	6
Moist-soil	19.6	4	1,031.7	11.4	2
Mudflats	15.5	5	444.6	4.9	4
Open water	11.2	6	6,602.5	73.0	1

[a] The proportion of observations during which Black Ducks were observed (Black Ducks/month) pooled across sites, refuges and years.

[b] Mean flooded area (ha/month) of wetland types (including exposed and shallowly flooded [< 45 cm] mudflats and unharvested, toppled corn), pooled across refuges and years.

[c] The proportion of flooded area (ha/month) among wetland types (including exposed and shallowly flooded, < 45 cm deep), pooled across refuges and years.

vegetation (2.1×) and aquatic bed (1.7×). Flooded corn was equally likely to be used as wooded wetlands (95% CI = 0.3–1.3), but the occurrence of Black Ducks was highly variable and inconsistent over time, reflecting variation in the availability and use of this resource (0.5 ± 0.4 s.e.; Table 2). Black Ducks were 1.7× more likely to be observed in December than February, but equally as likely to be observed in January as in December (0.2 ± 0.2, 95% CI = 0.3–1.2; Table 2).

Food availability

Plant dry weight biomass (kg ha^{-1}) at the mobile sites (n = 187) differed among wetland types during December–February in 2011/12–2012/13, within both the NWRs ($F_{4,161}$ = 24.0, P < 0.001; Table 3), and was approximately three times greater in moist-soil than wooded wetlands (t_{161} = 6.7, P < 0.001). The lowest biomass was recorded in mudflats and open water, with no detectable difference between these two wetland types (t_{161} = 0.8, P = 0.938, n.s.). Plant biomass did not differ by month at the mobile sites ($F_{2,161}$ = 2.6, P = 0.0997, n.s.) and net change in the plant abundance measures was < 10% on comparing sites used among months. Invertebrate biomass at the mobile sites differed among wetland

Table 2. Likelihood of use, odds ratios, confidence intervals and Wald c^2 statistics for the logistic regression model that best predicted relative habitat use compared to reference variables (*i.e.* wooded wetlands and December) by American Black Ducks during December–February in winters 2011/12–2012/13 at the Duck River Unit of the Tennessee NWR and the Cross Creeks NWR, Tennessee, USA.

Variable	**Predictor**	***n***	**Likelihood of use**	**Odds ratio (%)**	**Confidence intervals**		**Wald χ^2**	***P***
Wetland type	Unharvested flooded corn	45	–1.6	0.6	0.3	1.3	1.5	0.216
	Aquatic bed	155	–1.7	0.6	0.3	0.9	5.1	0.024
	Moist-soil	143	–2.1	0.5	0.3	0.82	8.1	0.004
	Mudflats	193	–2.9	0.3	0.2	0.6	17.3	< 0.001
	Open water	197	–4.3	0.2	0.1	0.4	27.1	< 0.001
Month	January	293	–1.2	0.8	0.6	1.2	0.8	0.372
	February	294	–1.7	0.6	0.4	0.9	5.9	0.015

Table 3. Mean (± s.e.) biomass (in dry kg ha^{-1}) of natural seeds, tubers and invertebrates apparently consumed by waterfowl and recovered from soil and aquatic samples taken from mobile sites during December–February in winters 2011/12–2012/13 at the Duck River Unit of the Tennessee NWR and the Cross Creeks NWR, Tennessee, USA.

Food type	**Month**	**Unharvested flooded corn[b] (*n* = 2, 11, 5)**		**Wooded wetlands (*n* = 19, 20, 25)**		**Mudflats (*n* = 5, 2, 5)**		**Moist-soil (*n* = 26, 19, 22)**		**Open water (*n* = 5, 8, 6)**		**Aquatic bed (*n* = 4, 3, 0)**	
		$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e**	$\bar{x}$	**s.e**	$\bar{x}$	**s.e**	$\bar{x}$	**s.e**
Plant	December	74.1	4.6	96.3	17.1	8.1	3.0	354.8	60.0	0	0	39.3	35.4
	January	80.0	19.2	121.0	48.7	26.1	22.1	352.5	58.7	0	0	11.7	10.5
	February	74.8	23.1	110.7	31.7	21.8	12.0	201.2	31.5	0	0	–	–
	Overall	77.9A	12.9	109.7A	19.8	16.8B	6.0	303.7C	32.3	0	0	27.5B	20.0
Invertebrates	December	2.2	1.6	46.0	14.5	29.6	7.4	18.9	5.5	0	0	4.0	3.5
	January	12.9	6.4	13.0	4.0	3.6	2.1	21.3	6.4	0	0	0.2	0.0
	February	9.5	5.3	22.9	6.5	17.4	8.2	35.2	13.6	0	0	–	–
	Overall	10.8AB	4.1	26.7A	5.3	20.2A	5.1	24.9A	5.3	0	0	2.3B	2.0
Combined	December	76.3	3.0	142.3	27.1	37.8	9.2	373.7	60.8	0	0	43.3	38.9
	January	92.9	23.4	134.0	48.2	29.7	24.0	373.8	58.3	0	0	11.9	10.6
	February	84.3	21.1	133.7	30.0	39.2	11.9	236.4	45.0	0	0	–	–
	Overall	88.7	15.1	136.4	20.4	37.1	6.7	328.6	32.9	0	0	29.8	22.2

[a] Means in the same row but with different capital letters indicate significant differences ($P < 0.05$) in the food ingested in the different habitats, based on Tukey-Kramer multiple pair-wise comparisons of least square means. Means without letters were not included in pair-wise comparisons.

[b] Does not include corn biomass, because core sampling did not sample corn cobs effectively, even after manipulation. Limited data from NWR staff indicates that the typical yield in corn fields is *c.* 100 bushel/acre or 6,274 k ha^{-1}.

types ($F_{4,161}$ = 2.8, P = 0.026) and was greatest in wooded wetlands (26.7 ± 5.3 s.e. kg ha^{-1}), followed by moist soil wetlands (24.9 ± 5.3 kg ha^{-1}) and mudflats (20.2 ± 5.1 kg ha^{-1}). Invertebrate biomass was approximately ten times lower in aquatic bed than in wooded wetlands (t_{161} = 2.8, P = 0.02) but did not differ among months at the mobile sites ($F_{2,161}$ = 0.9, P = 0.42).

Waterfowl activity

We completed 1,203 focal observations of Black Ducks across wetland types, including wooded wetland (n = 424), moist-soil (n = 346), open water (n = 131), aquatic bed (n = 110), mudflats (n = 106), and flooded corn (n = 86). The proportion of time spent in activities differed across wetland types (Wilks' λ = 0.9, $F_{5,\,1,197}$ = 5.7, P < 0.001; Table 4) and months (Wilks' λ = 1.0, $F_{2,\,1,200}$ = 3.8, P = 0.002; Table 5). Foraging, locomotion and resting dominated Black Duck activities in all wetland types (*c.* 90% combined). No differences in maintenance activities were observed across wetland types or between months. Contrasts of least-square means indicated greater foraging by Black Ducks in flooded corn, moist-soil vegetation, and mudflats (37.9%, 33.8% and 33.0%, respectively); less so in aquatic bed (17.5%) and open water (3.2%). Black Ducks spent more time at rest in open water (33.2%) but resting did not vary among other wetland types (22–27%). Locomotion comprised most of the time-budgets in open water and aquatic bed (53.2% and 49.9%, respectively). Black Ducks spent more time feeding in December (28.1%) and February (31.1%) than in January (22.3%), and a similar pattern existed for resting. Locomotion accounted for more than one-third of the time budgets among months (36.7%) and was greatest in February (39.1%).

Discussion

In our study, Black Ducks were apparently free to exploit all available food resources on and around NWRs, but they did not appear to maximise their use of the resources by distributing in relation to food availability. Yet if waterfowl forage efficiently in a food-limited or time-limited system, they should follow the marginal value theorem by distributing across the food resources in relation to the energy gained when feeding in a particular area (Miller *et al.* 2017). Because our study was conducted at two waterfowl sanctuaries, the birds should have been free from exogenous pressures of human predation risk, thus allowing food density to be the principal factor influencing distribution and activities. However, we detected consistent disproportional use of relative moderate- and low-density foraging patches, or of those containing less overall food biomass than at fixed sites in early and mid-winter and more than at those sites in late winter, suggesting that Black Duck distribution was unrelated to absolute food density, despite their extensive foraging behaviour.

There may be several explanations for Black Ducks failing to distribute according to food resource density. First, food density may not have been limiting and thus not a significant factor influencing the distribution and resource use of Black Ducks in our study area. The Black Ducks consistently used foraging patches with below-average

Table 4. Proportion of time engaged in seven activities[a] by American Black Ducks, and comparisons[b] among six wetland types surveyed from fixed and mobile sites during December–February in winters 2011/12–2012/13 at the Duck River Unit of the Tennessee NWR and the Cross Creeks NWR, Tennessee, USA.

Activity[a]	**Unharvested flooded corn (n = 86 birds)**		**Wooded wetlands (n = 424 birds)**		**Mudflats (n = 106 birds)**		**Moist-soil (n = 346 birds)**		**Open water (n = 131 birds)**		**Aquatic bed (n = 110 birds)**	
	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**
Foraging	37.9A	4.3	27.2B	1.8	33.0AB	4.0	33.8AB	2.1	3.2C	1.2	17.5B	3.1
Inactive	22.4A	2.4	24.8A	1.6	27.3A	3.9	24.3A	1.7	33.2A	3.2	22.0A	3.2
Locomotion	28.1A	3.7	35.4A	1.8	28.5A	3.4	32.2A	1.8	53.2B	3.3	49.9B	3.8
Maintenance	8.5A	2.2	8.0A	0.9	8.6A	2.1	5.7A	0.8	7.0A	1.4	6.9A	1.6
Alert	2.0	0.7	1.5	0.3	1.6	0.7	1.9	0.3	1.7	0.7	2.1	0.6
Agonostic	1.3	0.8	0.5	0.2	0.3	0.2	0.4	0.1	0.5	0.2	0.1	0.1
Courtship	0.2	0.1	2.0	0.3	0.3	0.2	0.9	0.2	1.1	0.5	1.5	0.6

[a] Means represent percentage of time expended during 1-min focal scans.

[b] Means within rows followed by unlike capital letters indicate a significant difference ($P < 0.05$) in the birds' activities in the different wetland types, based on Tukey-Kramer multiple pair-wise comparisons test of least squares means. Means without letter groupings were not included in pair-wise comparisons.

Table 5. Proportion of time engaged in seven activities[a] by American Black Ducks and comparisons[b] among months, for December–February in winters 2011/12–2012/13 at the Duck River Unit of the Tennessee NWR and the Cross Creeks NWR, Tennessee, USA.

Activity[a]	**December (n = 391)**		**January (n = 446)**		**February (n = 366)**	
	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**	$\bar{x}$	**s.e.**
Foraging	28.1A	1.8	22.3B	1.7	31.1A	2.1
Inactive	25.1A	1.7	29.1B	1.7	21.2A	1.7
Locomotion	34.7A	1.8	36.3A	1.8	39.1B	2.0
Maintenance	7.3A	0.9	8.0A	0.9	6.2A	0.9
Alert	1.7	0.3	2.3	0.3	1.2	0.3
Agonostic	0.4	0.1	0.9	0.2	0.0	0.0
Courtship	0.1	0.2	1.6	0.3	1.2	0.3

[a] Means represent percentage of time expended during one-minute focal surveys.

[b] Means within rows followed by unlike capital letters indicate significant difference (*i.e.* $P < 0.05$) between months in the birds' activities, based on Tukey-Kramer multiple pair-wise comparisons test of least squares means. Means without letter groupings were not included in pair-wise comparisons.

food energy densities, foraged in areas with little to no detectable food, and used flooded corn to a substantially lesser extent than other duck species (Osborn *et al.* 2017). Secondly, our method for sampling of food densities may not have been fully representative of the way that ducks access foraging patches, sample their environment, and perceive wetland quality. The detailed and systematic measures of food abundance taken at representative wetland types across the study area, including at both fixed and mobile plots, however, provides reasonable confidence in our assessment of the availability of food for the ducks. Indeed, we watched ducks exploit small areas in repeated and prolonged foraging bouts, then sampled these same areas intensively, so our estimates of food density in small patches should be as close as practicable to the Black Duck's perception of the foraging patch at that time. Thirdly, if competition with Mallards was driving resource selection by Black Ducks on these refuges, we should have witnessed behavioural interactions on recording the birds' activities. However, we did not see any apparent aggression from Mallards toward Black Ducks during our study, despite > 1,000 h of monitoring focal bird activities and anecdotal observations.

Whilst Schummer *et al.* (2020) found that female Black Ducks were deterred from feeding sites by Mallards, we suspect that the more artificial conditions in that study were not representative of food and space availability in our study area, where we observed no compelling evidence of competitive exclusion of Black Ducks by Mallards. Thus, our data support the conclusion that patch-level and larger-scale food densities are not predictors of site use by Black Ducks in Tennessee, and that management or conservation planning strategies using these assumptions may be suboptimal for the species.

Black Ducks used a range of habitat resources during the winter, but the proportion of daytime occurrence records was greatest for wooded wetlands. Although less frequented than wooded wetlands, flooded corn, moist-soil, mudflat, and aquatic bed resources were also used extensively by Black Ducks, concurring with previous studies of radio-marked Black Ducks in our study area (Monroe *et al.* 2021) and with sites elsewhere in the Atlantic Flyway (Bleau 2018; Droke 2018). Monroe *et al.* (2021) observed a shift in wetland use by female Black Ducks on and near the Tennessee NWR, from open water diurnally to emergent areas nocturnally, potentially consistent with nocturnal foraging. Prior to wetland loss and other landscape modification over the past century, wooded, herbaceous emergent, open water, and aquatic bed wetland types were likely prevailing resources for non-breeding Black Ducks in inland North America, including along the Mississippi Flyway (Baldassarre 2014). Our study reaffirmed the importance of this complex of habitat resources for Black Ducks, rather than a single source of high-energy food (*sensu* Pearse *et al.* 2012).

The total amount of food biomass recorded was lower in wooded wetlands than in moist-soil wetlands during our study, so Black Ducks likely had to forage more extensively in the former compared to the latter to obtain the same amounts of food. Alternatively, wooded wetlands may have been more important for other life history strategies than food acquisition, and foraging rates may simply have been opportunistic if the birds were not constrained by needing to meet their energy requirement in the study area (Hagy & Kaminski 2012a). For instance, Black Ducks on the mid-Atlantic Flyway have been found to select wooded wetlands for reasons such as courtship and loafing (Fino *et al.* 2017). Aquatic bed similarly contained little food during mid- and late winter after senescence of SAV, but were still used quite extensively. We observed greatest foraging effort by Black Ducks in February, which may have been related to pre-migratory hyperphagia, particularly for pre-breeding females (Miller 1985; Paulus 1983; Hagy & Kaminski 2012a) or, alternatively, food resources have become depleted over winter, causing increased search times towards the end of the winter season.

Whereas foraging was greatest in flooded corn and moist-soil wetlands, Black Ducks also spent some time foraging in wooded wetlands and mudflats, two areas with considerably less food. Locomotion was most common in aquatic bed, mudflats and wooded wetlands, perhaps because the

Black Ducks were searching for food or engaging in courtship activities. The ducks spent considerable time swimming and feeding in these areas with seemingly less food, suggesting that aquatic bed and wooded wetlands may be more relevant in providing other facilities to Black Ducks, for instance for pair segregation, hiding or escape cover (Newcomb *et al.* 2016; Monroe *et al.* 2021). More detailed research into the birds' diet would provide further insight into the relative importance of these different wetland types in relation to the Black Ducks' overall nutrient requirements and energy budgets during winter (White *et al.* 1993; Callicutt *et al.* 2011).

Black Ducks use a variety of wetland types throughout their range, including coastal marshes and interior palustrine wetlands (Baldassarre 2014). Byrd (1991) and White *et al.* (1993) suggested that Black Ducks wintering in Tennessee fed mostly on plant material, whereas diets in coastal regions consist of a greater proportion of invertebrates and other animal matter (Plattner *et al.* 2010; Cramer *et al.* 2012; Flores 2020). Generally, Black Ducks tend to consume more animal matter than do Mallards, at least in the northeastern parts of the Black Ducks' range (Jorde & Owen 1988; Baldassarre 2014). In our study, wooded and moist-soil wetlands and mudflats had the greatest abundance of aquatic invertebrates throughout winter and Black Ducks may have fed in these sites primarily to acquire protein and other essential nutrients from animal foods. Total food biomass estimates from other wetland types were considerably lower than those in moist-soil wetlands, and they were also lower than suggested forage profitability thresholds for waterfowl (180–200 kg ha^{-1}; Hagy & Kaminski 2015; Hagy *et al.* 2017). The greatest percentage of time spent foraging occurred in moist-soil wetlands and on corn, with the former typically containing abundant seeds, invertebrates, green shoots and tubers. These palustrine emergent herbaceous wetlands are an important component of wetland complexes for Black Ducks and other dabbling ducks in interior wintering regions (Brodsky & Weatherhead 1984; Jorde *et al.* 1984; Diefenbach *et al.* 1988; Osborn *et al.* 2017).

Food biomass sampled in foraging patches used by Black Ducks (*i.e.* mobile sites) remained consistent despite declining trends in biomass recorded at the fixed sites (Osborn *et al.* 2017). Given that food resources decompose or are exploited during winter in some wetland units, managers often flood other impoundments to provide new food resources and mimic historical flood events for wintering waterfowl (Fredrickson & Taylor 1982). The consistency in the food biomass estimates which we detected across months at the mobile sites suggests that Black Ducks adaptively exploited these newly inundated resources (Davis *et al.* 2009; Hagy *et al.* 2014). Perhaps Black Ducks within our study area selected patches with a minimum food density (but above a foraging threshold) rather than patches with the greatest food because they employed a risk-minimising strategy and were not limited by food density during winter (Hagy *et al.* 2017). Conversely, Black Ducks may meet their energetic needs in briefer periods of time when feeding in moist-soil and corn, which allowed them to rest in less food-rich areas, such as forested wetlands. For example, our seed and tuber biomass estimates in corn fields excluded grain, which often remained aggregated on cobs attached to partially-standing stalks after being manipulated (rolled) by farm machinery. Food density in corn fields exceeded all other resource types by at least 10-fold, so Black Ducks could have gained a large amount of resources there in a small amount of time. Although it was not part of our formal analyses, anecdotally, Black Ducks seemed to select emergent and open water areas bordered by wooded or scrub-shrub vegetation (Monroe *et al.* 2021). This habitat structure could enhance the birds ability to hide or escape from predators or competitors which, together with access to food resources, may improve their survival and ultimate fitness levels.

Black Ducks exploit waste grain when and where available throughout their winter range (Baldassarre 2014). Although evidence regarding the overall importance of agricultural crops to Black Ducks is inconclusive, our results combined with those of Monroe *et al.* (2021) suggest that they may be a relatively minor component of the wetland complex used by Black Ducks in the Tennessee River Valley. Research in this or other relevant regions to determine the energetic benefits (*e.g.* true metabolisable energy) of agricultural crops (*e.g.* corn, milo, millet) compared to natural foods (*e.g.* submersed aquatic vegetation, moist-soil seeds and tubers) for Black Ducks would be informative and help to guide management decisions (Coluccy *et al.* 2015). From the information currently available, diurnal resource use and behaviour of Black Ducks does not appear to be substantially influenced by food density, at least as detected by our ability to measure food availability in waterfowl sanctuaries in the Mississippi Flyway. We suspect that changes in the distribution of the breeding population or in the size of the US portion of the Mississippi Flyway breeding stock, along with the effects of climate change, are much more important factors to be considered than winter food abundance and distribution for conservation of the Black Duck population (Brook *et al.* 2009; Lavretsky *et al.* 2014; Meehan *et al.* 2021).

We recommend that wetland complexes containing a mix of herbaceous, woody and submersed aquatic vegetation are maintained or extended for Black Ducks in west Tennessee, which is consistent with their habitat selection tendencies, limited response to current food densities, and their activities therein (Monroe *et al.* 2021). We do not know the ideal proportional composition or juxtaposition of these resources (*sensu* Pearse *et al.* 2012), but incorporating hydrological, physical, chemical and other management techniques to produce a diverse wetland complex is consistent with the diverse needs of Black Ducks and other waterfowl wintering in Tennessee (Osborn *et al.* 2017). In particular, we recommend altering water management strategies to increase the production and availability of submersed aquatic vegetation to Black Ducks during winter, as this wetland community type has declined substantially within our study area over the last 20 years. These adaptive management strategies could include stabilising water levels in the

Tennessee River during vegetation growth periods, conducting partial drawdowns of deep aquatic bed areas during winter, and managing some impoundments for semi-permanent, emergent marsh vegetation (*e.g.* Hine *et al.* 2017; McClain *et al.* 2019). Partial drawdowns of impoundments and pumping off excess water in areas where submersed aquatic vegetation is overtopped or deep following senescence may increase the availability of foliage to Black Ducks and other waterfowl. Provision of mudflats in portions of these NWRs may also be a viable strategy where achievable, mimicking other important resources used by Black Ducks along coastal wetland areas of the Atlantic Flyway (Plattner *et al.* 2010). Mudflats remain something of an enigma, however, in that they generally contained little food yet the Black Ducks spent considerable time foraging about them. It could be that invertebrate "hotspots" exist within mudflats and that the Black Ducks are able to locate and exploit them, such as in the wetland systems of Long Island, New York (Plattner *et al.* 2010). Despite the apparently low densities of food in the mudflats, they also appeared to be an attractive habitat resource for Black Ducks in interior wetlands, by providing a safe place to rest and conduct other activities within our study area.

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