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Research Article

Habitat Selection and Activities of Dabbling Ducks during Non-Breeding Periods

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ABSTRACT Western Tennessee is an important region for waterfowl during non-breeding periods, supporting >40% of the Mississippi Flyway population of American black ducks (*Anas rubripes*). Understanding habitat selection and activities of waterfowl during the non-breeding period is important for directed habitat management on national wildlife refuges and in other wetlands important in meeting regional waterfowl conservation objectives. During November–February 2011–2013, we investigated diurnal habitat selection and activities of dabbling ducks (Anatini) among 5 common wetland types relative to emergent cover, water depth, and energetic carrying capacity (i.e., duck energy days [DEDs]) in western Tennessee, USA. We observed waterfowl daily and sampled food resources monthly at Tennessee and Cross Creeks National Wildlife Refuges. Mallard (*Anas platyrhynchos*), gadwall (*A. strepera*), northern pintail (*A. acuta*), and American green-winged teal (*A. carolinensis*) selected moist-soil wetlands over wooded, aquatic bed, and open water wetland types. Gadwall also selected deeper wetlands containing submersed aquatic vegetation. Foraging was the dominant activity of all dabbling ducks in mudflats and moist-soil wetlands, and it was also dominant in wooded wetlands for green-winged teal and gadwall. Deep, open water was avoided by dabbling ducks. Selection of wetland types was negatively correlated with increasing water depth and positively correlated with increasing emergent cover and DEDs. Shallowly flooded moist-soil and wooded wetlands provide high-energy foods and dense emergent cover, and are important to a diversity of dabbling ducks during winter. © 2017 The Wildlife Society.

KEY WORDS behavior, energetic carrying capacity, habitat selection, Mississippi flyway, Tennessee, waterfowl.

Since the early 1980s, researchers have recognized the need for additional information on the ecology of waterfowl during non-breeding periods in North America (Reinecke 1981, Anderson and Batt 1983, Weller 1988, Reinecke et al. 1989). Prior to discoveries linking winter habitat conditions to subsequent recruitment in mallard (*Anas platyrhynchos*) and northern pintail (*A. acuta*; Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Osnas et al. 2016), waterfowl ecologists believed the breeding season primarily influenced annual waterfowl population trajectories (Weller 1988). Indeed, nest success and survival of nesting females and neonates are important drivers of duck populations (Hoekman et al. 2002), but events and habitat conditions along migration and wintering areas also influence waterfowl recruitment (Kaminski and Gluesing 1987, Devries et al. 2008, Osnas et al. 2016).

The North American Waterfowl Management Plan (NAWMP) was created in 1986 and is considered a model for successful wildlife management and conservation planning (NAWMP 2012). The NAWMP is implemented through Joint Ventures (JV), which are regional partnerships among government and non-government natural resource organizations with a common conservation goal. Providing high-quality foraging habitat for waterfowl is a major goal of several JVs in regions primarily used by waterfowl during non-breeding periods (e.g., Lower Mississippi Valley Joint Venture). Non-breeding waterfowl are gregarious and often form mixed species flocks, so providing adequate food and other resources for diverse taxa that exhibit different life-history strategies and migration chronologies is a challenge for habitat managers (Fredrickson and Taylor 1982, Fredrickson and Reid 1988, Davis et al. 2014). Furthermore, waterfowl exploit habitat differently to meet specific

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physiological or behavioral needs. Mallards, for example, consume high-energy seeds and invertebrates in moist-soil, forested, and agricultural wetlands, but they may also use forested wetlands for pair-bonding or thermal cover (Heitmeyer 2006, Kross et al. 2008). Land managers are often tasked with provisioning wetland complexes to meet the needs of diverse guilds of waterfowl during migration and winter (Reinecke et al. 1989, Kross et al. 2008, Pearse et al. 2012). However, knowledge of key mechanisms that influence habitat selection in waterfowl, some of which certainly include food density and sanctuary conditions, is limited (Beatty et al. 2014, Kaminski and Elmberg 2014).

Western Tennessee, USA is an important stopover and wintering area for waterfowl in the Mississippi Flyway (Sanders et al 1995, Baldassarre 2014). Similar to many other areas of North America, much of the region's historical waterfowl habitat has been lost or degraded from flood control and river channelization, agriculture, and urban expansion (U.S. Fish and Wildlife Service [USFWS] 2014). Western Tennessee is also an important wintering area for American black ducks (*Anas rubripes*; black ducks), although the Mississippi Flyway population of the species continues to decline (Sanders et al. 1995, USFWS 2014, Osborn 2015, Newcomb et al. 2016). Several national wildlife refuges in this region prioritize habitat management practices to benefit black ducks. Previous studies have investigated habitat use and selection of black ducks in western Tennessee during autumn and winter (Chipley 1995, Clark 1996, Osborn 2015, Newcomb et al. 2016); however, these studies did not examine habitat selection among several dabbling duck species (Anatini), which may co-exist and potentially compete with black ducks. Osborn (2015) reported that black ducks primarily co-occurred with other dabbling ducks on mudflats in western Tennessee. Thus, effective wetland management for black ducks must consider habitat selection and activities of other species and determine if management activities targeting a diversity of species are complementary.

The objective of our study was to investigate habitat selection and activities of dabbling ducks in western Tennessee, relative to existing habitat and management strategies. We investigated trends in food density and other wetland resource characteristics among wetland types and dabbling duck associations with factors that may influence habitat use. We hypothesized that 1) dabbling ducks would select moist-soil over other wetland types because of relatively high food density; 2) proportional activity of dabblers would vary by wetland type, but time spent foraging by birds would increase in wetlands with greater food density; 3) there would be positive influences of emergent vegetation cover and energetic carrying capacity on duck abundance and negative associations of water depth and vehicle disturbance on duck abundance; and 4) selection of wetland types would vary by duck species.

STUDY AREA

We conducted our study at the Duck River Unit of Tennessee National Wildlife Refuge (TNWR, 35°57′30N 87°57′00W) and Cross Creeks National Wildlife Refuge (CCNWR, 36°29′36N 87°47′40W) in western Tennessee, USA, during November–February 2011–2013. The refuges lie within the floodplain of the Cumberland and Duck rivers, are flat or gently sloping, and generally at or near 107 m above sea level. The Lower Cumberland Tennessee Ecosystem climate typically experiences warm, humid summers ($\bar{x}$ temperature >20°C), mild winters ($\bar{x}$ >1°C), and rainfall well-distributed seasonally ($\bar{x}$ annual of 1,346 mm; USFWS 2014). Combined, the refuges provide >2,000 ha of impounded wetlands managed primarily for migrating and wintering waterfowl. Managed and natural wetlands within these refuges include moist-soil vegetation, open water, submersed aquatic vegetation, fields cultivated for row-crop agriculture, and isolated bottomland hardwood forests.

The refuges, separated by approximately 60 km, collectively support 150,000 migrating and wintering ducks annually and both include black ducks as a focal priority species for management (USFWS 2014). The Duck River Unit of TNWR is approximately 10,820 ha and located at the confluence of the Tennessee and Duck rivers in eastern Benton and western Humphreys counties, Tennessee. The CCNWR is approximately 3,586 ha and borders the main canal of the Cumberland River in Stewart County, Tennessee. Both refuges are managed as sanctuaries for waterfowl and other waterbirds during winter, and waterfowl hunting is prohibited with the exception of a limited-access resident goose season in early September. Wetland management at TNWR and CCNWR fosters moist-soil, grain-producing agriculture (e.g., corn, milo), and natural wetlands associated with riverine systems including mudflats, open water, wooded wetlands, and submersed aquatic vegetation (USFWS 2014). Each refuge consists of leveed impoundments that are gradually inundated in fall and winter as waterfowl migrate into and out of the region. Impoundments are flooded via pumping, gravity flow through water control structures, or through accumulation of precipitation.

METHODS

Experimental Design

Prior to fall arrival of waterfowl, we established 4 sites at each refuge for each of 5 wetland cover types commonly used by waterfowl. Wetland types included palustrine emergent with primarily annual, herbaceous vegetation (i.e., moist-soil); exposed and shallowly flooded mudflats; aquatic bed with submersed aquatic vegetation (SAV); deep (>45 cm), open water devoid of vegetation (i.e., open water); and palustrine forested and scrub-shrub (wooded wetlands; Cowardin et al. 1979). Moist-soil vegetation primarily occurred within impoundments where hydrology was managed and draw-downs occurred annually. Wooded wetlands occurred in managed impoundments and in low-elevation areas connected to rivers and streams where hydrology was less static. Wooded wetlands were typically narrow (≤100-m width) areas of open water and stream channels bounded by scrub-shrub and forest vegetation. Mudflats occurred along the

Duck, Tennessee, and Cumberland rivers where hydrology was highly variable and generally prevented growth of emergent vegetation. Open water and aquatic bed wetlands occurred within impoundments and portions of the Duck, Tennessee, and Cumberland rivers. We also established and sampled unharvested, flood corn sites; but these were inundated much later (mid-Jan) and for a shorter period of time (~2 weeks) than other sites and ultimately excluded from analyses. We separated sites by >200 m to alleviate issues of spatial dependence. Although varying in size because of natural occurrence, we believed wetland sites were of sufficient size (i.e., ≥0.5 ha) to aid in determining habitat selection among waterfowl species (Johnson 1980).

We enumerated dabbling ducks by species ≥1 time/week from camouflaged tree stands or ground blinds during early December through late February of each winter at all sites. We conducted surveys along pre-determined daily routes that rotated weekly among observers and occurred between sunrise and 5 hours thereafter (~0700–1200). We did not conduct evening or nocturnal sampling because of availability of adequate night-vision optics, distances from observation locations to sites, and potential for increased disturbance of waterfowl, but we assumed diurnal use was representative of habitat use and selection (Hagy and Kaminski 2012*b*). We placed white polyvinyl chloride markers at 100-m intervals from observation blinds 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 used the estimated distance of fixed objects with a high-precision laser rangefinder (Buckland et al. 2001, Bolduc and Afton 2004). When sites were >60% inundated, we systematically measured water depth at 10 locations along 2 random transects within each site and erected a fixed depth gauge so that average depth could be recorded during surveys without disturbing waterfowl (Hagy and Kaminski 2012*b*). We were unable to erect water gauges in open water and mudflat sites because of deep or fluctuating water levels in riverine areas.

If birds flushed or were disturbed from a site immediately prior to or during a survey, we censored the survey and returned at a later time. If a minor disturbance occurred, we waited ≤5 minutes to allow waterfowl to resume normal activities before initiating a count. We recorded average water depth and obtained an ocular estimate of percent horizontal emergent vegetation cover (nearest 5%) within the site during each survey. We conducted a single 180° scan of the site with binoculars or a spotting scope and used a digital voice recorder to simultaneously enumerate, identify, and record distances and instantaneous activities of dabbling ducks ≤200 m from the blind (Kaminski and Prince 1981, Smith et al. 1995, Beck et al. 2013). In mudflat and open water sites, we surveyed to the distance at which we could no longer reliably identify birds (Smith et al. 1995), which did not exceed 800 m. We estimated distance to individuals and groups of birds to the nearest 10 m to aid in density estimation in Distance 6.0 (Buckland et al. 2001). We classified waterfowl activities as foraging (surface feeding, tipping up), resting (sleeping, loafing, inactivity), locomotion (walking, swimming), aggression (chasing, biting, fighting), courtship (displaying, copulation), alert (inactive with head erect), and maintenance (preening, bathing, stretching; Kaminski and Prince 1981; Paulus 1984, 1988). We did not include birds in flight during surveys (Buckland et al. 2001), and we did not sample waterfowl in dense fog or if winds exceeded 30 km/hour (Hagy and Kaminski 2012*b*). Because observations constituted a non-invasive field study (Pauli et al. 2010), an animal care and use protocol was not required nor was a scientific collecting permit needed from the State of Tennessee. All data were collected under an agreement between the University of Tennessee at Knoxville and the USFWS.

We assessed food density monthly using a standard core sampler (10-cm diameter and depth) in all shallow emergent (≤45 cm) and mudflat sites and a modified Gerking box sampler in open water, aquatic bed, and deeply flooded emergent sites (>45 cm; Sychra and Adamek 2010). We collected 5 samples systematically along a random transect within each site, washed each sample in the field through a 500-μm aperture sieve bucket (Wildco, Buffalo, NY, USA), and placed them in polyethylene bags for transport and storage. We preserved core, sweep, and box samples in 70% ethyl alcohol and stored them at −10°C (Salonen and Sarvala 1985).

In the lab, we thawed food samples, stained them with 1% rose Bengal solution, washed combined sets of 5 samples through graduated sieves (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 and Kaminski 2012*a*). We identified and enumerated macroinvertebrates by order, dried them for 24 hours 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 it as previously described for macroinvertebrates. Following removal of macroinvertebrates and SAV, we air dried remaining material for 24–48 hours, extracted all seeds and tubers known to be consumed by dabbling ducks from number 4 and number 14 sieves, identified seeds and tubers to genus or species and dried them for 24 hours at 60°C, and weighed foods to the nearest 0.1 mg (Hagy and Kaminski 2012*a*).

To account for materials in the number 50 sieve, which were too numerous and laborious to extract using previously described methods, we subsampled small-sieve contents from 3 sites for each wetland type, refuge, and year to create correction factors for small seeds. We extracted seeds from a 25% portion by mass and identified, dried, and weighed seeds using previously described protocols (Reinecke and Hartke 2005, Hagy et al. 2011, Livolsi et al. 2014). We adjusted each biomass estimate by the appropriate correction factor for contents of the small sieve, corrected estimates for processing bias (Hagy et al. 2011), and converted final biomass (kg[dry]/ha) of seeds, tubers, SAV, and invertebrates to duck energy days (DED/ha; Reinecke et al. 1989, Gray et al. 2013) using published, taxon-specific true metabolizable energy values (TME; Sherfy 1999, Checkett et al. 2002, Kaminski et al. 2003, Ballard et al. 2004). We present mean (SE, 95% CI) monthly densities of plant foods (combined seed, tubers, and SAV) and invertebrates.

Statistical Analyses

Waterfowl density.—We estimated waterfowl densities by species, week, and site. We used multiple covariates distance sampling analysis in Distance 6.0 to account for potential visibility bias among wetland cover types with differing emergent vegetation cover (Smith et al. 1995, Marques et al. 2007). We excluded 2 moist-soil sites (1 in each year) at TNWR because of late and inconsistent flooding. We assumed 100% detectability of birds in mudflat, open water, wooded, and aquatic bed wetlands because vegetation did not obstruct view and observers could readily observe birds from survey blinds (Hagy and Kaminski 2012*b*). Because of infrequent observations of northern shovelers (*Anas clypeata*), American wigeon (*A. americana*), and black ducks, we excluded these species from individual analyses. We used a global detection function and average detection probability across all spatial and temporal levels and species to generate density estimates by species in moist-soil wetlands. We estimated flooded and observable area (ha) of each site for density estimates using aerial imagery, light detection and ranging (LiDAR) elevation maps, and water depth gauge data in ArcMap 10.1® (Environmental Systems Research Institute, Redlands, CA, USA). We estimated densities for all taxa by dividing raw weekly abundances by flooded area within each site (ha) estimated monthly as previously described for mudflat, open water, wooded, and aquatic bed wetlands.

Waterfowl activity.—We summed counts for each activity and species (including dabbling ducks) by wetland type, and we performed chi-square tests of homogeneity by species to compare the percent occurrence of activities among wetlands for dabbling duck activities (PROC FREQ in SAS version 9.3; Zar 1999). Observations of aggression, courtship, maintenance, and alert were low (7% of observations); therefore, we excluded these activities from total counts and final analyses.

Habitat selection.—Flooding coverage was not uniform among impoundments, study areas, and years; thus, we averaged densities (ducks/flooded ha) of dabbling ducks across weekly surveys to calculate a monthly average for each site, wetland type, refuge, and year. We modeled densities of each species and all dabbling ducks combined as a function of wetland cover type using separate linear mixed models (PROC MIXED in SAS version 9.3; SAS Institute, Cary, NC, USA; Littell et al. 2006). For each taxon, we designated wetland type as a fixed effect, year and refuge as random effects, and month as a repeated effect. We included only mudflats, moist-soil, and wooded wetlands for green-winged teal (*Anas carolinensis*) because of infrequent observations of this species in other wetland types. We included only mudflats and moist-soil sites for northern pintail because of infrequent detections in other wetland types. We interpreted a significant effect of wetland type using effect size and $\alpha = 0.05$.

We used Spearman rank correlations (PROC CORR in SAS version 9.3) to examine associations between duck taxa and water depth, emergent vegetation cover, and combined DEDs of plant foods and macroinvertebrates (Isola et al. 2000, McKinney et al. 2006). We used this approach because of missing values among water depth estimates, abundance of zeros in weekly dabbling duck densities, non-normality of vegetation cover estimates, and lack of variation in water depths in open water and aquatic bed. Prior to analyses, we grouped water depth estimates into functional categories (3–9 cm, 10–25 cm, 26–45 cm, and >45 cm; Isola et al. 2000, Taft et al. 2002). For rank correlations involving water depth and vegetation cover, we used all weekly survey data to increase sample size. We excluded mudflats from water depth correlations because depths could not be estimated. We used dabbling duck densities recorded on or closest to the day when we collected food samples in each site for rank correlations involving DEDs. We interpreted a significant effect using effect size and $\alpha = 0.05$.

To infer habitat selection, we used available habitat shapefiles from 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 to estimate refuge-wide flooded areas (ha) of each wetland type in ArcMap 10.1. Observers delineated flooded area monthly based on hand-drawn field maps. We calculated mean proportions of each species of dabbling duck in relation to total dabbling duck estimates among weekly surveys. We also estimated total flooded area (ha) among wetland types across refuges and years. We ranked proportions of flooded wetland availability and waterfowl densities (PROC RANK), and compared them to make inferences on selection among wetland types (Johnson 1980).

Table 1. Global parameter estimates from detection models in Distance 6.0 (Thomas et al. 2009) estimating dabbling duck densities in moist-soil wetland sites from November 2011 and 2012 through February 2012 and 2013 at the Duck River Unit of Tennessee National Wildlife Refuge (TNWR) and Cross Creeks National Wildlife Refuge (CCNWR), Tennessee, USA.

Study area	Habitat	K[a]	AIC[b]	ΔAIC[c]	n[d]	$g(y)$[e]	SE	% CV	95% CI
TNWR	Moist-soil wetlands	5	21,677.5	229.9	260	0.58	0.01	0.72	0.56–0.58
CCNWR	Moist-soil wetlands	5	7,320.9	111.2	232	0.65	0.01	0.98	0.64–0.66

[a] Number of model terms, including those for adjustment and covariate levels.
[b] Akaike's Information Criterion.
[c] Difference between top model and other models in the set.
[d] Number of weekly surveys.
[e] Mean probability of detecting an individual given its distance from the observer.

Disturbance.—We placed 8 TRAFx® vehicle counters (TRAFx Research, Canmore, Alberta, Canada) along major refuge roads to monitor and index disturbances at TNWR in each year. Counters continuously recorded the number of vehicle disturbances detected in hourly intervals across 24-hour periods. We downloaded data from each counter monthly from late December to late February. To make inferences about potential effects of disturbance on waterfowl selection, we summed dabbling duck densities for all sites that occurred within 500 m of each counter (Korschgen and Dahlgren 1992), and we plotted weekly densities against the number of detections among counters. We were unable to obtain data from the second year of study because of equipment malfunctions and because counters were not available for deployment at all sites.

Table 3. Monthly Spearman rank correlations[a] (ρ) of factors affecting wetland use by dabbling ducks from November 2011 and 2012 through February 2012 and 2013 at the Duck River Unit of Tennessee National Wildlife Refuge and Cross Creeks National Wildlife Refuge, Tennessee, USA.

	Water depth[b]		Vegetation cover[b]		DED/ha[c]	
Period	***n***	**ρ**	***n***	**ρ**	***n***	**ρ**
Dec	209	−0.283	274	0.448	50	0.488
Jan	209	−0.183	267	0.384	57	0.451
Feb	209	−0.174	266	0.426	58	0.437
Dec–Feb	627	−0.227	807	0.424	165	0.481

[a] All significant correlations using $\alpha = 0.05$.
[b] Covariates estimated during weekly surveys.
[c] Duck energy days (DED/ha) estimated once at the end of each month, and duck densities represent those estimated on or closest to the day of food samples collection.

RESULTS

Waterfowl and Energy Density

Global detection probabilities of dabbling ducks in moist-soil wetlands were approximately 58% at TNWR and 65% at CCNWR (Table 1). Duck densities differed among wetland types for all species (Table 2). Mean densities of mallard, northern pintail, gadwall (*Anas strepera*), green-winged teal, and combined dabbling ducks were greatest in moist-soil wetlands, but use of other wetland types varied by species (Table 2). Across species, duck densities in open water and mudflats were least among wetland types. Densities of dabbling ducks were negatively correlated with increasing water depth and positively correlated with increasing emergent vegetation cover and DEDs among wetland types (Table 3). We observed positive correlations between DEDs and densities of mallard ($\rho = 0.509$, $n = 50$), northern pintail ($\rho = 0.392$, $n = 50$), and green-winged teal ($\rho = 0.493$, $n = 50$) in December. Mallard densities were positively correlated with increasing emergent vegetation cover ($\rho = 0.404$–0.443) and DEDs ($\rho = 0.402$–0.509) in each month. Approximately 80% of total dabbling duck densities >0 occurred in 0–25% emergent vegetation cover ($n = 481$ surveys), and approximately 14% of total dabbling duck densities >0 occurred in water depths <45 cm. The greatest total dabbling duck density estimates occurred in flooding depths between 30 cm and 90 cm and in areas with 0–50% emergent vegetation cover.

During November–December, plant biomass was greatest in moist-soil, followed by wooded, aquatic bed, mudflat, and open water wetlands (Table 4). Plant food biomass (kg[dry]/ha) generally declined among wetland types during November–February ($\bar{x} = 61.8\% \pm 12.1$), with greatest declines in moist-soil (75.9%) and aquatic bed (88.5%) wetlands. Invertebrate biomass was greatest in mudflats, followed by wooded, moist-soil, aquatic bed, and open water wetlands in November–December (Table 4). Invertebrate biomass declined substantially from November to February in mudflat (79.4%) and aquatic bed (94.9%) wetland types, but it did not decline substantially in wooded (+70%) or moist-soil wetlands (39.2%). We did not detect measureable biomasses of plant or invertebrate foods in open water during any sampling period.

Waterfowl Activity

Proportional occurrence of activities differed among wetland types for mallard, gadwall, northern pintail, green-winged teal, and combined dabbling ducks (Fig. 1). Foraging was the primary activity of all species in moist-soil wetlands, including mallard (37%), gadwall (48%), green-winged teal (69%), northern pintail (58%), and combined dabbling ducks (46%). Both foraging (40%) and locomotion (42%) were predominant activities among combined dabbling ducks using mudflats. Foraging was the most common activity in mallard (41%), green-winged teal (91%), and

Table 2. Dabbling duck densities (birds/ha/month/site) and comparisons[a] among 5 common wetland types during November 2011 and 2012 through February 2012 and 2013 at the Duck River Unit of Tennessee National Wildlife Refuge and Cross Creeks National Wildlife Refuge, Tennessee, USA. Densities averaged across weekly surveys for each month prior to analyses.

	Wooded ($n = 44$)		Mudflat ($n = 45$)		Moist-soil ($n = 33$)		Open water ($n = 47$)		Aquatic bed ($n = 36$)	
Species	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**
Mallard	17.1B	7.7	4.0BC	1.0	55.8A	9.2	1.0C	0.5	10.9B	2.8
Gadwall	6.4BC	1.3	3.6BC	1.0	21.1A	7.8	0.2C	0.1	15.8AB	2.9
Northern pintail	0.2	0.1	0.1B	0.0	15.2A	7.8	0.0	0.0	0.3	0.1
Green-winged teal	16.4AB	5.9	0.5B	0.2	31.4A	18.0	0.0	0.0	0.7	0.5
Total	38.5B	9.0	8.2B	1.6	123.9A	33.2	1.3B	0.7	27.7B	4.8

[a] Means in the same row but with different capital letters are significantly different ($P < 0.05$) based on Tukey–Kramer multiple pairwise comparisons test of least squares means. Means without letter groupings were not included in pairwise comparisons.

Table 4. Densities (kg[dry]/ha/site) of waterfowl foods recovered from benthic and nektonic samples taken monthly from 5 common wetland types[a] used by waterfowl from November 2011 and 2012 through February 2012 and 2013 at the Duck River Unit of Tennessee National Wildlife Refuge and Cross Creeks National Wildlife Refuge, Tennessee, USA.

	Wooded ($n = 56$)			Mudflat ($n = 60$)			Moist-soil ($n = 45$)			Aquatic bed ($n = 28$)		
Taxon and month	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI
Plant[b]												
Nov	164.6	82.5	0–348.4	16.2	3.7	8.7–24.0	633.5	140.8	314.9–952.1	26.2	13.1	0–58.3
Dec	233.2	112.0	0–475.3	10.5	3.7	2.6–18.4	518.1	118.8	253.3–782.9	0.6	0.4	0–1.6
Jan	162.8	70.8	12.0–313.7	14.6	5.3	3.3–25.9	257.5	84.0	72.7–442.4	0.4	0.3	0–1.1
Feb	89.2	38.7	3.7–171.8	10.2	4.2	1.2–19.1	152.4	63.3	13.0–291.8	3.0	3.0	0–10.2
Invertebrate												
Nov	18.8	5.9	5.6–32.0	165.5	64.2	27.7–303.3	16.6	6.1	2.8–30.4	13.9	4.1	3.9–23.9
Dec	42.1	12.4	15.4–68.9	133.9	52.4	21.5–246.4	20.8	7.0	5.2–36.5	0.2	0.1	0–0.5
Jan	13.8	4.6	3.9–23.7	46.8	25.2	0–100.8	17.4	8.3	0–35.6	0.0	0.0	0–0.1
Feb	32.1	10.0	10.9–53.4	34.0	23.7	0–85.0	10.1	3.5	2.4–17.9	0.7	0.7	0–2.2

[a] Open water produced no measurable food biomass during sampling ($n = 30$).
[b] Combined estimate of seeds, tubers, and vegetation commonly consumed by waterfowl.

northern pintail (63%) observed on mudflats. Locomotion was the predominant activity among gadwall (55%) and common among mallard (40%) using mudflats.

Similar to mudflats, foraging (40%) and locomotion (37%) were the dominant activities among combined dabbling ducks using wooded wetlands. For mallard, locomotion (43%) and resting (39%) were dominant activities, whereas gadwall (57%) and green-winged teal (53%) primarily foraged in wooded wetlands. Locomotion was the dominant activity observed among combined dabbling ducks (56%) using aquatic bed wetlands. Locomotion dominated there for mallard (55%) and gadwall (57%). Foraging and resting were also frequently observed among mallard (22% and 24%, respectively) and gadwall (21% and 22%, respectively) in aquatic bed. Foraging was dominant among green-winged teal in this wetland type (49%). Mallard and gadwall constituted 98% of species observed in open water (73% and 25%, respectively). There, the primary activity was locomotion for mallard (76%) and gadwall (50%). Gadwall also spent 39% of their time resting in open water wetlands.

Habitat Selection and Disturbance

Among refuges and years, open water was the most available wetland type ($\bar{x} = 6{,}602.5 \pm 48.3$ ha/month), but ranked proportions of dabbling duck abundances were least in open water (Table 5). Proportional abundances of all species except gadwall were greatest in moist-soil, which was the second-most available wetland type ($\bar{x} = 1{,}031.7 \pm 67.6$ ha/month). Gadwall were most abundant in aquatic bed, which was the least available wetland type ($\bar{x} = 387.0 \pm 30.1$ ha/month). Additionally, all species used aquatic bed and mudflats in greater ranked proportion than available. Green-winged teal was the only species to use wooded wetlands in greater proportion than ranked availability, which was the

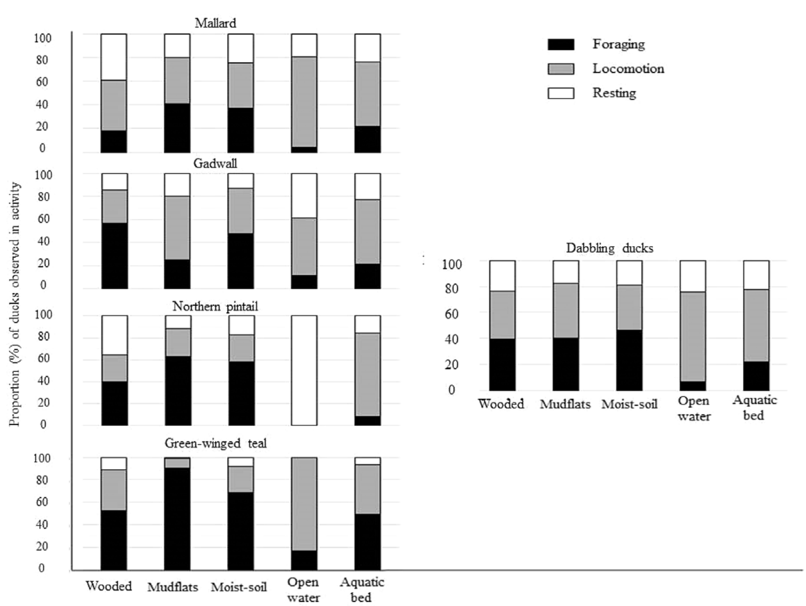

Figure 1. Proportional occurrence of foraging, locomotion, and resting observed among mallard, gadwall, northern pintail, American green-winged teal, and combined dabbling ducks among 5 wetland types during November 2011 and 2012 through February 2012 and 2013 at the Duck River Unit of Tennessee National Wildlife Refuge and Cross Creeks National Wildlife Refuge, Tennessee, USA.

third-most available wetland type ($\bar{x} = 546.9 \pm 10.1$ ha/month).

Vehicle counters at TNWR detected 3.5 ± 0.3 disturbances/day/counter in December, 6.8 ± 1.5 disturbances/counter/day in January, and 5.4 ± 0.4 disturbances/counter/day in February. Among the 8 vehicle counters placed at TNWR, 4 counters functioned throughout winter and had duck observation sites occurring within 500 m, which consisted of 4 wooded and 2 moist-soil wetlands. Dabbling duck densities and vehicle disturbances showed inverse trends from mid-December through early January (Fig. 2), although disturbance explained little variation in waterfowl densities ($r^2 = 0.1$), likely because of the small number of vehicle counters ($n = 4$).

DISCUSSION

Habitat complexes provide diverse wetland resources to help meet needs of wintering waterfowl in and near the lower Mississippi Valley (Reinecke et al. 1989, Pearse et al. 2012, Lancaster et al. 2015). Our results identified mechanisms underlying the importance of multiple wetland types to support the diverse needs of many different species of dabbling ducks in our study area. We identified a diversity of food resources among various natural wetland types in western Tennessee and documented the rapid decline of those resources where abundant. Throughout most of winter, open water, wooded, and aquatic bed wetlands likely provide less food energy to most species of dabbling ducks compared to moist-soil wetlands, and primarily served other habitat functions (e.g., sanctuary, pair bonding, thermal cover). Conversely, food resources in moist-soil and mudflat wetlands were apparently used during November through January until mean levels were likely too low to provide substantial energy to foraging birds (Hagy and Kaminski 2015, Hagy et al. 2017*b*). Although densities of most species were greatest in moist soil where food densities were also greatest, this trend was inconsistent across other wetland types and patterns of habitat use and selection were likely influenced by many factors within our study area.

Because many managed wetlands on public and private lands used by wintering waterfowl are hunted or are open to public use in the Lower Mississippi Valley, identifying true patterns of habitat selection based on resource availability and need can be challenging (Pearse et al. 2012). Disturbance to waterfowl (e.g., hunting and traffic) on our study area was minimal when compared to surrounding public and private habitat and perhaps approximates true habitat selection in terms of resource exploitation (Fretwell and Lucas 1970; *sensu* Wiens 1976, 1977, 1985). Although our sample size was small and trends in duck densities may have been related to other factors (e.g., food abundance and changes in migratory behavior), our results support previous research suggesting human disturbance influences dabbling duck distribution and behavior. Incremental effects of disturbances from refuge personnel, researchers, and others (e.g., refuge visitors) may negatively waterfowl activities and thus should be minimized within areas designated as sanctuaries (Hagy et al. 2017*a*). Human disturbance, for example, may stress waterfowl and cause them to forage more, which could result in declines in energetic carrying capacity (Platteeuw and Henkens 1997). Waterfowl also show variable responses to human disturbances based on their frequency, duration, and nature of disturbance (Platteeuw and Henkens 1997, Pease et al. 2005), but we did not test this in our study. Although Pease et al. (2005) suggested that waterfowl can become conditioned to disturbance from humans, Conomy et al. (1998) cautioned that such conditioning to disturbance may be species specific. We hypothesize that dabbling ducks may not have fully acclimated to disturbances in our study, otherwise we would have predicted that densities would have increased or stabilized with increasing disturbance, but we saw no such patterns. The topic of human disturbance in and around areas designated as sanctuaries requires additional research to determine if linkages exist between disturbance and demographic rates, such as survival. Additional research should be conducted to evaluate the effect of human disturbance (e.g., from researchers, wetland managers), on and near national wildlife refuges intended to provide sanctuary for resting and foraging waterfowl during the non-breeding period (McKinney et al. 2006).

Moist-soil, aquatic bed, and mudflat wetlands provide important resources for waterfowl today, but they also represent wetlands that birds encountered during autumn and winter in eras prior to deforestation, flood control, and agriculture conversion in the Mississippi Alluvial Valley. Dabbling ducks primarily foraged in moist-soil wetlands during our study, but several species also extensively foraged in other natural wetland types such as mudflats, aquatic bed, and wooded wetlands. In both Europe and North America, green-winged teal exploit tidal and other mudflats for food (Johnson and Rohwer 2000, Guillemain and Elmberg 2014). Mudflats in our study area contained high densities of invertebrates, primarily aquatic snails (Gastropoda) and midge larvae (Diptera), important foods for green-winged teal and northern pintail (Euliss and Harris 1987, Anderson et al. 2000). Mudflats along reservoirs and large rivers of western Tennessee may provide important foraging habitat, but management of mudflats is complex and relies on the timing of reservoir drawdowns conducted by multiple

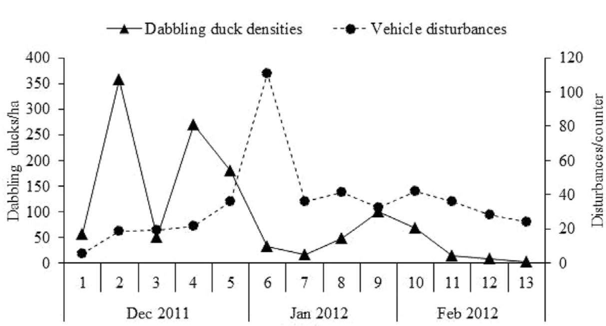

Figure 2. Weekly trends in the mean number of vehicle disturbances detected by counting devices ($n = 4$) and dabbling duck densities occurring in sites within 500 m of counters along major roads during early December 2011 through late February 2012 at the Duck River Unit of Tennessee National Wildlife Refuge, Tennessee, USA.

Table 5. Estimates and ranks (in parenthesis) of percent dabbling duck occurrence (birds/month pooled across sites, refuges, and years) and availability among of 5 common wetland cover types from November 2011 and 2012 through February 2012 and 2013 at the Duck River Unit of Tennessee National Wildlife Refuge and Cross Creeks National Wildlife Refuge, Tennessee, USA.

Wetland type	Mallard	Gadwall	Northern pintail	Green-winged teal	Availability[a]
Open water	2.7 (5)	1.6 (5)	0.1 (5)	0.1 (5)	73.5 (1)
Moist-soil	45.2 (1)	21.1 (3)	91.7 (1)	51.0 (1)	11.5 (2)
Wooded	6.6 (4)	7.1 (4)	0.7 (4)	29.3 (2)	6.1 (3)
Mudflats	32.4 (2)	31.9 (2)	5.2 (2)	15.4 (3)	4.6 (4)
Aquatic bed	13.1 (3)	38.3 (1)	2.4 (3)	4.2 (4)	4.3 (5)

[a] The proportion of flooded area (ha/month) among wetland types studied (includes exposed and shallowly flooded mudflats [<45 cm]), pooled across refuges and years.

agencies (e.g., Tennessee Valley Authority [TVA]; Laux 2008, Wirwa 2009). Cooperation among USFWS, TVA, and other responsible agencies is necessary to ensure sufficient mudflats are available to dabbling ducks and other waterbirds at critical times during the non-breeding period.

Foraging was the dominant activity observed among green-winged teal, gadwall, and northern pintail in wooded wetlands, but not among mallard. We noted few red oaks (*Quercus* spp.) or other acorn-producing trees within wooded sites and assert that their value as foraging habitat was probably limited to moist-soil vegetation along the margins produced during natural summer drawdowns (Reinecke et al. 1989, Davis et al. 2009). We speculate based on the moderate food densities and mixed dominance of foraging and non-foraging activities among duck species that species may select these cover types for different resource needs. For instance, wooded wetlands during our study mimicked vegetated openings in forested wetlands that may have occurred incidentally within expansive bottomland forests that once covered the Lower Mississippi Valley. Forested wetlands are consistently used by as many as 8 species of waterfowl during the non-breeding period (Fredrickson and Heitmeyer 1988), and mallard, northern pintail, and green-winged teal have all been previously reported to have positive associations with forested and scrub-shrub wetland types in the southeastern United States (Gordon et al. 1998). The importance and value of wooded wetland cover in our study likely ranged from provision of foraging habitat for green-winged teal and gadwall to provision of isolated areas for pair bonding or cover for mallard.

Aquatic bed was most extensively used by gadwall and mallard, although there was evidence of selection by all dabbling duck species observed. Unlike other dabbling ducks, gadwall primarily feed on SAV (Paulus 1982, 1984; McKnight and Hepp 1998), which was not abundant in moist-soil or other wetland types during our study. Food densities in aquatic bed declined >90% from November to December, most likely because of senescence of SAV and increases in water depth. At that time, gadwall may have shifted to foraging on abundant high-energy seeds in moist-soil or other wetland types (Paulus 1982, Euliss and Harris 1987, Benedict and Hepp 2000). Use of moist-soil seeds presumably would have reduced foraging time and increased energetic gains if gadwall can extract energy from seeds and tubers similar to other waterfowl species (MacArthur and Pianka 1966). Aquatic bed may be an important wetland type for several species of dabbling ducks, even after senescence of SAV reduces its foraging value.

Across wetland types, densities of dabbling ducks generally declined with increasing water depth but increased with emergent vegetation cover. Wetlands flooded 10–25 cm deep often attract the greatest abundances and promote foraging in dabbling ducks (Isola et al. 2000, Hagy and Kaminski 2012*b*); however, most wetland use occurred in areas flooded >30 cm in our study. Within our study area, impoundments often flooded quickly and to mean depths beyond 10–25 cm by the time peak abundances of dabbling ducks occurred. Most dabbling duck species, however, can readily exploit deeper flooding depths by shifting their foraging strategy, and deeper flooding depths may facilitate resource partitioning and less competition among species (Guillemain et al. 2000, 2002). Densities of dabbling ducks were also positively correlated with greater emergent cover. Positive relationships between dabbling duck densities and interspersion of emergent vegetation has been previously documented (Kaminski and Prince 1981, Gordon et al. 1998, Smith et al. 2004, Moon and Haukos 2008, Webb et al. 2010). Emergent vegetation creates structural complexity and edge (Kaminski and Prince 1981, Smith et al. 2004), may be associated with reduced predation risk (Euliss and Harris 1987, Moon and Haukos 2008), provides thermal cover during cold periods (Jorde et al. 1984), and provides visual isolation for courtship and pair formation (Rave and Baldassarre 1989). The proximate cues of interspersed cover and water to birds may be indicative of aspects of habitat quality, such as food density and availability.

Densities of dabbling ducks in our study area were positively correlated with energy density (i.e., DEDs) throughout winter. Gordon et al. (1998) and Cox and Afton (1997) also observed associations between habitat use of dabbling ducks and the area of wetlands containing abundant foods. Research is limited that formally tests the hypothesis of food limitation on waterfowl during non-breeding periods (Hagy and Kaminski 2015, Hagy et al. 2017*b*). Food limitation during non-breeding periods may reduce body condition and have carry-over effects on subsequent survival and recruitment during the breeding season, but the relationship between waterfowl and food densities is complex (Hagy et al. 2014, Williams et al. 2014). Factors such as the distribution and quality of foods among and within wetlands (Charnov 1976) and across landscapes (Beatty et al. 2014), water depth (Isola et al. 2000), species morphological limitations (Pöysa 1983), disturbance (McKinney et al. 2006), and climate or weather conditions (Jorde et al. 1984, Osnas et al. 2016, Petrie et al. 2016) can directly or indirectly influence the availability, accessibility, and profitability of foods (Krapu and Reinecke 1992). Additionally, metabolic rates and metabolizability of foods also vary among waterfowl species, which further complicates estimates of carrying capacity (Williams et al. 2014). Thus, our results suggest the importance of formally testing the food limitation hypothesis in regions used by migrating and wintering waterfowl to better understand the importance of providing high-quality foraging habitats.

Our estimate of plant food densities in moist-soil wetlands in western Tennessee (633.5 kg/ha) is similar to estimates reported in the Mississippi Alluvial Valley (550 kg/ha; Kross et al. 2008), the Upper Mississippi River Valley/Great Lakes regions (377–570 kg/ha; Brasher et al. 2007), and the Illinois River Valley (691.3 kg/ha; Stafford et al. 2011). Moreover, our estimate is considerably greater than was reported in palustrine emergent wetlands in the Upper Midwest during spring (208 kg/ha; Straub et al. 2012) and in Wetland Reserve Program easements in the Mississippi Alluvial Valley during winter (263.5 kg/ha; Olmstead et al. 2013). These differences may be attributed to wetland management strategies, climate, and regional and seasonal plant succession patterns (Hagy et al. 2014). Variation may also have arisen among regional food density estimates because of ambiguity regarding foods and non-food taxa of waterfowl (Hagy and Kaminski 2012*a*). Despite moist-soil wetlands having the greatest plant biomass in early winter in our study, foods quickly declined in mid-late winter (i.e., late Jan) and apparently became similar to other wetland types. Although moist-soil wetlands provide important values to waterfowl and other wildlife (Fredrickson and Taylor 1982), this wetland type alone cannot satisfy the life-history requirements of a diverse assemblage of dabbling duck species during the entire non-breeding season, so provision of wetland complexes is encouraged for waterfowl during the non-breeding period (Reinecke et al. 1989, Pearse et al. 2012, Beatty et al. 2014).

Occurrence of row-crop agriculture is extensive in western Tennessee and is used by land managers to provide food for migrating waterfowl (USFWS 2009, 2010), particularly late in winter when natural foods and waste grains in harvested fields have significantly declined (Foster et al. 2010). Pearse et al. (2012) determined that landscapes with as much as 50% flooded agriculture were associated with greatest abundances of mallards and other dabbling ducks in western Mississippi. Although row-crop fields containing harvested and unharvested corn were managed for waterfowl at both CCNWR and TNWR during our study, most areas were extensively flooded only briefly during late winter ($\leq$3 weeks), which prevented a direct comparison of waterfowl use and food availability with other wetland cover types. Once flooded, densities of mallard (140–2,455 ducks/ha) and northern pintail (0.7–52.2 ducks/ha) in unharvested corn were high (McClanahan 2015), likely because of high food densities that have been previously reported to exceed 69,000 DEDs/ha in the region (Foster et al. 2010). High waterfowl densities, foraging rates (McClanahan 2015), and potential energy densities (Foster et al. 2010) suggest that flooding unharvested agricultural crops, such as corn, may be a suitable practice to increase energetic carrying capacity for waterfowl in late winter when food resources in natural wetland types have been depleted or are near an energetic profitability threshold (Hagy and Kaminski 2015).

MANAGEMENT IMPLICATIONS

Effective management of non-breeding waterfowl relies on finding efficient methods to accommodate numerous co-existing species within fragmented landscapes where wetlands are potentially limited. Because habitat selection and activity patterns in western Tennessee varied among dabbling duck species, we recommend that conservation planners and wetland managers provide a diversity of wetland types in habitat complexes. Research continues to advocate for provisioning moist-soil and wooded wetlands within primary foraging areas to meet the needs of these and other dabbling ducks. We recommend incremental flooding of impoundments to ensure seed availability during winter. Generally, providing a diversity of high-quality habitat flooded at different times during the autumn–winter non-breeding period may be required (Pearse et al. 2012). Lastly, human disturbance may affect wetland use by non-breeding waterfowl and habitat managers should carefully consider their frequency or intensity of disturbance if sanctuary is a primary management goal (Hagy et al. 2017*a*).

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