Wetlands (2012) 32:859–869
DOI 10.1007/s13157-012-0317-5

ARTICLE

Local and Landscape Associations Between Wintering Dabbling Ducks and Wetland Complexes in Mississippi

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Received: 5 August 2011 / Accepted: 20 June 2012 / Published online: 10 July 2012
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Abstract Landscape features influence distribution of waterbirds throughout their annual cycle. A conceptual model, the wetland habitat complex, may be useful in conservation of wetland habitats for dabbling ducks (Anatini). The foundation of this conceptual model is that ducks seek complexes of wetlands containing diverse resources to meet dynamic physiological needs. We included flooded croplands, wetlands and ponds, public-land waterfowl sanctuary, and diversity of habitats as key components of wetland habitat complexes and compared their relative influence at two spatial scales (i.e., local, 0.25-km radius; landscape, 4-km) on dabbling ducks wintering in western Mississippi, USA during winters 2002–2004. Distribution of mallard (*Anas platyrhynchos*) groups was positively associated with flooded cropland at local and landscape scales. Models representing flooded croplands at the landscape scale best explained occurrence of other dabbling ducks. Habitat complexity measured at both scales best explained group size of other dabbling ducks. Flooded croplands likely provided food that had decreased in availability due to conversion of wetlands to agriculture. Wetland complexes at landscape scales were more attractive to wintering ducks than single or structurally simple wetlands. Conservation of wetland complexes at large spatial scales (≥5,000 ha) on public and private lands will require coordination among multiple stakeholders.

Keywords Anatidae · Landscape · Mississippi Alluvial Valley · Wetland complex · Winter

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Introduction

Conservation of wintering waterfowl involves sustaining habitats birds use while meeting their annual-cycle events, including foraging, acquisition of nutrient reserves, pair formation, and molt (Heitmeyer 1988a, b; Lower Mississippi Valley Joint Venture Management Board 1990; Baldassarre and Bolen 2006). Conservation planning and implementation in waterfowl wintering regions, such as the Mississippi Alluvial Valley (MAV), are based on determining demand by waterfowl for food energy (assuming this resource may be limited) using daily ration models and allocating resulting habitat objectives to public and private lands in support of target population levels (Reinecke et al. 1989; Reinecke and Loesch 1996). Although useful for designing regional wetland conservation strategies, this process cannot determine the desired proportion or distribution of structurally and functionally different wetlands across landscapes (Reinecke and Baxter 1996). Because habitat features at local and landscape scales influence avian community structure, abundance, distribution, survival, and ultimately reproductive success of waterbirds (Fretwell 1972; Naugle et al. 2000; Fairbairn and Dinsmore 2001;

Riffell et al. 2003), investigating habitat associations of birds at multiple spatial scales remains a priority for conservation and management.

A conceptual model representing interactions among waterfowl, wetlands, and their habitat resources is the "wetland habitat complex" (hereafter, wetland complex; Dwyer et al. 1979; Brown and Dinsmore 1986; Fredrickson and Heitmeyer 1988). The premise of this model is that individual wetlands do not contain the variety of resources birds need; thus, birds seek a defined area with multiple wetlands providing diverse resources to meet daily and seasonally dynamic requirements (e.g., Krapu 1974; Dwyer et al. 1979). Although numerous field observations describing diverse wetland use by ducks are consistent with this conceptual model (Baldassarre and Bolen 2006:264–267), it has not been explicitly defined or evaluated for waterfowl during winter.

Herein, we use the conceptual framework of the wetland complex to examine relations between diurnal presence and abundance of wintering dabbling ducks (Anatini) and local and landscape features in the MAV portion of Mississippi. We combined data on duck locations and abundances collected during aerial surveys in this region during January 2003–2005 with contemporary satellite imagery classified into multiple wetland types for assessment of duck use of wetlands at both aforementioned scales (Pearse et al. 2008a). Our objectives were to 1) evaluate factors potentially related to components of the wetland complex that influenced occurrence and abundance of wintering ducks, 2) determine if local or landscape metrics most influenced duck distributions, and 3) describe landscape features important for waterfowl use of space. Fulfillment of these objectives represents an important step toward developing spatially explicit strategies for conservation and management of wintering waterfowl habitats at local and landscape scales in the MAV and potentially elsewhere.

Methods

Study Area

The MAV is a continentally important region for migrating and wintering waterfowl in North America (Reinecke et al. 1989). The MAV is the floodplain of the lower Mississippi River, covering 10 million ha and portions of seven states. Historically, the region was an extensive bottomland hardwood ecosystem composed of various hard- and soft-mast producing trees that provided forage and other resources for waterfowl and other wildlife (Fredrickson et al. 2005). Extensive landscape changes occurred during the 20th century, and large portions of the MAV were cleared of trees and used for agriculture and urban development (Reinecke et al. 1989). Our study area encompassed most of the MAV within the state of Mississippi (1.9 million ha) and was bounded to the south and east by the loess hills of the lower Mississippi River Valley and on the west by the Mississippi River (Pearse et al. 2008a).

Aerial Surveys

We located ducks during three aerial surveys conducted during 8–13 January 2003, 5–9 January 2004, and 24–27 January 2005, following Reinecke et al. (1992) and modified for our study (Pearse et al. 2008a). We conducted additional surveys each winter, but the three surveys conducted in January were temporally closest to acquisition dates of satellite images used to quantify habitat variables. The pilot navigated transects using a global positioning system (GPS) receiver and flew at a constant altitude of 150 m. The observer sat in the right-front seat and determined a 0.25-km wide transect boundary on that side of the plane with markers placed on the wing strut and window (Norton-Griffiths 1975). We recorded numbers of mallards (*Anas platyrhynchos*) and other dabbling ducks (e.g., northern pintail [*A. acuta*], American wigeon [*A. americana*], northern shoveler [*A. clypeata*], green-winged teal [*A. crecca*]) observed within each transect. Additionally, we recorded habitat type and a GPS location associated with each group of dabbling ducks observed (≥1 bird; Pearse 2007).

Habitat Data Layer

We obtained spatial data layers of wetlands present during surveys from Ducks Unlimited, Inc. (C. Manlove, Ducks Unlimited, Inc., Ridgeland, Mississippi, USA, unpublished data). Primary data layers were rasters representing vegetative land cover and presence of surface water. Land-cover maps were compiled annually from a combination of National Agriculture Statistics Service data (National Agricultural Statistics Service 2002–2004) and forest cover (Twedt and Loesch 1999). Distribution of surface water during winter was classified from Landsat-5 Thematic Mapper images, and we considered only flooded sites as potential waterfowl habitat because wintering ducks rarely used dry lands in the MAV and elsewhere (Fleskes et al. 2003; also see Pearse 2007). We designated water features present in winter images as permanent if they also were present in images from summer 2001. We used the combined land-cover and surface-water layers to represent potential wetlands available to waterfowl on 4 January 2003, 30 December 2003, and 17 January 2005. Although surface-water data did not correspond exactly with aerial survey dates, the data layers provided a reasonable representation of availability of surface water during that timeframe.

Using combined land-cover and surface-water layers, we identified nine structurally different land types to include in analyses: flooded soybean, flooded rice, flooded corn or grain sorghum, other flooded croplands, seasonal-emergent wetland, forested wetland, aquaculture pond, Mississippi River, and other permanent wetlands (e.g., oxbow lake). We defined flooded crops as areas with standing or harvested crops and inundated during surveys. We combined corn and grain sorghum because these were difficult to differentiate from the airplane and each covered a relatively small portion of the flooded area in our study (corn = 0.7 %; grain sorghum = 0.1 %; National Agricultural Statistics Service 2002–2004). We combined other croplands (e.g., cotton) into a single category because they apparently have minimal foraging or other values for waterfowl (Reinecke and Loesch 1996). Seasonal-emergent wetlands included wetlands dominated by natural herbaceous plants (e.g., moist-soil wetlands; Kross et al. 2008). Forested wetlands comprised all wetlands dominated by trees or shrubs (Fredrickson et al. 2005). We classified permanent wetlands including ponds, rivers, streams, and lakes into one category with two exceptions. We created separate categories for aquaculture ponds because they were especially attractive to northern shovelers and for the Mississippi River channel because few waterfowl were observed there.

Landscape Characteristics and Model Development

A central tenet of the wetland complex is that ducks disproportionately use areas with diverse and interspersed habitats because such areas provide daily and seasonally varying resources needed by wintering waterfowl (Fredrickson and Heitmeyer 1988; Reinecke et al. 1989). Implicit in the concept is that different wetlands of the complex exist within proximity of each other. Fredrickson and Heitmeyer (1988) speculated that habitats ≤10 km apart may constitute a wetland complex, but gave no empirical or theoretical basis for this criterion. We measured variables associated with locations of duck groups at two spatial scales. We designated a 0.25-km radius as the local scale and based this value on accuracy of GPS locations, which were approximate rather than exact because duck groups were distributed over 0.25 km perpendicular to the plane. Also, a radius of 0.25 km is equivalent to a circular area of 19.6 ha, which approximates the average size of managed wetlands on public and private lands in Mississippi (23.0 ha; U.S. Fish and Wildlife Service 2002). We based our selection of a landscape scale (4-km radius; 5,024 ha) on the average size of state and federal wildlife management areas in western Mississippi during our study (5,027 ha; U.S. Fish and Wildlife Service 2002).

We created polygons bounding local- and landscape-scale areas for each duck group from year-specific habitat layers in a geographic information system (GIS) and used program FRAGSTATS to quantify local and landscape-level habitat variables from these coverages (Table 1; McGarigal and Marks 1992). For each scale of analysis, we calculated proportion of area represented by each habitat type and other landscape metrics (Table 1). We quantified additional variables of interest, such as distance to and occurrence of sanctuary on public land within local and landscape scales, using ArcGIS 9.0 (Environmental Systems Research Institute 1996). Sanctuary included any area located on public lands with a policy of prohibiting harassment or hunting of waterfowl during winter. We obtained a spatial database of waterfowl sanctuaries from the LMVJV (B. Elliott, LMVJV, Vicksburg, Mississippi, unpublished data) but were able to include only sanctuaries on public lands because sanctuaries on private lands had not been surveyed.

We developed models a priori to explain occurrence and abundance of wintering ducks using five habitat components to represent the wetland complex hypothesis (i.e., flooded croplands, seasonal and permanent wetlands, managed sanctuary, habitat complexity, and the proportion of area flooded independent of habitat type). The five habitat components measured at two spatial scales represented ten a priori models of duck distribution and were constructed using covariates extracted from habitat layers (Table 1).

We grouped flooded soybean, rice, corn or grain sorghum, and other crop fields as one habitat component to represent the contribution of agricultural lands that provide high-energy food for wintering ducks (Reinecke et al. 1989; Stafford et al. 2006; Foster et al. 2010). Another habitat component grouped wetlands and ponds, including seasonal-emergent wetlands, permanent wetlands, forested or scrub-shrub wetlands, and aquaculture ponds. These wetlands are structurally different from croplands and provide natural seeds, tubers, and aquatic invertebrates consumed by waterfowl (Fredrickson and Taylor 1982; Fredrickson et al. 2005; Kross et al. 2008). Aquaculture ponds are classified as agricultural lands rather than jurisdictional wetlands (Mitsch and Gosselink 2007), but they provide important habitat for species such as northern shovelers (Dubovsky and Kaminski 1992).

At the local scale, we included a binary variable indicating presence or absence of managed sanctuary on public land within the area. At the landscape scale, we used distances from observations of duck groups to the nearest sanctuary and percentages of sanctuary within the spatial context as covariates. We recognize our analysis of dabbling duck association with sanctuaries was incomplete because we only were able to determine presence of sanctuaries on public lands. Nonetheless, we reasoned analysis of duck associations with known sanctuaries was important based on previous research indicating ducks respond positively to their availability (Madsen 1998; Evans and Day 2002; St. James 2011).

We used multiple measures to index complexity of wetlands used by ducks (Table 1). We quantified interspersion of

Table 1 Variables (acronyms) measured at local (0.25-km radius) and landscape (4-km radius) scales were grouped to represent five components of a wetland habitat complex and used to construct ten models describing distributions of wintering dabbling ducks in western Mississippi, January 2003–2005

Component	Local scale	Landscape scale
Flooded croplands	Presence of flooded soybean field (BEAN_LO)	Percent (%) of wetland area as flooded soybean field (BEAN_LA)
	Presence of flooded rice field (RICE_LO)	% of wetland area as flooded rice field (RICE_LA)
	Presence of flooded corn or grain sorghum field (CORN_LO)	% of wetland area as flooded corn or grain sorghum field (CORN_LA)
	Presence of other flooded croplands (OCROP_LO)	% of wetland area as other flooded croplands (OCROP_LA)
Wetlands and ponds	Presence of seasonal-emergent wetland (EMERG_LO)	% of wetland area as seasonal-emergent wetland (EMERG_LA)
	Presence of forested wetland (FW_LO)	% of wetland area as forested wetland (FW_LA)
	Presence of permanent wetland (PERM_LO)	% of wetland area as permanent wetland (PERM_LA)
	Presence of aquaculture pond (FISH_LO)	% of wetland area as aquaculture pond (FISH_LA)
Managed sanctuary	Presence of managed waterfowl sanctuary within area (REF_LO)	Distance of managed sanctuary from observation (REF_DIST)
		Presence of managed waterfowl sanctuary (REF_LA)
Complexity	Contagion index (CONTAG_LO)	Contagion index (CONTAG_LA)
	Average perimeter-area ratio for wetland patches within area (PARA_LO)	Average perimeter-area ratio for wetland patches within area (PARA_LA)
Flooded area	Presence of >50 % of area designated as seasonally or permanently flooded (WET_LO)	% of area designated as seasonally or permanently flooded (WET_LA)

habitats with two metrics: (1) contagion and (2) average perimeter-area ratio. For our analyses, contagion jointly represented interspersion (i.e., proximity of different wetlands to one another), dispersion (i.e., distribution of individual habitat types; McGarigal and Marks 1992), and wetland diversity (i.e., richness and evenness). The contagion metric ranged from 0 to 100; low values indicated high levels of interspersion and dispersion (i.e., greater habitat complexity) and high values indicated landscapes with low wetland diversity and interspersion. Based on the wetland-complex concept, we predicted occurrence and abundance of ducks to be negatively associated with the contagion index because low contagion (i.e., increased habitat complexity) would result in a positive waterfowl response. Perimeter-area ratio reflected the complexity of patch shapes within the landscape; small values represented simple shapes and large values represented complex shapes. We predicted duck occurrence and abundance would be associated positively with the average perimeter-area ratio among patches within landscapes.

Statistical Analyses

We conducted separate analyses for mallards and dabbling ducks other than mallards, because we suspected species-specific responses to wetland complexes but did not have large enough sample sizes for separate analyses of dabbling ducks other than mallards. The presence or absence of ducks was a binomial response; hence, we used general linear models with a logit-link function to model occurrence (GENMOD procedure; SAS Institute 2004). Because aerial surveys did not record locations where no ducks were observed, we generated these locations randomly from a GIS layer representing areas that had been surveyed, contained wetlands potentially attractive to ducks, and were >250 m from duck observations to ensure separation between used and random sites. The number of random locations selected each year equaled the number of sightings of duck groups in each winter survey. To model abundance of groups of mallards or of other dabbling ducks, we fit general linear models to observed group size (GENMOD procedure; SAS Institute 2004). Because the dependent variables were counts of individuals, we used a natural logarithm transformation to approximate a normal distribution (Gotelli and Ellison 2004).

We merged data from all three surveys for analysis and included year as a fixed effect in all models because we were most interested in detecting associations that were consistent among years rather than year-specific phenomena. We compared a priori models among all categories of habitat components representing the wetland complex (Table 1). We evaluated multicollinearity among covariates within models using variance inflation factors and found all values (i.e., ≤2.9) were within acceptable levels (<5; Montgomery et al. 2006). We fit models using maximum likelihood estimation and examined output statistics including second-order Akaike's Information Criterion (AIC_c), differences between AIC_c of the current model and minimum AIC_c in the model

set (ΔAIC_c), and model weights (w_i; Burnham and Anderson 2002). We also assessed the fit of global models containing all covariates by calculating a coefficient of determination (R^2; Nagelkerke 1991).

We performed supplementary analyses to compare habitat composition of landscapes occupied by different sized groups of ducks. For this comparison, we categorized flooded habitats into four classes that have importance for wetland managers: flooded croplands, seasonal-emergent wetlands, forested or scrub-shrub wetlands, and permanent wetlands. We compared proportional habitat composition among landscapes where we observed three contrasting levels of duck abundance (i.e., large groups, small groups, and none). Observations of large groups were those in the upper 5 % of the overall distribution of group sizes for mallards (≥100 individuals) and other dabbling ducks (≥200 individuals); observations of small groups were those where at least some ducks were present but abundance was less than large groups. Locations not used by ducks were the random locations described previously. We analyzed wetland composition of landscapes surrounding these locations using multivariate analysis of variance (GLM procedure; SAS Institute 2004). Dependent variables included proportions of wetlands surrounding locations, and the independent variable was categorized group size of ducks associated with the location. We used Wilks' Lambda to test the null hypothesis of no difference among groups and, when results were significant (α=0.05), we examined univariate tests and conducted multiple comparisons of group means using Tukey-Kramer adjustments for post hoc comparisons.

Results

Distributions of Mallards

We observed 522 groups of mallards during surveys in 2003, 155 groups in 2004, and 162 groups in 2005. A global model explained 34 % of variation in occurrence of mallard groups. The model respresenting flooded croplands at the local scale had greatest support (w_i=1.00; Table 2). The likelihood of mallard groups occurring at the local scale was 3.3 times (95 % CI: 2.5–4.4) greater in the presence of flooded soybean fields than when absent, 2.1 times (95 % CI: 1.6–2.7) greater with other associated croplands, 1.3 times (95 % CI: 0.9–1.6) greater with corn or grain sorghum present, and 1.1 times (95 % CI: 0.8–1.3) greater with ricefields present. The next two highest-ranked models of occurrence represented effects at the landscape scale and included covariates related to wetlands and flooded croplands. Models representing habitat complexity, wetland area, and managed sanctuary had no support.

The global model containing all potential covariates explained 20 % of the variation in abundance of mallard groups. The model representing croplands at the landscape scale accounted for 97 % of model weight. A model representing complexity at the landscape scale received the remaining model weight; thus, landscape-scale models accounted for all model weight (Table 2). The percentage of flooded rice and soybean lands at the landscape scale related positively to the size of mallard groups. Group size increased 6 % (95 % CI: 1–12 %) for each 1 % increase in flooded ricefields and 3 % (95 % CI: 1–4 %) for each 1 % increase in flooded soybean fields. Percentage of corn or grain sorghum and other flooded croplands were positively related to mallard abundance but confidence intervals included zero. Models representing wetlands and ponds and managed sanctuary performed poorly compared to the preceding models ($\Delta AIC_c \geq 29.5$, Table 2).

The configuration of wetlands in landscapes varied among locations associated with large mallard groups (≥100 individuals), small groups (<100 individuals), and areas that were not used (Wilks' lambda = 0.940, $F_{6,3346}$=17.5, P<0.001). Percentage of wetland area in croplands was greatest for the large mallard groups (47 %), 34 % for small mallard groups, and 27 % for areas not used by mallards (Table 4). Additionally, large groups of mallards occurred in landscapes with 20 % emergent and 20 % forested or scrub-shrub wetlands; small groups and areas without mallards were associated with decreased percentages of emergent wetland habitat (15–16 %) and increased percentages of forested wetlands (25–27 %). Percentage of wetlands designated as permanent was lowest for the large mallard groups (13 %), 25 % for small groups, and 31 % for areas not used. Overall, large mallard groups were observed in landscapes with 42 % (95 % CI: 37–48 %) of the total area flooded; small groups where 25 % of the area was flooded (95 % CI: 24–27 %), and landscapes where no mallards were observed were 27 % (95 % CI: 26–28 %) flooded.

Distributions of Other Dabbling Ducks

We observed 262 groups of dabbling ducks other than mallards in 2003, 83 groups in 2004, and 247 groups in 2005. A global model explained 29 % of variation in occurrence of dabbling duck groups. Models representing effects at the landscape scale had all model weight. A model representing flooded croplands at the landscape scale received greatest support (w_i=0.99; Table 3). The increase in likelihood of occurrence of dabbling ducks other than mallards for each 10 % increase in area of flooded habitat at a location was 1.3 (95 % CI: 1.1–1.8) for soybean fields, 2.1 (95 % CI: 1.3–3.2) for other croplands, 2.9 (95 % CI: 0.1–69.4) for corn or grain sorghum, and 1.1 (95 % CI: 0.5–2.7) for rice. Models representing sanctuary provided the least support in explaining variation in occurrence of other dabblers (Table 3).

Table 2 Model selection statistics summarizing effects of metrics representing components of a wetland habitat complex on the distributions (i.e., occurrence and abundance) of mallard groups observed during aerial surveys in western Mississippi, January 2003–2005

Response	Category[a]	Scale[b]	Model[c]	k[d]	ΔAIC_c[e]	w_i[f]
Occurrence	Croplands	Local	Y, BEAN_LO, RICE_LO, CORN_LO, OCROP_LO	8	0.0	1.00
	Wetlands	Landscape	Y, EMERG_LA, PERM_LA, FW_LA, FISH_LA	8	84.8	0.00
	Croplands	Landscape	Y, BEAN_LA, RICE_LA, CORN_LA, OCROP_LA	8	92.6	0.00
	Wetlands	Local	Y, FW_LO, EMERG_LO, FISH_LO, PERM_LO	8	93.7	0.00
	Complexity	Landscape	Y, CONTAG_LA, PARA_LA	6	111.8	0.00
	Complexity	Local	Y, CONTAG_LO, PARA_LO	6	162.8	0.00
	Flooded area	Landscape	Y, WET_LA	5	175.5	0.00
	Flooded area	Local	Y, WET_LO	5	180.3	0.00
	Sanctuary	Landscape	Y, REF_LA, R_DIST	6	183.3	0.00
	Sanctuary	Local	Y, REF_LO	5	208.6	0.00
Abundance	Croplands	Landscape	Y, BEAN_LA, RICE_LA, CORN_LA, OCROP_LA	8	0.0	0.97
	Complexity	Landscape	Y, CONTAG_LA, PARA_LA	6	6.8	0.03
	Croplands	Local	Y, BEAN_LO, RICE_LO, CORN_LO, OCROP_LO	8	18.4	0.00
	Complexity	Local	Y, CONTAG_LO, PARA_LO	6	21.9	0.00
	Flooded area	Landscape	Y, WET_LA	5	22.7	0.00
	Wetlands	Landscape	Y, EMERG_LA, PERM_LA, FW_LA, FISH_LA	8	29.5	0.00
	Flooded area	Local	Y, WET_LO	5	50.6	0.00
	Sanctuary	Local	Y, REF_LO	5	56.5	0.00
	Wetlands	Local	Y, FW_LO, EMERG_LO, FISH_LO, PERM_LO	8	59.1	0.00
	Sanctuary	Landscape	Y, REF_LA, R_DIST	6	66.5	0.00

[a] Conceptual category of theoretical wetland complex

[b] Spatial scale (local, 0.25-km radius; landscape, 4-km radius)

[c] Acronyms defined in Table 1

[d] Number of estimated parameters

[e] $\Delta AIC_c = AIC_{c\ i} - AIC_{c\ \min.}$ Min for occurrence = 2077.9; Min for abundance = 2579.0

[f] Model weight

The global model explained 18 % of variation in abundance of dabbling duck groups. Habitat complexity at local and landscape scales received most of the model weight ($\sum w_i$= 0.82; Table 3), and wetland area at local and landscape scales received the remainder. Models describing wetland complexes at local and landscape scales had similar model weight ($\sum w_i$= 0.58 vs. 0.42). These models indicated positive associations between group size and increasing habitat complexity at local and landscape scales (CONTAG_LA = −0.018, 95 % CI: −0.011, −0.024; CONTAG_LO = −0.013, 95 % CI: −0.008, −0.018; Fig. 1). Models describing effects of flooded croplands and public land sanctuary ranked last in the model set.

The configuration of wetlands in landscapes varied among locations associated with large groups (≥200 individuals), small groups (<200 individuals), and areas that were not used by dabbling ducks other than mallards (Wilks' lambda = 0.940, $F_{6,3346}$=17.5, P<0.001). Percentage of wetland area in flooded croplands was greatest (51 %) for large groups of other dabbling ducks, 33 % for small groups, and 28 % for areas that were not used (Table 4). Percentage of emergent wetlands varied little (10–12 %) relative to the occurrence or abundance of dabbling ducks. Large and small groups used landscapes with 20–24 % forested wetlands, whereas area of forested wetlands increased to 34 % where no dabbling ducks were observed. Percentage of wetlands designated as permanent was lowest (17 %) for large groups of dabbling ducks, 33 % for small groups, and 29 % for areas that were not used. Overall, the percentage of total landscape area flooded was 41 % (95 % CI: 34–48 %) for large groups of dabbling ducks, 29 % (95 % CI: 28–31) for small groups, and 28 % (95 % CI: 27–31 %) for locations where no ducks were observed.

Discussion

The wetland-complex concept has application for describing landscapes used by ducks during breeding (Brown and Dinsmore 1986; Krapu and Duebbert 1989), migration (Webb et al. 2010), and wintering seasons (Reinecke et al. 1989). We used this conceptual model as a framework for exploring relations between distributions of wintering ducks and wetlands in an agriculture-dominated landscape. Model

Table 3 Model selection statistics summarizing effects of metrics representing components of a wetland habitat complex on the distributions (i.e., occurrence and abundance) of groups of dabbling ducks other than mallards observed during aerial surveys in western Mississippi, January 2003–2005

Response	Category[a]	Scale[b]	Model[c]	k[d]	ΔAIC_c[e]	w_i[f]
Occurrence	Croplands	Landscape	Y, BEAN_LA, RICE_LA, CORN_LA, OCROP_LA	8	0.0	0.99
	Complexity	Landscape	Y, CONTAG_LA, PARA_LA	6	8.9	0.01
	Croplands	Local	Y, BEAN_LO, RICE_LO, CORN_LO, OCROP_LO	8	21.9	0.00
	Flooded area	Landscape	Y, WET_LA	5	51.3	0.00
	Wetlands	Landscape	Y, EMERG_LA, PERM_LA, FW_LA, FISH_LA	8	55.7	0.00
	Wetlands	Local	Y, FW_LO, EMERG_LO, FISH_LO, PERM_LO	8	60.6	0.00
	Complexity	Local	Y, CONTAG_LO, PARA_LO	6	77.1	0.00
	Sanctuary	Local	Y, REF_LO	5	78.1	0.00
	Sanctuary	Landscape	Y, REF_LA, R_DIST	6	80.1	0.00
	Flooded area	Local	Y, WET_LO	5	81.6	0.00
Abundance	Complexity	Landscape	Y, CONTAG_LA, PARA_LA	6	0.0	0.46
	Complexity	Local	Y, CONTAG_LO, PARA_LO	6	0.5	0.36
	Flooded area	Landscape	Y, WET_LA	5	2.6	0.12
	Flooded area	Local	Y, WET_LO	5	4.2	0.06
	Wetlands	Landscape	Y, EMERG_LA, PERM_LA, FW_LA, FISH_LA	8	14.2	0.00
	Croplands	Landscape	Y, BEAN_LA, RICE_LA, CORN_LA, OCROP_LA	8	15.0	0.00
	Wetlands	Local	Y, FW_LO, EMERG_LO, FISH_LO, PERM_LO	8	19.0	0.00
	Sanctuary	Local	Y, REF_LO	5	21.5	0.00
	Croplands	Local	Y, BEAN_LO, RICE_LO, CORN_LO, OCROP_LO	8	21.8	0.00
	Sanctuary	Landscape	Y, REF_LA, R_DIST	6	27.5	0.00

[a] Conceptual category of theoretical wetland complex

[b] Spatial scale (local, 0.25-km radius; landscape, 4-km radius)

[c] Acronyms defined in Table 1

[d] Number of estimated parameters

[e] $\Delta AIC = AIC_{c\ i} - AIC_{c\ min.}$ Min for occurrence = 1556.9; Min for abundance = 1856.3

[f] Model weight

selection indicated flooded croplands were an important component of wetland complexes for wintering ducks in western Mississippi. Agriculture currently is the dominant land use in the MAV and winter flooded croplands are a large component of seasonally available flooded lands in this region. We found strongest associations between wintering dabbling ducks and flooded soybean, rice, and other croplands. These working lands apparently provided some of the same opportunities as natural wetlands for wintering ducks to feed, rest, court, and perform other daily activities (Delnicki and Reinecke 1986; Elphick 2000; Stafford et al. 2010b). Although flooded croplands provide waste grains containing 10–50 % more metabolizable energy than native seeds (Kaminski et al. 2004), few harvested croplands in the MAV have high densities of these foods, especially by midwinter when most grains have decomposed or been consumed (Nelms and Twedt 1996; Stafford et al. 2006; Foster et al. 2010). Elphick (2008) reported duck densities on flooded ricefields increased with area of flooded ricelands within 5 km. We found positive associations between flooded croplands and duck distributions at local and landscape scales, providing further support for flooded agricultural land as part of wetland complexes for wintering dabbling ducks in this region despite their dynamic food resource availability.

Diversity and interspersion of flooded croplands and wetlands (i.e., habitat complexity) positively influenced abundance of wintering dabbling ducks other than mallards. Including habitat complexity provided only modest improvement in models describing distributions of mallards, although contagion indices covaried with numbers of mallards observed similar to their effect on other dabbling ducks (Fig. 1). Diversity of contiguous or nearby wetlands may have afforded dabbling ducks with increased diversity of food and other resources at local and landscape scales (Fleming 2010). Gordon et al. (1998) observed a similar association between abundance of wintering mallards and green-winged teal and habitat heterogeneity in coastal South Carolina wetlands. Riffell et al. (2001) reported mallards in Michigan used more structurally diverse habitats during

Table 4 Mean percentage of wetland habitats in landscapes (4-km radius) surrounding locations where different-sized[a] groups of mallards (large = ≥100; small = <100; no use = 0) and other dabbling ducks (large = ≥200; small = <200; no use = 0) were observed during aerial surveys in western Mississippi, January 2003–2005

Wetland habitat	Mallard						Other dabbling ducks					
	Large (n=71)		Small (n=768)		No use (n=839)		Large (n=30)		Small (n=562)		No use (n=592)	
	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI
Cropland	47A[b]	43–51	34B	32–35	27C	26–28	51A	43–59	33B	32–35	28C	26–29
Emergent	20A	17–22	16B	15–17	15B	14–16	12A	8–16	10A	8–11	11A	10–12
Forest	20A	18–23	25B	24–27	27B	25–28	20A	15–25	24A	23–26	32B	30–34
Permanent	13A	10–16	25B	24–27	31C	30–33	17A	8–25	33B	31–35	29C	27–31

[a] Large groups of mallards and dabbling ducks other than mallards were defined as those in the upper 95th percentile of group size distributions; small groups were all observations with fewer ducks; and no use were randomly selected sites from a habitat layer of potentially occupied sites

[b] Letters represent differences among group types and within species groups at the α=0.05 level based on Turkey-Kramer multiple comparisons

summer, with the influence of habitat complexity most apparent within sampled wetlands. Furthermore, complexity and diversity of wetland vegetation types within wetlands were positively associated with mallard use of wetlands in the Illinois River Valley (Stafford et al. 2010a). Habitat and landscape complexities are key components of the wetland-complex concept because they represent occurrence of multiple habitats within a complex (Fredrickson and Heitmeyer 1988). Our results indicating positive effects of habitat complexity on distribution at multiple spatial scales provide additional support for the integration of wetland complexity and diversity in conservation and management of habitats for wintering waterfowl in the MAV.

We found little evidence that distributions of wintering ducks were influenced by sanctuary on public lands. Similarly, Elphick (2008) reported that presence of waterfowl refuges within radii of 2, 5, and 10 km had little influence on duck use of ricefields in California during winter. However, most studies of habitat use by ducks report extensive use of sanctuaries during hunting seasons (e.g., Cox and Afton 1997; Evans and Day 2002; Guillemain et al. 2008; St. James 2011) as well as at other times in fall, winter, and spring (e.g., Madsen and Fox 1995; Madsen 1998; McKinney et al. 2006; Stafford et al. 2007, 2010a). We suspect that lack of support for effects of sanctuaries was a consequence of the data used in our analyses (i.e., only public land sanctuaries). We did not have data identifying sanctuaries on private lands or areas on public and private lands that may function as sanctuaries intermittently due to infrequent hunting or self-imposed restrictions. Omission of these critical data may have resulted in poor performance of models describing sanctuary effects. Additionally, our choice of spatial extents may not have been large enough to detect sanctuary effects for species that make more extensive daily movements than the diameter of landscape we investigated (4 vs. 8.7–24.4 km; Cox and Afton 1996).

Distribution of dabbling ducks was best described by aspects of the wetland complex (i.e., croplands, complexity) measured at the landscape scale (i.e., average size of publically managed areas in Mississippi MAV; ~5,000 ha), yet we also found support for certain factors measured at the local level. Dabbling ducks migrating to the MAV may exhibit hierarchical habitat selection (Johnson 1980), and we speculate that wintering ducks may have perceived and responded initially to wetland complexes at the scale of public management areas and subsequently to site-specific characteristics. Elphick (2008) also found landscape characteristics at a similar scale (i.e., 5-km radius) had the greatest influence on distributions of ducks using ricefields in California. Similarly, dabbling ducks responded to features measured at a 10-km scale in Nebraska during spring migration (Webb et al. 2010). We observed large groups of mallards and other dabbling ducks in landscapes with more available wetland area than landscapes with less wetland area. Previous studies have reported positive relations between species richness and abundance of waterfowl and wetland area throughout the annual cycle (e.g., wintering, Heitmeyer and Vohs 1984; migration, LaGrange and Dinsmore 1989; breeding, Kaminski and Weller 1992). We also found certain combinations of habitats were associated with the presence and abundance of duck groups. For example, large groups of mallards were associated with landscapes that had approximately 50 % flooded croplands, 20 % emergent wetlands, 20 % forested wetlands, and 10 % permanent wetlands. Large groups of other dabbling ducks showed similar associations, with landscapes comprising approximately 50 % flooded croplands, 10 % emergent wetlands, 20 % forested wetlands, and 20 % permanent wetlands. Our results suggest complexes of wetlands containing diverse resources influence distribution of wintering dabbling ducks, although we recognize these habitat associations may be specific to the study area and habitats available during our study.

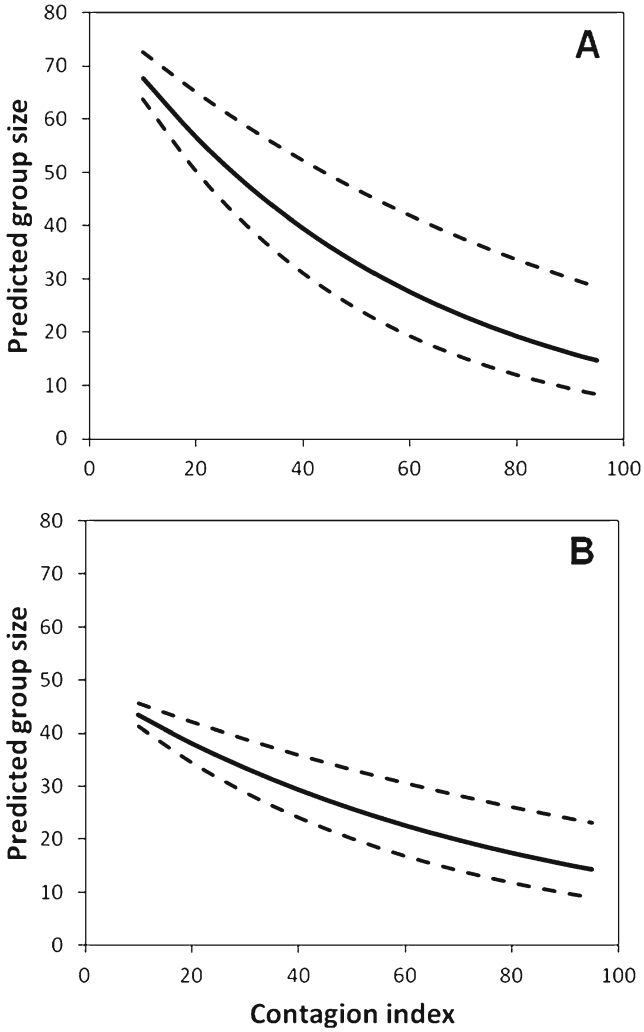

Fig. 1 Predicted relationships (*solid line*) and 95 % confidence intervals (*dashed lines*) between group size of dabbling ducks other than mallards and contagion indices, which measured habitat complexity, at landscape (**a**; 4-km radius) and local (**b**; 0.25-km radius) spatial extents for observations collected during aerial surveys in western Mississippi, January 2003–2005. Lower values for contagion indicate greater habitat complexity and higher values for contagion indicate lower habitat complexity

Using aerial survey data to study duck landscape associations is subject to certain limitations. We only observed ducks diurnally when weather conditions allowed aerial observations. Ducks also are active at night (Cox and Afton 1997; Anderson and Smith 1999; Davis et al. 2009), but we have no information regarding nocturnal habitats used by ducks. Additionally, our analysis was restricted to the mid-winter period when wetland data from satellite imagery were available. Mid-winter is an important time, because it tends to be the period of greatest duck abundance in Mississippi during winter (Pearse et al. 2008a). The influence of local and landscape features may be different at other times during winter. Moreover, aerial surveys have inherent visibility biases (Pollock and Kendall 1987), and results in our study may have been influenced by decreased rates of detecting duck groups in forested versus open wetlands (72 vs. 95 % estimated detection probability in forested vs. open wetlands for groups of 30 individuals; Pearse et al. 2008b). This limitation would be more serious if our study analyzed wetland-specific associations instead of wetland complexes. However, quantifying use of specific wetlands was not a primary interest, and results and conclusions from our study were valid assuming observed ducks were associated with local and landscape scale covariates in the same manner as ducks not detected. Finally, our models that included selected characteristics of wetland complexes explained less than half the variation in distributions of wintering ducks; presumably, remaining variation was due to factors not included in our models, such as weather, disturbance, and food availability.

Implications for Conservation and Management

The MAV in Mississippi changed considerably during the 20th century from a landscape dominated by bottomland hardwoods to one dominated by agriculture, and likely agriculture will continue to dominate this landscape for the foreseeable future. The strong positive associations between distributions of dabbling ducks and flooded agricultural fields support the notion that these lands represent a basic component of habitat complexes for wintering ducks in this region. Wintering ducks likely used flooded agriculture fields as foraging and loafing sites, functions that forested and emergent wetlands served before being converted to croplands. Flexibility of waterfowl and other waterbirds to exploit resources on cultivated lands, especially when agriculture replaced natural wetlands, has been well documented in North America and worldwide (e.g., Reinecke and Krapu 1986; Czech and Parsons 2002). Certain flooded crop types have characteristics that emulate natural wetlands (e.g., ricelands; Elphick 2000), whereas other crops provide resources of reduced quality or quantity compared to flooded forests or seasonal-emergent wetlands (e.g., soybean fields; Loesch and Kaminski 1989; Kaminski et al. 2004). Therefore, agricultural lands in modern landscapes may be viewed as replacing some of the resources once obtained by wintering dabbling ducks from natural wetlands but not as superior to these former systems. In agriculture-dominated landscapes like the MAV, programs that promote winter flooding of croplands would ensure availability of this habitat component of wetland complexes while providing environmental and economic benefits (Manley et al. 2009).

Wildlife management areas might increase habitat complexity for waterfowl by modifying current practices to increase diversity and abundance of foods available (e.g., natural or agricultural seeds), vegetative structure (e.g., emergent and forested wetlands), or topography and thus

corresponding variation in water depths and permanency (e.g., Hagy and Kaminski 2012). Further insight into how ducks discern diversity of wetlands within landscapes and how use of diverse wetlands influences distribution, body condition, and survival would be useful. Management of wetland complexes should be considered at multiple spatial extents, although our results suggest integrating the wetland-complex concept into waterfowl habitat conservation at the scale of management areas (e.g., approx. 5,000 ha) may be most effective in the MAV and similar landscapes. Management at this scale will require support from private landowners and coordination by public agencies to provide stakeholders with an appreciation of conservation objectives and how individual wetlands integrate into complexes to provide quality habitat for waterfowl.

Acknowledgments The Mississippi Department of Wildlife, Fisheries, and Parks was our primary sponsor with funding from the state's migratory bird stamp program. Other sponsors providing financial and logistical support included the Anderson-Tully Company; Delta Wildlife; Forest and Wildlife Research Center, Mississippi State University; Ducks Unlimited, Inc., Southern Regional Office; Jack H. Berryman Institute; Mississippi Cooperative Fish and Wildlife Research Unit (Research Work Order 74); U.S. Department of Agriculture, Animal and Plant Health Inspection Service–Wildlife Services–National Wildlife Research Center; and the Science Support Program jointly administered by the U.S. Fish and Wildlife Service and U.S. Geological Survey. We thank A. Nygren for expert pilot services and P. Gerard and S. Riffell for statistical advice. J. Anderson, M. Guillemain, and anonymous reviewers provided valuable comments for this manuscript. Our manuscript was approved for publication as Mississippi State University–Forest and Wildlife Research Center Journal Article WF–356. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government.

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