Habitat associations of wintering dabbling ducks in the Arkansas Mississippi Alluvial Valley: implications for waterfowl management beyond the mallard

Authors: Herbert, John A., Chakraborty, Avishek, Naylor, Luke W., and Krementz, David G.

Source: Wildlife Biology, 2021(1)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00792
Habitat associations of wintering dabbling ducks in the Arkansas Mississippi Alluvial Valley: implications for waterfowl management beyond the mallard

John A. Herbert, Avishek Chakraborty, Luke W. Naylor and David G. Krementz

Mallard *Anas platyrhynchos* ecology drives current habitat management strategies for most waterfowl; however, are these management strategies suitable for other dabbling duck species? Migratory waterfowl, in addition to mallards, in the lower Mississippi Alluvial Valley experience heavy hunting pressure, so management strategies should be appropriate for a broader array of species. We investigated habitat associations of dabbling ducks (dabblers) in the Arkansas portion of the Mississippi Alluvial Valley and factors driving winter distributions. We modeled winter aerial survey data over seven years with Bayesian spatio–temporal models to test what landscape covariates most affected dabbler habitat use. We found that dabbler distributions were closely associated with open water, habitat inundated with surface water and agricultural habitat such as rice, soybeans and fallow fields. Surface water extent and rice field extent were the key drivers of high dabbler abundances. These habitat–covariate associations were the same as used by mallards, suggesting landscape management focused on mallards likely is appropriate for dabblers, at least at the broad scale of our study.

Keywords: aerial survey, Arkansas, dabbling ducks, habitat use, Mississippi Alluvial Valley, spatial random effect, species distribution modeling, waterfowl

Understanding the ecological factors influencing the spatial distribution of a species is essential to proper wildlife management and planning (Runge et al. 2014, Aagaard et al. 2015, Lonsdorf et al. 2016). The North American Waterfowl Management Plan was developed to enhance waterfowl populations and habitat (U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS), USFWS and CWS 1986). Joint ventures (JV) were established through this plan to coordinate the biological planning and habitat conservation activities necessary to support waterfowl and other migratory birds (USFWS and CWS 1986). Further, migratory waterfowl use different habitats throughout the year in North America, making coordination amongst JVs and management flyways essential for sustainable populations (USFWS et al. 2012). The Mississippi Flyway is one of the four major flyways for migratory birds in North America and is the most heavily used flyway by waterfowl in the United States (Bellrose 1980, Davis et al. 2014).

Within the Mississippi flyway, the lower Mississippi Alluvial Valley (MAV) provides essential wetland habitat for overwintering waterfowl, and conservation planning for migratory birds in this region is led by the Lower Mississippi Valley Joint Venture (LMVJV) (Reinecke et al. 1989, Reinecke and Loesch 1996, USFWS et al. 2012). Waterfowl planning in the LMVJV leans heavily on the ecology of mallards *Anas platyrhynchos* for management decisions, in part because of greater information availability. However, conservation planning and implementation should incorporate other dabbling ducks (dabblers), to better understand the habitat preferences of all waterfowl to refine management strategies (Petrie et al. 2011, Pearse et al. 2012, Williams et al. 2014). Dabblers are among the most frequently harvested species by hunters in North America, with harvest totaling in the millions each year. Mallards are harvested in greater numbers than any other duck species, however, dabblers also are harvested in high numbers (Raftovich et al. 2019, USFWS 2019).
Within the MAV, dabblers are associated with ‘wetland-complex’ landscapes composed of approximately 50% flooded croplands, 20% forested wetlands, 20% permanent wetlands and 10% emergent wetlands (Pearse et al. 2012). Dabblers need a variety of habitat to meet their needs during the winter season – especially because habitat can be quickly altered by harsh weather and flooding events (Guillemain et al. 2013, Herbert et al. 2018) and often move long distances quickly to find available resources (Ji and Jeske 2000, Baldassarre and Bolen 2006). Changes in resources will often alter duck distributions throughout the wintering period, especially in dynamic landscapes such as the MAV (Nichols et al. 1983, Reinecke et al. 1989, Davis et al. 2014, Hagy et al. 2014, Herbert et al. 2018). For instance, habitat use by mallards within the MAV varies with changing surface water extent, and it is assumed but rarely tested if this applies to other dabblers (Reinecke and Loesch 1996, Davis et al. 2014, Herbert et al. 2018). Pearse et al. (2012) found that sanctuary sites on public lands explained little of the variation in dabbler occurrence in the Mississippi portion of the MAV. Recently, Herbert et al. (2018) found that mallard distributions in the MAV fluctuate within and among years, particularly driven by dynamic surface water availability, cropland landcover and colder conditions. Dabblers are assumed to behave in a similar nomadic fashion to find resources, but little is known about how dabblers use wintering landscapes. This information is needed for managers to best meet the resource needs of these populations, because these species may have different habitat associations than mallards (Bellrose 1980, Baldassarre and Bolen 2006, Stafford et al. 2010).

Therefore, in this study we focus on the spatial distribution of wintering dabblers in the Arkansas portion of the MAV (ARMAV). To our knowledge, this is the largest-scale, landscape-use assessment for these species undertaken to date. Our objectives were to analyze seven years of systematic aerial waterfowl survey data from the ARMAV to determine habitat characteristics influencing abundance and distribution of wintering dabblers and to evaluate these findings in relation to mallard abundance and distributions during the same period.

**Methods**

**Study area**

We maintain the same study region as described in Herbert et al. (2018). The MAV is the floodplain for the Mississippi River covering 10 million ha, of which Arkansas encompasses 3.7 million ha. Topography is flat in the region, with elevations rarely exceeding 10 m above normal Mississippi River flowlines, making the MAV subject to winter flooding from precipitation and overflowing tributaries (Reinecke et al. 1989). However, hydrology and bottomland hardwood forest extent in the MAV have been severely altered by agricultural development and flood control (Reinecke et al. 1988). Crowley’s Ridge lies within the region, but we did not include this area in our study (Fig. 1). Prominent land cover types in the ARMAV during our study included soybean fields (*Glycine* spp.), rice fields (*Oryza* spp.), fallow fields (uncultivated), corn fields (*Zea* spp.), wetlands (bottomland hardwood forests and herbaceous wetlands) and permanent water (USDA-NASS 2009–2015).

**Survey design**

We used observations from Arkansas Game and Fish Commission diurnal aerial surveys (n = 25) over seven wintering periods from 2009 to 2016. Survey periods each year were mid-November, mid-December, early-January and late-January, except for the final three years that did not include late-January surveys. Fixed width (250 m) transects were randomly selected within geographic strata based on expert opinion in the first two years (strata: n = 5; Reinecke et al. 1992), and then divided into watersheds the final five years (strata: n = 11; Lehnen 2013). Total survey length ranged from 3700 to 5600 km per survey. At each duck observation, surveyors recorded the date, species, number of individuals and coordinates. Non-mallard dabblers were recorded to species when possible; however, surveyors lumped dabblers at times for logistic reasons (Lehnen 2013). Therefore, we lumped all dabbler species for this analysis. Dabblers included were: wood duck *Aix sponsa*, gadwall *Mareca strepera*, northern pintail *Anas acuta*, American wigeon *M. americana*, northern shoveler *Spatula clypeata* and green-winged teal *A. crecca*.

**Covariates**

We used 10 covariates previously found to have the most influence on wintering mallard abundance and distribution in the ARMAV to test what covariates were most important for dabblers (Herbert et al. 2018). We used four agriculture land covers: 1) rice (*Oryza* spp.) (covariate 1); 2) soybean (*Glycine* spp.) (covariate 2); 3) corn (*Zea* spp.) (covariate 3); and fallow fields (uncultivated farmland in the preceding growing season) (covariate 4). Bottomland hardwood forests and herbaceous emergent wetlands were combined into wetlands covariate (covariate 5). Open (permanent) water, which consisted of rivers, ponds and aquacultures facilities, was an additional covariate (covariate 6). All six land cover covariates had no temporal changes within a season but did change among years. All land cover covariates were obtained using the Cropland Data Layer (CDL) (USDA NASS 2009–2015). We tested environmental effects by including surface water extent (covariate 7) (indicative of rainfall and overbank flooding) and weather as covariates within our models. We conducted an unsupervised classification of Landsat imagery to classify surface water at the time of each survey (details in Herbert et al. 2018). Weather was classified using the winter severity index (WSI) (covariate 8) outlined in Schummer et al. (2010) and weather data from the United States Historical Climatology Network (Menne et al. 2015) at nine weather stations throughout the ARMAV (details in Herbert et al. 2018). We averaged WSI values over days within surveys and interpolated averaged values among weather stations to create a smooth gradient of WSI values within the ARMAV during each survey period (Herbert et al. 2018). Negative WSI values indicate temperatures above 0°C with no snow cover and positive WSI values indicate temperatures below 0°C with snow cover (Schummer et al. 2010).
Thus, we interpreted negative parameter estimates for WSI as selection for areas with warmer conditions and less snow (Herbert et al. 2018). Finally, to evaluate the contributions of public lands often managed for waterfowl, we combined federal and state-managed land into one covariate (managed land, covariate 9) and included restored wetlands in the Wetlands Reserve Program (WRP) (covariate 10). Linear dependence among covariates was tested prior to model fitting using the variance inflation factor (VIF) (VIF = 1/1 - r²).

Statistics

Because our goal was to analyze dabbling duck survey data as was done for mallard survey data in Herbert et al. (2018), we used the same statistical methods (see the Supplementary information for details). We divided the ARMAV into 4-km² grid cells, and each covariate was given a proportional value (0.0–1.0) for amount of land cover the covariate had within a cell. WSI values were continuous and based on the calculated value by cell. Dabbler abundance was separated as a categorical response for each cell as 0: no observed dabblers, 1: 1–15 dabblers, 2: 16–100 dabblers, 3: over 100 dabblers.

We used the categorical abundance of dabblers to be a discretized version of an underlying latent potential abundance (PA) surface over the ARMAV, modeled as a linear function of covariates. The PA surface indicated how suitable a specific cell within the region was for dabblers. Thus, the higher the value of a PA surface, the higher the probability that we would encounter more dabblers in that cell. The representation of categorical data as latent continuous variables provided a convenient tool for linking the environmental covariates with the variation in dabbler prevalence (Albert and Chib 1993). We also incorporated a spatial random effect (θ) to capture autocorrelation in dabbler prevalence among adjacent cells (Gelfand et al. 2005). Inclusion of this spatial term allowed us to overcome model inadequacy arising from: 1) possible non-linearity in the response–covariate relationship and 2) lack of data on all
potentially important covariates, in addition to utilizing the spatial dependence to enhance the predictive efficiency in unsampled regions within the ARMAV (Gelfand et al. 2005, Chakraborty et al. 2010). We used a two-stage model, where the first stage explained the likelihood of a nonzero observation at a specific cell (dabller presence/absence) and the second stage explained, conditional on at least one dabller observation in a cell, the abundance category of that sighting.

We estimated covariate effects on dabller presence for each survey (stage 1), covariate effects for the conditional abundance for each survey (stage 2) and covariate-specific effects for temporal dependence across surveys (survey effect) and years (year effects). We linked abundance data to covariate data through a latent variable to model presence/absence in the first stage. We modeled the observed abundance category, given presence of dabblers in a cell. For each stage, the model has three parts: 1) a fixed effect mean expressed as a linear combination of covariates; 2) a spatial random effect (θ) to capture spatial autocorrelation; 3) and a pure error term accounting for residual variation (ε). Our dataset included dabller observations collected over multiple surveys and years, so we extended the model into a spatio–temporal setting. We focused on analyzing dependence between models at different points of time, anticipating temporal dependence across surveys as well as years (Supplementary information Eq. A3). The temporal association parameters $\Gamma_{\text{survey}}$ and $\Gamma_{\text{year}}$ facilitated borrowing of information across different surveys for each covariate. We assigned diffused normal priors to their components. For the vectors of spatial random effects at any time point, we used conditional autoregressive (CAR) priors (Banerjee et al. 2004). We wrote a Markov chain Monte Carlo (MCMC) estimation scheme (chain length = 35 000, burn-in = 25 000, then thinned at every fifth iteration) and ran all models in Program R (Gilks 2005, <www.r-project.org>).

We used the same six competing candidate models to evaluate the spatio–temporal effects on dabblers that were used for mallards in Herbert et al. (2018), except we removed covariates for mallards that were found to be non-significant, to make a more informative model set. The models were developed to assess: 1) agriculture fields (agriculture model); 2) surface water and land cover classes known to be used by dabblers (habitat model); 3) surface water and managed land (managed land model); 4) the five most important covariates expected to affect dabller abundance determined from the scientific literature (waterfowl importance model) (Reinecke et al. 1992, Stafford et al. 2006, Davis et al. 2014); and, 5) surface water and open water (water model). We included the full model with all main effects as our sixth and final candidate model (full model) (Table 1).

We conducted a posterior predictive check for all candidate models with the Bayesian $\chi^2$ goodness of fit summary statistic, with a value close to 0.5 indicating adequate model fit (Johnson 2004). We then evaluated candidate models with the Bayesian predictive information criterion (BPIC; Ando 2007). The model with the smallest BPIC value was considered the best performing model (Supplementary information). We interpreted any covariate with 95% credible intervals not overlapping zero as positively (>) zero or negatively (<) zero) affecting dabller distribution and abundance, and covariates with 95% credible intervals overlapping zero as having no effect on dabller distributions. Additionally, we ranked covariate importance for each survey by dividing the posterior mean of each covariate effect by corresponding standard deviation (SD) (Supplementary information).

We produced maps of spatial random effects (θ) for each survey to examine trends in covariate importance among regions within the ARMAV. Overestimation of dabller abundance by the covariates is represented by negative θ values, whereas underestimation of dabller abundance is represented by positive θ values. Thus, θ values closer to zero

| Model    | Description                                      | Covariates                          | $\chi^2$ BPIC | $\chi^2$ ΔBPIC | $\chi^2$ pD | $\chi^2$ Bayesian GoF |
|----------|--------------------------------------------------|-------------------------------------|--------------|----------------|-------------|------------------------|
| Full     | All main effects                                 | Rice field + soybean field + wetland + corn field + surface water + open water + fallow field + managed land + WRP + WSI | 39 802       | 0              | 320         | 0.48                   |
| Habitat  | Surface water and known land covers that dabblers use | Rice field + soybean field + wetland + surface water + fallow field + managed land + WRP + WSI | 39 808       | 6              | 250         | 0.53                   |
| Waterfowl importance | Most important covariates for dabller from previous research | Rice field + wetland + surface water + open water + WSI | 40 130       | 2337          | 209         | 0.51                   |
| Managed Land | Surface water and managed land | Wetland + WRP + managed land + open water + surface water + WSI | 40 282       | 2489          | 242         | 0.49                   |
| Water    | How water alone affects dabller abundance distributions. | Surface water + open water | 40 692       | 2899          | 141         | 0.55                   |
| Agriculture | Agriculture fields and post-harvest waste grain left in fields. | Rice field + soybean field + corn field + fallow field | 41 321       | 3528          | 182         | 0.52                   |

1 Bayesian predictive information criterion.
2 Effective number of parameters.
3 Bayesian goodness of fit, measured by $A = P[R^2 > \chi^2]$. Values closer to 0.50 are indicative of model adequacy.
represent regions where the covariates within the model accurately predicted dabbler abundance. Random variation in $\theta$ across the cells indicate a lack of spatial dependence, whereas a smooth pattern with little differences in $\theta$ values among nearby cells but showing smooth transitions among far away cells is considered evidence of spatial association. Finally, we developed spatial probabilities of dabbler abundance across the ARMAV. We generated posterior maps with the estimated categorical abundance probabilities throughout the ARMAV for each survey. We then compared the predicted distributions of dabblers to previously published mallard results (Herbert et al. 2018) to see if dabblers are using the same habitat in the same regions as mallards, or if they are using the same habitat type but in different locations. We compared the distributions by calculating the Euclidean distance among categorical abundances in each cell across the ARMAV for each survey. At any cell, calculated values close to zero indicated similar categorical abundance probabilities for mallards and dabblers for that cell. Whereas, at any other cell, a large positive value indicated strong discrepancy between the categorical abundance probabilities of mallards and dabblers for that cell (Furrer et al. 2009).

**Results**

We counted 620 105 individual dabblers over 25 surveys. Gadwall were the most abundant species, followed in rank order by American green-winged teal, northern pintail, northern shoveler, wood duck and American wigeon. Most (64%) dabblers, excluding mallards, observed were not identified to species. Transects from all surveys intersected 9657 cells (~20% of total extent), 2515 of which had at least one dabbler observation. The values of the goodness of fit summary statistic were close to 0.5 for all models, indicating adequate model fit in all cases, potentially due to the role of spatial random effects in compensating for any inadequacy of fixed-effect parts. The delta BPIC of the habitat model compared to the full model was only 6, so we consider both models performing equally well. Therefore, because the habitat model had fewer covariates, we consider the habitat model the best performing model (Table 1). Here, we report results only from the habitat model.

We found surface water, open water, rice fields, soybean fields and fallow fields, positively influenced dabbler presence (stage 1 of model) in most (> 20/25) surveys. WSI most often had a negative effect on dabbler presence (17/25 surveys), suggesting dabblers sought regions of higher temperatures with less freezing temperatures and snow. Surface water and rice fields most often had the highest influence (stage 1), and rice fields, open water and surface water had a positive correlative effect on dabbler presence (stage 1), and rice fields, open water and surface water had a positive correlative effect on dabbler abundance (stage 2) within the same year. We found that rice fields, fallow fields, surface water and open water had a positive correlative effect on dabbler presence (stage 1), and rice fields, open water and surface water had a positive correlative effect on dabbler abundance (stage 2) among surveys conducted during the same month across years (Table 3).

The maps of spatial effects had a generally smooth pattern for all months indicating good model performance, because the values had little variance among nearby cells (i.e. spatial correlation). We found a general spatio–temporal pattern for dabbler presence, as seen in the example in Fig. 2. In most surveys (19/25), we found that values close to zero were in the central portion of the MAV (34–35.5° latitude), indicating that the covariates used in our models were good predictors of dabbler presence in that region (Supplementary information). We found greater spatio–temporal variation in values in the northern (> 35.5° latitude) and southern (< 34° latitude) portions of the MAV. The models found that less dabblers were present than predicted (~0) in the northern portion of the MAV during the December–January (14/18) surveys. This suggests that due to colder and more extreme cold weather in the northern latitudes, dabblers were seeking warming (i.e. more southerly) regions, which supports our findings of WSI negatively influencing dabbler presence throughout the ARMAV. During the November surveys, the northern and southern portions did not show a pattern among years, which could primarily be due to warmer temperatures throughout the MAV earlier in the wintering period. Additionally, we found higher dabbler abundance (category 3) predicted in the north (above 35° latitude) in November but moved farther south to the cen-

---

**Table 2.** Posterior covariate estimates for winter dabbling duck presence and abundance in the ARMAV from 2009 to 2016. Results are from the habitat model, which performed best by BPIC. Numbers represent the frequency at which 95% credible intervals for a covariate did not overlap 0 and positively or negatively influenced dabbler abundance for the 25 surveys. The last column represents the number of times a covariate was the most important for a survey, ranked by dividing the covariate mean by the standard deviation (SD). Stage 1 modeled presence and absence of mallards and stage 2 modeled dabbler abundance where mallards were present.

| Covariate     | Stage 1 (pos/neg) | Stage 2 (pos/neg) | Stage 1 | Stage 2 |
|---------------|-------------------|-------------------|---------|---------|
| Rice field    | 23/0              | 18/0              | 7       | 10      |
| Soybean field | 20/0              | 7/0               | 0       | 2       |
| Wetland       | 10/0              | 0/0               | 1       | 0       |
| Surface water | 23/0              | 17/0              | 14      | 7       |
| Open water    | 24/0              | 2/0               | 0       | 0       |
| Fallow field  | 21/0              | 1/0               | 2       | 1       |
| WSI           | 3/17              | 7/1               | 1       | 4       |
Table 3. Survey effect and year effect posterior estimates from the combined year-habitat model explaining dabbling duck distribution in the ARMAV. Stage 1 (top) modeled dabbler presence and absence and stage 2 (bottom) modeled dabbler abundance only where dabblers were present. Covariates with a 95% confidence interval for effects not overlapping zero are highlighted in gray.

| Survey effect | Year effect |
|---------------|-------------|
| 95% CI lower  | Mean        | 95% CI upper |
| Stage 1       |             |             |
| Rice field    | −0.02       | 0.42        | 0.84          | 0.25          | 0.63          | 1.0           |
| Soybean field | −0.01       | 0.66        | 1.30          | −0.23         | 0.33          | 0.90          |
| Wetland       | −0.24       | 0.39        | 1.02          | −0.14         | 0.40          | 0.94          |
| Surface water | 0.07        | 0.30        | 0.54          | 0.46          | 0.69          | 0.91          |
| Open water    | −0.06       | 0.34        | 0.77          | 0.32          | 0.70          | 1.07          |
| Fallow field  | 0.18        | 0.63        | 1.06          | 0.14          | 0.49          | 0.289         |
| WSI           | 0.13        | 0.62        | 1.14          | −0.16         | 0.29          | 0.72          |
| Stage 2       |             |             |
| Rice field    | −0.11       | 0.22        | 0.60          | 0.41          | 0.79          | 1.13          |
| Soybean field | −0.15       | 0.45        | 1.05          | −0.16         | 0.42          | 1.01          |
| Wetland       | −0.62       | 0.16        | 0.89          | −0.63         | 0.13          | 0.76          |
| Surface water | −0.09       | 0.13        | 0.62          | 0.39          | 0.88          | 1.14          |
| Open water    | −0.16       | 0.39        | 0.95          | 0.02          | 0.67          | 1.09          |
| Fallow field  | −0.48       | 0.41        | 1.21          | −0.77         | 0.31          | 1.10          |
| WSI           | −0.08       | 0.51        | 1.08          | −0.22         | 0.30          | 0.84          |

Central and southern portions of the MAV (below 35° latitude) in December and January.

Visual examination of predicted abundance maps (Fig. 3, Supplementary information) indicated locations of dabbler abundance were near land covers associated with managed lands, even though managed lands were not in the top performing model (Supplementary information). We attribute the very low percentage of spatial coverage wildlife refuges have within the ARMAV (< 5%, Supplementary information) for not performing well in the models. We found similar spatial categorical abundance distributions of mallards (Herbert et al. 2018) and dabbling ducks in all surveys. Generally, the distribution extent of dabblers was smaller than those of mallards, which is expected since we observed fewer dabblers during these surveys and may have accounted for some differences among spatial abundances. However, one difference of not was that we found higher abundances of mallards compared to dabbler abundances in habitat corridors with higher prevalence of bottomland hardwood forests in December–January when these habitats were more likely flooded (Supplementary information).

Discussion

We used data from a long-term, systematic aerial waterfowl survey (Lehnen 2013) and modeled both fixed and transitory resources across a large scale heterogeneous landscape to predict the spatial and temporal abundance and distribution of migratory dabbling ducks in the ARMAV (Pearse et al. 2012, Hagy et al. 2014, McGarigal et al. 2016). Similar to results for more abundant mallards in the MAV (Herbert et al. 2018), the coverage and distribution of surface water associated with selected land cover and weather (rice fields, soybean fields, fallow fields, WSI) had the greatest influence on dabbler presence and abundance (rice fields, soybean fields, WSI) within a winter. Our ability to include temporal variation in surface water and WSI allowed us to improve the predictability of our distribution model (Pickens and King 2014, Aagaard et al. 2015, Yackulic and Ginsberg 2016). Among winters, surface water in combination with rice fields were the most important drivers of dabbler presence and abundance. In addition, our modeled distribution patterns at the landscape scale were improved by including covariates into our hierarchical models (e.g. surface water, WSI) at smaller scales, given that some land cover covariates were nearly constant at larger scales. For example, cropland data within a year is constant. However, we examined cropland data among years, allowing for more reliable predictions (USDA-NASS 2009–2015). Thus, one important difference in our modelling approach compared to how the wetland-complex concept (Väänänen 2001, Pearse et al. 2012) affects dabbler distributions, was our ability to examine ephemeral covariates at several scales through time, something that Pearse et al. (2012), Hagy et al. (2014) and Aagaard et al.

Figure 2. Spatial random effects (θ) for the presence/absence of dabbling ducks across the Arkansas Mississippi Alluvial Valley (ARMAV) for the December 2014 waterfowl survey. Scale of θ explains the performance of covariates used in the model. Positive θ values represent cells with more dabbling ducks than expected and negative θ values represent cells with less dabbling ducks than predicted. The entire surface of θ values across the ARMAV equals 1.0. A correlated spatial pattern is shown, because a smooth gradient of θ values exists, whereas a mixed gradient of θ values would indicate no spatial pattern present.
considered an important next step in better understanding dabbler habitat use and distributions.

Dabbler abundance and distribution through time was consistently influenced by croplands more so than by managed lands (Pearse et al. 2012, Hagy et al. 2014). This finding is similar to that for mallards in the ARMAV (Reinecke et al. 1992, Beatty et al. 2014a, Herbert et al. 2018) and dabblers in the Mississippi portion of the MAV (Pearse et al. 2012). Both Pearse et al. (2012) and Herbert et al. (2018) remarked that, in addition to croplands in this region being the primary landcover, waterfowl concentrations predicted to be on agricultural fields often were part of a complex of habitats that included publicly managed wetlands within short distances (~< 10 km, Beatty et al. 2014b). While flooded croplands provide waste grains that meet many of the energetic and nutrient needs of waterfowl, the availability of those foods throughout winter can be uncertain across space and time (Nelms and Twedt 1996, Stafford et al. 2006, Kross et al. 2007, Hagy et al. 2014). The combination of flooded agricultural fields in proximity of managed public wetlands allows dabblers to seek out food resources that change in availability (Pearse et al. 2012, Davis et al. 2014, Hagy et al. 2014). Predicted abundance maps highlighted this habitat complex association. For instance, managed public lands such as Dale Bumpers White River National Wildlife Refuge and Rex Hancock Black Swamp Wildlife Management Area run through the central portion of the ARMAV, and dabblers were consistently found to be in that surrounding area. Additionally, dabbler concentrations were common in the proximity of other clusters of managed wetlands in the southwest portion of the ARMAV and Big Lake Wildlife Management Area in the northeastern part of the ARMAV (Supplementary information).

Cropland use by dabblers within and among winters was consistently important, but of those cropland types we examined, both rice and soybeans explained dabbler presence, abundance and distribution more consistently than any other. Reinecke et al. (1992) also found mallards in the ARMAV used flooded rice and soybean fields heavily during the winter. Stafford et al. (2006) described rice fields as critical habitat for meeting seasonal requirements of waterfowl. The attractiveness of rice fields likely resulted from nutrient content of waste rice that is needed during the winter months as well as the physical structure of standing stubble when present (Kross et al. 2007, Pernollet et al. 2015). Further, the decomposition of rice is relatively slow compared to the rapid decomposition of soybeans once exposed to water (Nelms and Twedt 1996, Stafford et al. 2006). Reinecke et al. (1992) suggested that the use of naturally flooded rice fields represented most of
the habitat use on private lands in the MAV by mallards. Despite the relative lack of standing stubble in soybean fields as well as the short-term nature of available waste soybeans in harvested fields, dabblers do use soybean fields (Stafford et al. 2006). As Herbert et al. (2018) hypothesized, the high abundance (31–34% of total extent in the ARMAV) of soybean fields in part explains their use.

We found dabblers redistributed throughout winter from being predominantly located in the northern parts of the ARMAV during early winter, then relocating to the southern parts of the ARMAV during late winter. This redistribution was coincident with increasing WSI in the northern portion of the ARMAV. Distribution changes of dabblers in the MAV during winter is not a new observation; however, the cause of that redistribution has been attributed to weather effects and changes in food/habitat availability (Nichols et al. 1983, Pearse et al. 2012). So, our findings that WSI related to the temporal changes in dabbler distributions could suggest that increasing weather severity reduces food availability and freezes wetlands, while concomitantly increasing thermal stress on dabbler populations (Schummer et al. 2010, Guillemaing et al. 2013). Dabblers thus need to relocate for warmer conditions with available resources, which are more likely to be found in the southern portions of the MAV during late winter. Other dabbler studies have found that lower temperatures (< −7°C) eliminate evening flights and force dabblers to select favorable microclimates during non-foraging periods (Baldassarre and Bolen 1984, Hepp 1985). We offer that dabblers are sensitive to thermal stress and modify their behaviors to use different regions and habitats with increased available energy.

While we have found many factors such as unmanaged flooding, cropland use and WSI are important in interpreting dabbler presence, abundance and distribution within and among years in the MAV, these factors do not explain the underlying drivers of dabbler habitat use. For example, Aagaard et al. (2015) found that dabbler habitat use models had a large amount of variation present in the system that was not well explained by the variables they incorporated – many variables of which we included in our models. We offer several additional behavioral mechanisms that may be contributing to this unexplained variation in dabbler habitat use. First, as explained above, thermal stress is a continuing mechanism that needs to be further examined and included in waterfowl habitat use models (Hepp 1985). Second, we offer that predator avoidance should be examined. Gadwall, green-winged teal and northern pintails have been found to redistribute during the day to avoid predators (Euliss and Harris 1987, Dooley et al. 2010, Casazza et al. 2012). Additionally, we propose that hunting pressure needs to be examined (Tamisier 1976, Williams and Nichols 2001, Dinges et al. 2015). Hunting pressure likely also affected diurnal distributions in our study. Hunting pressure in the MAV can be intense, especially on publicly managed lands (St. James et al. 2013). Such pressure can cause dabblers to move away from areas of high hunting pressure (e.g. wildlife management areas) to sanctuary habitat both on public and private lands, thus impacting dabbler distributions (Reinecke et al. 1992, St. James et al. 2013, Dinges et al. 2015). Evidence of predator and hunting pressure avoidance we found was the use of open water. Open water habitats are relatively free of predators and hunters, thereby affording dabblers the opportunity to roost, preen and conduct courtship activities while avoiding disturbance (Bell et al. 1997, Casazza et al. 2012, Beatty et al. 2014b).

One aspect of flooding that has not been formally incorporated into modelling efforts is water depth (Pearse et al. 2012, Hagy et al. 2014, Aagaard et al. 2015). Dabblers are recognized to use water depth as a means for segregating habitat use and typically prefer shallow water (Guillemaing and Fritz 2002). For example, Euliss and Harris (1987) found that green-winged teal and northern pintails used significantly different water depths for foraging and while resting on open wetlands. Aagaard et al. (2015) suggested that mallards used deeper water depths than northern pintails and that in the Mississippi Flyway during autumn, northern pintails, northern shovelers and green-winged teal habitat use was best explained by water depth. Documenting water depth at the spatial and temporal scales of this study presents substantial logistical challenges. Nonetheless, we suggest that, when feasible, future researchers incorporate water depth in conjunction with landscape covariates into habitat use models to better explain presence, abundance and distribution of wintering waterfowl in the MAV and other wintering regions (Guillemaing and Fritz 2002).

Finally, one aspect of our modelling effort worthy of further exploration is species groupings. Bell et al. (1997) suggested that wintering waterfowl groups likely have overlapping habitat requirements, therefore modelling groups of waterfowl may be an important step in understanding waterfowl distributions. Aagaard et al. (2015) found two dabbling duck habitat use groupings during autumn in the Mississippi Flyway: 1) gadwall, green-winged teal, blue-winged teal Anas discors, northern shovelers and American wigeon; and, 2) northern pintail and mallards. Davis (2014) observed that mallards, northern shovelers and gadwall would associate on aquaculture ponds during the winter in the MAV. We encourage future researchers to examine habitat use of dabblers by considering such possible species groupings.

Conclusions

We found dabblers used approximately the same wetland-complexes as mallards and that dabblers redistributed themselves largely in response to the same variables as mallards. Although we found higher abundances of mallards in forested wetlands late in the winter compared to dabbler abundances then, these differences are most likely attributed to species-specific habitat preferences, where more mallards redistributed to forested wetlands and dabblers remained in the rice fields, soybean fields and open water (Davis and Afton 2010). Mallards were still present in similar abundances throughout the landscape in the desired habitat of dabblers, therefore we believe that using the mallard as a surrogate for developing conservation plans for dabbling ducks in the MAV is appropriate. This finding is important because we know relatively less about the winter ecology of dabblers other than mallards in the MAV. Thus, using the mallard in planning will allow biologists to take full advantage of the greater knowledge base on mallards. However, we note that some dabblers (e.g. gadwall), have very different winter...
habitats, so we encourage continued examination of these less-abundant but common species (Paulus 1984, Devineau et al. 2010). We further encourage biologists to investigate the winter ecologies of diving ducks and other wetland-dependent waterbirds (e.g. Rallidae), which may be impacted by habitat management designed for mallards (Fournier et al. 2019). In summary, adaptive management strategies driven by mallard ecology likely are sound for broader conservation goals, but more detailed studies such as this one are needed to ensure population goals are met for all species (Elmberg et al. 2006, Holopainen et al. 2018, USFWS 2019).

Acknowledgements – Thanks to AGFC employees Jason Jackson, Jason Carbaugh and J.J. Abernathy for conducting the aerial surveys. We also thank Kristen L. Herbert, Sarah E. Lehnen, Michael Mitchell and Henry T. Pittman. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Funding – This research was funded by the U.S. Geological Survey Arkansas Cooperative Fish and Wildlife Research Unit, the University of Arkansas, the Arkansas Audubon Society. Aerial surveys were funded by the Arkansas Game and Fish Commission. High performance computing resources were provided by Technology Services at Tulane University.

Author contributions – JAH, LWN and DGK conceived the study, JAH and AC analyzed the data, and DGK led the writing. All authors made substantial contributions to previous drafts and have approved the final version.

Conflicts of interest – None of the authors have any conflicts of interest.

Permits – No waterfowl were handled during this study.

References

Aagaard, K. et al. 2015. Evaluating predictors of local dabbler abundance during migration: managing the spectrum of conditions faced by migrants. – Wildfowl 65: 100–120.

Albert, J. and Chib, S. 1993. Bayesian analysis of binary and polychotomous response data. – J. Am. Stat. Assoc. 88: 669–679.

Ando, T. 2007. Bayesian predictive information criterion for the evaluation of hierarchical Bayesian and empirical Bayes models. – Biometrika 94: 443–458.

Baldassarre, G. A. and Bolen, E. 1984. Field-feeding ecology of waterfowl wintering on the southern High Plains of Texas. – J. Wildl. Man. 48: 63–71.

Baldassarre, G. A. and Bolen, E. 2006. Waterfowl ecology and management, 2nd edn. – Krieger Publishing Company, Florida.

Banerjee, S. et al. 2004. Hierarchical modeling and analysis for spatial data. – Chapman & Hall/CRC Press.

Beatty, W. S. et al. 2014a. Landscape effects on mallard habitat selection at multiple spatial scales during the non-breeding period. – Landscape Ecol. 29: 989–1000.

Beatty, W. S. et al. 2014b. The role of protected area wetlands in waterfowl habitat conservation: implications for protected area network design. – Biol. Conserv. 176: 144–152.

Bell, M. C. et al. 1997. Wintering waterfowl community structure and the characteristics of gravel pit lakes. – Wildl. Biol. 3: 65–78.

Bellrose, F. C. 1980. Ducks, geese and swans of North America, 3rd edn. – Stackpole Books, Pennsylvania.

Casazza, M. L. et al. 2012. Hunting influences the diel patterns in habitat selection by northern pintails Anas acuta. – Wildl. Biol. 18: 1–13.

Chakraborty, A. et al. 2010. Modeling large scale species abundance with latent spatial processes. – Ann. Appl. Stat. 4: 1403–1429.

Davis, B. E. and Atton, A. D. 2010. Movement distances and habitat switching by female mallards wintering in the lower Mississippi Alluvial Valley. – Waterbirds 33: 349–356.

Davis, B. E. et al. 2014. Habitat and resource use by waterfowl in the Northern Hemisphere in autumn and winter. – Wildfowl Spec. Iss. 4: 17–69.

Devineau, O. et al. 2010. A comparison of green-winged teal Anas crecca survival and harvest between Europe and North America. – Wildl. Biol. 16: 12–24.

Dinges, A. J. et al. 2015. Effects of the light goose conservation order on non-target waterfowl distribution during spring migration. – Wildl. Biol. 21: 88–97.

Dooley, J. L. et al. 2010. Effects of hunting season structure, weather and body condition on overwintering mallard Anas platyrhynchos survival. – Wildl. Biol. 16: 357–366.

Elmberg, J. et al. 2006. The scientific basis for new and sustainable management of migratory European ducks. – Wildl. Biol. 12: 121–127.

Euliss Jr., N. H. and Harris, S. W. 1987. Feeding ecology of northern pintails and green-winged teal wintering in California. – J. Wildl. Manage. 51: 724–732.

Fournier, A. M. et al. 2019. Evaluating tradeoffs in the response of sora (Porzana carolina) and waterfowl to the timing of early autumn wetland inundation. – Waterbirds 42: 168–178.

Furrer, R. et al. 2009. Package ‘fields’. – R Foundation for Statistical Computing, Vienna, Austria. <https://github.com/NCAR/Fields>.

Gelfand, A. E. et al. 2005. Modelling species diversity through species level hierarchical modelling. – J. R. Stat. Soc. Ser. C Appl. Stat. 54: 1–20.

Gilks, W. R. 2005. Markov chain Monte Carlo. – Wiley.

Guillemain, M. and Fritz, H. 2002. Temporal variation in feeding tactics: exploring the role of competition and predators in wintering dabblers. – Wildl. Biol. 8: 81–90.

Guillemain, M. et al. 2013. Effects of climate change on European ducks: what we do know and what we need to know? – Wildl. Biol. 19: 404–419.

Hagy, H. M. et al. 2014. Annual variation in food densities and factors affecting wetland use by waterfowl in the Mississippi Alluvial Valley. – Wildfowl Spec. Iss. 4: 436–450.

Hepp, G. R. 1985. Effects of environmental parameters on the foraging behavior of three species of wintering dabblers (Anatini). – Can. J. Zool. 63: 289–294.

Herbert, J. A. et al. 2018. Effects of landscape structure and temporal habitat dynamics on wintering mallard abundance. – Landscape Ecol. 33: 1319–1334.

Holopainen, S. et al. 2018. Sustainable management of migratory European ducks: finding model species. – Wildl. Biol. 2018: wlb.00336.

Ji, W. and Jeske, C. 2000. Spatial modeling of the geographic distribution of wildlife populations: a case study in the lower Mississippi River region. – Ecol. Model. 132: 95–104.

Johnson, V. E. 2004. A Bayesian χ² test for goodness-of-fit. – Ann. Stat. 32: 2361–2384.

Kross, J. P. et al. 2007. Conserving waste rice for wintering waterfowl in the Mississippi Alluvial Valley. – J. Wildl. Manage. 72: 1383–1387.

Lehnen, S. 2013. Monitoring the effects of climate change on waterfowl abundance in the Mississippi Alluvial Valley: optimizing sampling efficacy and efficiency. – USGS Unpublished Report, <https://ecos.fws.gov/ServCat/Reference/Profile/65874>.

Lonsdorf, E. V. et al. 2016. A generalizable energetic-based model of avian migration to facilitate continental-sale waterbird conservation. – Ecol. Appl. 26: 1136–1153.
McGarigal, K. et al. 2016. Multi-scale habitat selection modeling: a review and outlook. – Landscape Ecol. 31: 1161–1175.
Menne, M. J. et al. 2015. United States historical climatology network daily precipitation, and snow data. – Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory. <http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html>.
Nelms, C. O. and Tweedt, D. L. 1996. Seed deterioration in flooded agriculture fields during winter. – Wildl. Soc. Bull. 24: 85–88.
Nichols, J. D. et al. 1983. Factors affecting the distribution of mallards wintering in the Mississippi Alluvial Valley. – Auk 100: 932–946.
Paulus, S. L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. – J. Wildl. Manage. 48: 371–380.
Pearse, A. T. et al. 2012. Local and landscape associations between wintering dabblers and wetland complexes in Mississippi. – Wetlands 32: 859–869.
Pernollet, C. A. et al. 2015. A comparison of wintering duck numbers among European rice production areas with contrasting flood regimes. – Biol. Conserv. 186: 214–224.
Petrie, M. J. et al. 2011. Guidelines for establishing joint venture waterfowl population abundance objectives. North American waterfowl management plan science support team technical report No. 2011-1. – U.S. Fish and Wildlife Service, Washington D.C., USA.
Pickens, B. A. and King, S. L. 2014. Linking multi-temporal satellite imagery to coastal wetland dynamics and bird distribution. – Ecol. Model. 285: 1–12.
Rafrovich, R. V. et al. 2019. Migratory bird hunting activity and harvest during the 2017–2018 and 2018–2019 hunting seasons. – U.S. Fish and Wildlife Service, Laurel, Maryland, USA.
Reinecke, K. J. and Loesch, C. R. 1996. Integrating research and management to conserve wildfowl (Anatidae) and wetlands in the Mississippi Alluvial Valley, USA. – Giber Faune Sauvage Game Wildl. 13: 927–940.
Reinecke, K. J. et al. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. – In: Weller, M. S. (ed.), Waterfowl in winter. Univ. of Minnesota Press, Minneapolis, pp. 325–337.
Reinecke, K. J. et al. 1992. Evaluation of aerial transects for counting wintering mallards. – J. Wildl. Manage. 56: 515–525.
Reinecke, K. J. et al. 1989. Mississippi Alluvial Valley. – In: Smith, L. M. et al. (eds), Habitat management for migrating and wintering waterfowl in North America. Texas Tech Univ. Press, pp. 203–247.
Runge, C. A. et al. 2014. Conserving mobile species. – Front. Ecol. Environ. 12: 395–402.
Schummer, M. L. et al. 2010. Weather-related indices of autumn–winter dabbler abundance in middle North America. – J. Wildl. Manage. 74: 94–101.
Stafford, J. D. et al. 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. – J. Wildl. Manage. 70: 61–69.
Stafford, J. D. et al. 2010. Factors associated with hunter success for ducks on state-owned lands in Illinois, USA. – Wildl. Biol. 16: 113–122.
St. James, E. A. et al. 2013. Effect of weekly hunting frequency on duck abundances in Mississippi wildlife management areas. – J. Fish Wildl. Manage. 4: 144–150.
Tamisier, A. 1976. Diurnal activities of green-winged teal and pintail wintering in Louisiana. – Wildfowl. 27: 19–32.
USDA-NASS (National Agricultural Statistics Service Cropland Data Layer) 2009–2015. Published crop-specific data layer. – USDA-NASS, Washington, D.C., <http://nassgeodata.gmu.edu/CropScape/>.
USFWS and CWS (U.S. Dept of Interior and Canadian Wildlife Service) 1986. North American waterfowl management plan. – U.S. Dept of Interior, Washington, D.C. and Dept of the Environment, Ottawa, Canada. <https://nawmp.org/sites/default/files/2018-01/1986%20OriginalNAWMP.pdf>.
USFWS (U.S. Fish and Wildlife Service) 2019. Adaptive harvest management: 2020 hunting season. – U.S. Dept of Interior, Washington, D.C., <www.fws.gov/birds/management/adaptive-harvest-management/publications-and-reports.php>.
USFWS (U.S. Fish and Wildlife Service, Canadian Wildlife Service, Secretaria de Medio Ambiente Recursos Naturales) 2012. U.S North American waterfowl management plan 2012: People Conserving Waterfowl and Wetlands. - U.S. Dept of Interior, Washington, D.C., Department of the Environment, Ottawa, Canada, and Minister of the Environment, Mexico City, Mexico. Available online at <www.fws.gov/migratory-birds/pdf/management/NAWMP/2012NAWMP.pdf>.
USGS (U.S. Geological Survey) 2009–2016. Data available from the USGS. – <http://glovis.usgs.gov/>.
Väänänen, V. M. 2001. Hunting disturbance and the timing of autumn migration in Anas species. – Wildl. Biol. 7: 3–9.
Williams, B. K. and Nichols, J. D. 2001. Systems identification and the adaptive management of waterfowl in the United States. – Wildl. Biol. 7: 223–236.
Williams, C. K. et al. 2014. Estimating habitat carrying capacity for migrating and wintering waterfowl: considerations, pitfalls and improvements. – Wildlflowl Spec. Iss. 4: 407–435.
Yackulic, C. B. and Ginsberg, J. R. 2016. The scaling of geographic ranges: implications for species distribution models. – Landscape Ecol. 31: 1195–1208.

Supplementary information (available online as Appendix wlb-00792 at <www.wildlifebiology.org/appendix/wlb-00792>).