

RESEARCH ARTICLE

Effects of landscape structure and temporal habitat dynamics on wintering mallard abundance

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Abstract

Context Management of wintering waterfowl in North America requires adaptability because constant landscape and environmental change challenges existing management strategies regarding waterfowl habitat use at large spatial scales. Migratory waterfowl including mallards (*Anas platyrhynchos*) use the lower Mississippi Alluvial Valley (MAV) for wintering habitat, making this an important area of emphasis for

improving wetland conservation strategies, while enhancing the understanding of landscape-use patterns.

Objectives We used aerial survey data collected in the Arkansas portion of the MAV (ARMAV) to explain the abundance and distribution of mallards in relation to variable landscape conditions.

Methods We used two-stage, hierarchical spatio-temporal models with a random spatial effect to identify covariates related to changes in mallard abundance and distribution within and among years.

Results We found distinct spatio-temporal patterns existed for mallard distributions across the ARMAV

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and these distributions are dependent on the surrounding landscape structure and changing environmental conditions. Models performing best indicated seasonal surface water extent, rice field, wetland and fallow (uncultivated) fields positively influenced mallard presence. Rice fields, surface water and weather were found to influence mallard abundance. Additionally, the results suggest weather and changing surface water affects mallard presence and abundance throughout the winter.

Conclusions Using novel datasets to identify which environmental factors drive changes in regional wildlife distribution and abundance can improve management by providing managers additional information to manage land over landscapes spanning private and public lands. We suggest our analytical approach may be informative in other areas and for other wildlife species.

Keywords Species distribution modeling · Spatial random effect · Species-habitat relationships · *Anas platyrhynchos* · Waterbird · Waterfowl

Introduction

Effective wildlife management and planning require an understanding of the ecological factors influencing the distribution of species in space and time (Pressey et al. 2007). Investigations of spatial patterns and relationships within a study system are necessary to enhance the predictive ability of distribution models (Merow et al. 2014; Yackulic and Ginsberg 2016). Additionally, species distributions are inherently determined by ecological processes across a landscape, and tend to fluctuate temporally, especially when considering the ecology of highly mobile migratory species (Greenberg and Marra 2005; Beatty et al. 2014a). Thus, migratory species pose unique challenges for habitat managers, and knowledge on temporal habitat dynamics across a landscape could improve management strategies (Pickens and King 2014; Runge et al. 2016).

Species distribution models typically include prior knowledge of ecological relationships at appropriate spatio-temporal scales, and numerous studies have examined the effects of spatial and temporal scaling on species distribution models (Wiens 1989; Merow et al.

2014; Holland and Yang 2016). However, challenges arise when incorporating both local- and landscape-scale characteristics into species distribution models because ambiguity exists without categorization of meaningful biological scales (Mazerolle and Villard 1999; Thornton et al. 2011). For example, spatial patterns can be overlooked in a study that only examines an ecological variable as a function of discrete patches compared to a study that examines a variable as a function of a continuous landscape (Chakraborty et al. 2010). As species distributions are predicted to be impacted by the effects of climate change and landscape modification, studies incorporating neighborhood effects and spatial patterns into distribution models can improve management planning (Almaraz et al. 2012; Anderson 2013; McGarigal et al. 2016).

The mallard (*Anas platyrhynchos*) provides one example of a highly mobile species that behaviorally adapts to spatial and temporal fluctuations in the availability of resources. Specifically, the abundance and distribution of wintering mallards vary spatially within and among years in the lower Mississippi Alluvial Valley (MAV) (Nichols et al. 1983). Theory suggests that migratory waterfowl select habitat in order of geographic scale, from (1) geographic region, (2) wetland systems, (3) site-specific locations and, lastly, (4) microhabitat (Johnson 1980; Kaminski and Elmberg 2014; Beatty et al. 2014a). For example, mallards demonstrate different habitat selection patterns as a function of behavior (Beatty et al. 2014a). However, a specific link between the spatio-temporal distribution of mallards to temporal variation in landscape conditions will provide valuable insight into the effects of landscape conditions on the ecology of a migratory bird (Ji and Jeske 2000; Pernollet et al. 2015). Consequently, understanding the potential ecological drivers of mallard winter movement and habitat selection will improve waterfowl management and conservation (Heitmeyer 2006; Baldassarre and Bolen 2006).

The mallard is the most abundant waterfowl species in North America and the MAV winters the majority of the continental population in most years (Bellrose 1980; Green and Krementz 2008; USFWS et al. 2012). As such, waterfowl biologists in the MAV prioritize mallard populations in developing hunting regulations and wetland management plans (USFWS and CWS 1986; Drilling et al. 2002). Pearse et al. (2012)

previously modelled mallard habitat associations, but robust statistical models of spatio-temporal variation for winter mallard distributions have not been developed. Studies have analyzed the relationships of certain covariates to mallard habitat use in the MAV, but only at local sites or at sites with mallards present (Pearse et al. 2012; Beatty et al. 2014a; Hagy and Kaminski 2015). Thus, a need exists for insight into large-scale spatio-temporal waterfowl habitat availability (Haig et al. 1998; Almaraz et al. 2012). An expansion in the understanding of mallard spatial ecology will benefit not only mallards, but other wetland-dependent species in the MAV (Pearse et al. 2012).

In this study, we used a novel dataset of landscape-scale mallard observations to examine the effects of landscape composition on mallard abundance and distribution in the MAV in the state of Arkansas, USA (ARMAV). Specifically, our objectives were to: (1) evaluate the effects of landscape composition and temporally dynamic environmental conditions on the distribution and abundance of non-breeding mallards over time and space throughout the winter over a seven-year period; (2) assess the performance of landscape composition in predicting the distribution and abundance of mallards across the ARMAV; and (3) develop spatially explicit probabilities of mallard abundance within the ARMAV. To meet our objectives, we developed two-stage, hierarchical Bayesian spatio-temporal models with spatial random effects. We then predicted mallard abundance in both sampled and unsampled areas in spatially and temporally dynamic habitat. We evaluated the spatial performance of the model to identify areas where the model fully or partially explained local mallard abundance.

Methods

Study area

The MAV covers 10 million ha and includes areas of six states in the southern United States; Arkansas contains approximately 37% of the MAV (Reinecke et al. 1989). 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) (Fig. 1).

Survey design

We used diurnal mallard observations collected from 25 Arkansas Game and Fish Commission aerial surveys of fixed-width (250 m) transects in the ARMAV from 2009 to 2016. Surveys were randomly stratified and observers recorded the date, number of individual mallards detected and geographic coordinates of mallard observations. In the first 4 years of the study, four surveys were completed each year in mid-November, mid-December, early-January and late-January. The final 3 years did not include late-January surveys. Transects were randomly chosen with selection weighted by strata. The first 2 years of the study the ARMAV was separated into five strata based on expert opinion, and in the next 5 years, the ARMAV was divided into 11 strata based on the watersheds (Lehnen 2013). Total length of combined transects for each survey ranged from 3700 to 5600 km.

Covariates

We quantified 13 covariates known to influence mallard habitat use in winter (Nichols et al. 1983; Allen 1987; Reinecke et al. 1989; Heitmeyer 2006; Beatty et al. 2014a, b). Overall landscape composition within the ARMAV varied among years, and land cover covariates were from the annual cropland data layer (USDA NASS 2009–2015): rice fields (covariate 1), soybean fields (covariate 2), corn fields (covariate 3), permanent water (covariate 4), wetlands (covariate 5), and fallow (uncultivated agriculture) fields (covariate 6).

Seasonal surface water that varied among each survey (hereafter surface water) was used to describe the extent of seasonally-flooded land across the landscape (covariate 7). We used Landsat imagery to identify and quantify surface water for each survey using the Normalized Water Diversity Index and surface water was identified with an overall average of 90% accuracy among the 25 classifications (McFeters 1996; USGS 2009–2016). All geoprocessing was performed in ESRI ArcGIS (ESRI 2015, see supplementary material).

Land that is publicly managed for wildlife by state and federal agencies (i.e. national wildlife refuges and

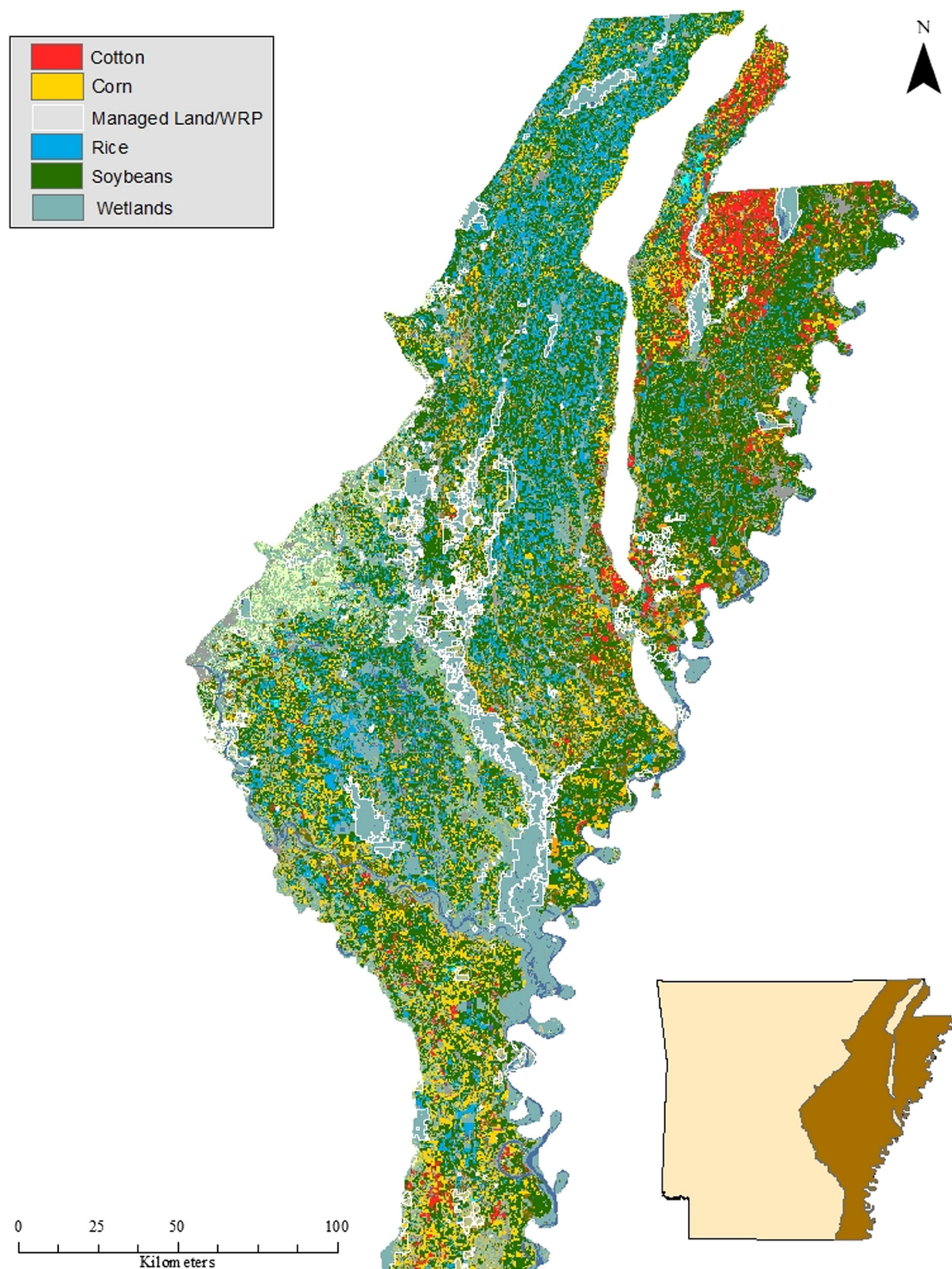


Fig. 1 Land cover from the annual cropland data layer within the ARMAV (2013). Figure only represents land cover covariates used during one of 7 years. Legend shows land cover relevant to the study (USDA NASS 2013)

state wildlife management areas) was combined as a covariate, hereafter managed land (covariate 8). Wetlands enrolled in the Agricultural Conservation Easement Program (ACEP), hereafter referred to as the Wetland Reserve Program (WRP), were added to assess the potential impact of the program on mallard habitat use (covariate 9). Covariates 1–9 were quantified as a percentage of area per grid cell (see below).

Waste grain from crops that remain in a field post-harvest are a food source for waterfowl and can positively influence mallard space use (Stafford et al. 2006; Kross et al. 2007). To estimate availability of waste seeds, we used annual county harvest yields for rice (kg/ha) (covariate 10) and soybean (bushel/ha) (covariate 11) from the United States Department of Agriculture (USDA) annual crop data (USDA-NASS 2015). Due to high linear dependence, we did not include waste corn as a covariate in the analysis. We assumed a higher crop yield at the county level resulted in a greater density of waste seeds. The USDA values were used for November surveys and decreased in value for each following survey by applying decomposition rates (Nelms and Twedt 1996). When cells overlapped two or more counties, we calculated a mean yield for that cell.

We evaluated the effects of weather on mallard distribution and abundance with the weather severity index (WSI; covariate 12) within the ARMAV (Schummer et al. 2010). We obtained weather data from United States Historical Climatology Network data at nine weather stations (Menne et al. 2015) and WSI values were calculated following Schummer et al. (2010). 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. Negative WSI values indicate temperatures above 0 °C with no snow and positive WSI values indicate temperatures below 0 °C with snow (Schummer et al. 2010). Thus, we interpreted negative parameter estimates for WSI as selection for areas with warmer conditions and less snow. Linear dependence among covariates was tested prior to model

fitting based on the Variance Inflation Factor ($VIF = 1/(1 - r^2)$) for each covariate, with r^2 being the multiple correlation coefficient calculated by regressing that covariate on all other covariates.

Statistical analysis

We developed a grid of 2 km × 2 km cells to facilitate modeling mallard distribution and abundance in the ARMAV. We selected 4 km² cells because this value corresponded with mean daily movement distance estimates (3.46 km) for non-breeding mallards and provided a reasonable computation time (Beatty et al. 2014a). Each cell was assigned a value for each covariate as a proportion (0.0–1.0; land cover) or continuous value (WSI, food availability). Given that detectability of mallards can vary among habitat types, especially if canopies are closed, we assigned mallard abundance per cell to four categories to reduce potential uncertainty in aerial surveys due to variable detection among habitats. Categorical response values reduced the variability associated with errors from raw counts, which helped to capture important patterns in abundance data across spatial as well as temporal scales (Smith et al. 1995; Chakraborty et al. 2010). The four categories were: Category 0: no observed mallards, Category 1: 1–15 mallards, Category 2: 16–100 mallards, and Category 3: ≥100 mallards.

We conceptualized the observed categorical abundance 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 is for mallards. Thus, the higher the value of a PA surface, the higher the probability that we would encounter more mallards 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 mallard prevalence (Albert and Chib 1993). We also incorporated a spatial random effect (θ) to capture autocorrelation in mallard 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; (2) lack of data on all potentially important covariates; (3) lack of data in

unsampled regions within the ARMAV (Gelfand et al. 2005; Chakraborty et al. 2010).

Species prevalence data usually contain a large proportion of category 0 (absences), and a single PA surface cannot adequately explain variation in abundance that ranges from category 0 to 3 (Royle and Nichols 2003). That is, using one surface (one set of covariate and spatial effects) to model zeros and nonzeros together may result in poor predictive properties for the model (Potts and Elith 2006; Wenger and Freeman 2008). In Bayesian ecological modeling, there are instances of two-stage modeling for species prevalence such as the suitability/availability modeling in Gelfand et al. (2005) or the potential/transformed abundance approach of Chakraborty et al. (2010). Therefore, we used a two-stage model, where the first stage explained the likelihood of a nonzero observation at a specific cell (mallard presence/absence) and the second stage explained, conditional on at least one mallard observation in a cell, the abundance category of that sighting.

We estimated covariate effects on mallard 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 (see supplemental material Eq. 1). To model presence only in the second stage, we modeled the observed abundance category, given presence of mallards in a cell (see supplemental material Eq. 2). 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; and (3) a pure error term accounting for residual variation (ε). Our dataset included mallard 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 (see supplemental material Eq. 3). The temporal association parameters Γ_{survey} and Γ_{year} facilitated borrowing of information across different surveys for each covariate. We assigned diffused normal priors to their components.

We assumed univariate normal distributions for independent pure error terms with zero means, which

results in a probit regression model for each stage of the model. For identifiability reasons, variance of ε terms were fixed at 1. It should be noted that fixing the error variance at 1 does not impose any constraint. If we parametrized the error standard deviation as σ , it can be shown that the category-specific probabilities are only functions of β/σ . This implies the coefficients can only be identified relative to a fixed value of σ . Generally, we solve this by setting $\sigma = 1$. Since the measure of significance of a covariate effect is independent of its scale, this assumption does not limit flexibility of the model. 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; R Core Team 2015).

Model development

We developed a set of six competing candidate models to evaluate the spatio-temporal effects on mallard abundance. The models were developed to assess: (1) agriculture fields and waste grain abundance; (2) interactions among surface water and land cover classes known to be used by mallards; (3) managed land and their interaction with surface water; (4) the five most important covariates expected to affect mallard abundance determined from the scientific literature; and (5) surface water and permanent water. We included the full model with all main effects and no interactions as our sixth and final candidate model (Table 1).

We conducted a posterior predictive check for all candidate models with the Bayesian χ^2 goodness of fit statistic where p values close to 0.5 indicate adequate model fit (Johnson 2004). We then evaluated candidate models with the Bayesian predictive information criterion (BPIC; Ando 2007). The BPIC criterion modifies the commonly used deviance information criterion of Spiegelhalter et al. (2002) by strengthening the penalty on model size. The model with the smallest BPIC value was considered the best performing model (supplementary material). We interpreted any covariate with 95% credible intervals not overlapping zero as positively (> 0) or negatively (< 0) affecting mallard distribution, and covariates

Table 1 The six competing models to explain winter mallard abundance and distribution within the ARMAV from 25 aerial surveys from 2009 to 2016

Model	Description	Covariates	BPIC ^a	ΔBPIC	pD ^b	Bayesian <i>p</i> value ^c
Full	All main effects	All main effects	56791	0	386	0.55
Habitat	Known land covers that mallards use and their interaction with water	Rice field + soybean field + wetland + surface water + fallow field + permanent water + WSI	56848	57	268	0.517
Waterfowl Importance	Most important covariates for mallards from previous research	Surface water + rice field + wetland + permanent water + WSI	57364	573	217	0.548
Managed Land	Land associated with managed land and their interaction with water	Wetland + WRP + managed land + permanent water + surface water + WSI	57533	742	255	0.496
Water	How water alone affects mallard abundance distributions.	Surface water + permanent water	58431	1640	144	0.504
Agriculture	Agriculture fields and post-harvest waste grain left in fields.	Rice field + soybean field + corn field + fallow field + waste rice + waste soybean	59058	2267	233	0.492

Competing models included a subset of covariates based on knowledge from previous research. Model performance was ranked by BPIC and the full model best explained the abundance and distribution of mallards

^aBayesian Predictive Information Criterion

^bEffective number of parameter

^cModel fit measured by $A[R^B > \chi^2]$. Values closer to 0.50 (from either direction) are indicative of model adequacy

with 95% credible intervals overlapping zero had no effect on mallard distributions. Additionally, we ranked covariate importance for each survey by dividing the mean of the covariate by the standard deviation (SD).

We produced maps of spatial random effects (θ) for each survey to examine trends in covariate performance among regions within the ARMAV. Overestimation of mallard abundance by the covariates is represented by negative θ values, whereas underestimation of mallard abundance is represented by positive θ values. Thus, θ values closer to zero represent regions where the covariates within the model accurately predicted mallard abundance. Random variation in θ across the cells indicate a lack of spatial dependence, whereas a smooth pattern with little differences in θ values among nearby cells, but showing smooth transitions among far away cells, is considered evidence of spatial association. Finally, we developed spatial probabilities of mallard abundance across the ARMAV. We generated posterior maps with the estimated categorical abundance probabilities

throughout the ARMAV for each survey (see supplemental material Eq. 4).

Results

We counted 924,098 individual mallards over all 25 surveys. Transects from all surveys intersected 9657 cells ($\sim 20\%$ of total extent), 3327 of which had at least one mallard observation. The median amount of surface water cover in the ARMAV increased every survey among years (November (1.6%), December (4.6%), early-January (4.5%), late-January (5.1%)) in every year. The late-January 2013 and early-January 2014 were the only surveys to have above 10% total surface water coverage across the ARMAV (12 and 35% coverage, respectively). WSI values ranged from -12.9 to 9.2 and the mean WSI values for all surveys was -4.5 , with early-January (0.26) having the highest WSI values, followed by late-January (-5.7), December (-6.4), and November (-10).

All posterior predictive check *p* values were close to 0.5 for all models, which indicated all models

adequately fit. The presence of spatial random effects contributed to adequacy of models with smaller set of covariates. As expected, the pD values decrease as we gradually reduce the number of covariates. According to BPIC, the full model performed best, yet, the habitat model produced a BPIC value close to the full model, even with significantly smaller number of parameters (Table 1). Here, we report results only from the full model.

The presence of mallards (stage 1) was most influenced by surface water, wetlands, rice fields, fallow fields, WSI, open water, and waste rice. Mallard abundance (stage 2) was most influenced by only surface water, rice fields, and WSI. WSI negatively influenced the presence of mallards, indicating severe weather (i.e. high WSI) reduced mallard presence whereas milder weather increased mallard presence. In contrast, among locations where mallards were present, WSI positively influenced abundance, which implied where mallards were present, severe weather made it more likely for mallard distributions to clump. Overall, we found many covariates provided information of what affects mallard presence, but only a few of them are informative about to what extent abundance will occur (Table 2 and supplemental tables).

Surface water was typically the most important covariate to positively influence mallard presence (12 of 25 surveys) and abundance (12 of 25 surveys) (Table 2 and supplementary tables). Temporally, surface water, wetlands, rice fields, waste rice and open water positively influenced presence and abundance from November to late-January (supplementary tables). We found WSI positively influenced mallard presence in November but then negatively influenced mallard presence from December to late-January, which coincides with an increase in severe weather conditions (supplementary tables). With respect to the temporal dependence in covariate effects, we found surface water, wetlands, rice, soybean, and fallow fields had positive associations for the presence of mallards across surveys within the same year. Only surface water and WSI were found to have positively correlated effects on abundance between successive months (Table 3). For surveys conducted at same month in consecutive years, surface water, wetlands, open water, rice and fallow fields were positively associated with presence, whereas only surface water and rice field positively influenced abundance. All significant temporal parameters among years had a posterior mean between 0 and 1 indicating stationary pattern of these covariate effects in the long run

Table 2 Posterior covariate estimates for winter mallard abundance distributions in the ARMAV from 2009 to 2016

Covariate	Effect on Mallards		Total highest mean/SD	
	Stage 1 (Pos/Neg)	Stage 2 (Pos/Neg)	Stage 1	Stage 2
Rice field	20/0	18/0	6	5
Soybean field	10/0	3/0	0	0
Wetland	25/0	0/3	5	1
Corn field	0/1	0/0	0	0
Surface water	23/0	21/0	12	12
Open water	17/0	1/1	1	0
Fallow field	20/0	0/0	0	0
Managed land	2/1	6/0	0	0
WRP	3/1	0/0	0	0
WSI	5/12	12/0	2	7
Waste rice	13/1	0/0	0	0
Waste soybean	6/1	0/0	0	0

Results are from the full 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 mallard abundance for the 25 surveys. 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 mallard abundance where mallards were present

Table 3 Survey effect and year effect posterior estimates from the combined year full model explaining mallard distribution in the ARMAV

	Survey Effect			Year Effect		
	95%CI Lower	Mean	95%CI Upper	95%CI Lower	Mean	95%CI Upper
Stage 1						
Rice field	0.0235	0.4098	0.8389	0.2731	0.6404	1.0001
Soybean field	0.0809	0.7683	1.4920	– 0.1237	0.4381	0.9617
Wetland	0.1204	0.5400	0.9409	0.1679	0.5222	0.8648
Corn field	– 0.7008	– 0.0855	0.5034	– 0.7924	– 0.0231	0.9623
Surface water	0.0897	0.2958	0.5476	0.4854	0.7247	0.9321
Open water	– 0.1068	0.3511	0.9298	0.2154	0.6753	1.0730
Fallow field	0.0238	0.3909	0.8211	0.3564	0.7443	1.0916
Managed land	– 0.9061	0.0483	1.1019	– 1.1593	– 0.1107	0.9209
WRP	– 0.3872	0.2949	0.9172	– 0.2597	0.4347	1.0915
WSI	– 0.0786	0.2943	0.6695	0.1728	0.4536	0.7343
Waste rice	– 0.4628	0.4170	1.2500	– 0.4235	0.3516	1.1171
Waste soybean	– 0.6572	0.1001	0.8831	– 0.8159	– 0.0041	0.8786
Stage 2						
Rice field	– 0.0309	0.3131	0.9227	0.1344	0.6586	0.9932
Soybean field	– 0.2832	0.4301	1.0806	– 0.4470	0.2724	0.8844
Wetland	– 0.1265	0.4246	0.9459	– 0.8591	– 0.0429	0.9343
Corn field	– 1.0641	0.3724	1.5116	– 0.7564	0.1501	0.8629
Surface water	0.0034	0.3395	0.7735	0.3127	0.6955	1.0388
Open water	– 1.2444	– 0.2025	0.6949	– 0.4817	0.2843	1.0584
Fallow field	– 0.6665	0.4564	1.3864	– 0.6213	0.1393	0.7512
Managed land	– 0.2648	0.1978	0.7168	– 0.1277	0.6527	1.1983
WRP	– 0.5748	0.1508	0.8653	– 0.6767	0.1953	0.9808
WSI	0.2155	0.7459	1.2125	– 0.0483	0.3003	0.7453
Waste rice	– 0.6277	0.2217	1.0610	– 0.9854	– 0.1428	0.6645
Waste soybean	– 0.6031	0.2648	1.0561	– 1.0281	– 0.2811	0.5056

Stage 1 (top) modeled mallard presence and absence and stage 2 (bottom) modeled mallard abundance where mallards were present. Covariates with 95% confidence intervals not overlapping zero are highlighted in gray

(Table 3). However, given that we have only 7 years of data, a longer dataset is necessary to confirm any long-term pattern of yearly association.

We found the presence of mallards was spatially correlated in all surveys (Fig. 2 and supplementary figures). The spatial effects (θ) for the presence of mallards at latitudes between 34 and 36° generally had θ values close to zero, suggesting the covariates explained mallard presence well. The western portion (longitudes – 91.5 to – 92.0°) of the ARMAV had high positive θ values in 11 of 25 surveys. Negative θ values tended to be in the southern (below 34°) and northern (above 36°) latitudes of the ARMAV (Fig. 2

and supplementary figures). A spatial pattern also was apparent in the presence of mallard abundance probabilities. In five of seven November surveys, the probability for the presence of mallards was higher in the northern portion of the ARMAV. In six of seven December surveys and all of the early-January and late-January surveys, the probability for the presence of mallards redistributed south (supplementary figures). The probability of absence was high throughout the ARMAV and consistent among surveys, implying that a large portion of the ARMAV is of lower value for mallards. We found the probability of absence was highest in the northeastern portion of the ARMAV east

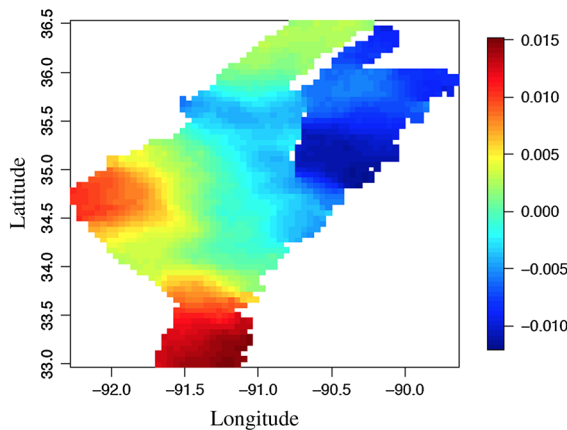


Fig. 2 Spatial random effects (θ) for the presence/absence of mallards across the ARMAV for the early-January 2014 waterfowl survey from the full model. Values of θ explain the performance of covariates used in the model. Positive θ values represent cells with more mallards than expected and negative θ values represent cells with less mallards than predicted. A correlated spatial pattern is shown, because a smooth gradient of θ values exists. The entire surface of θ values across the ARMAV equals 1.0

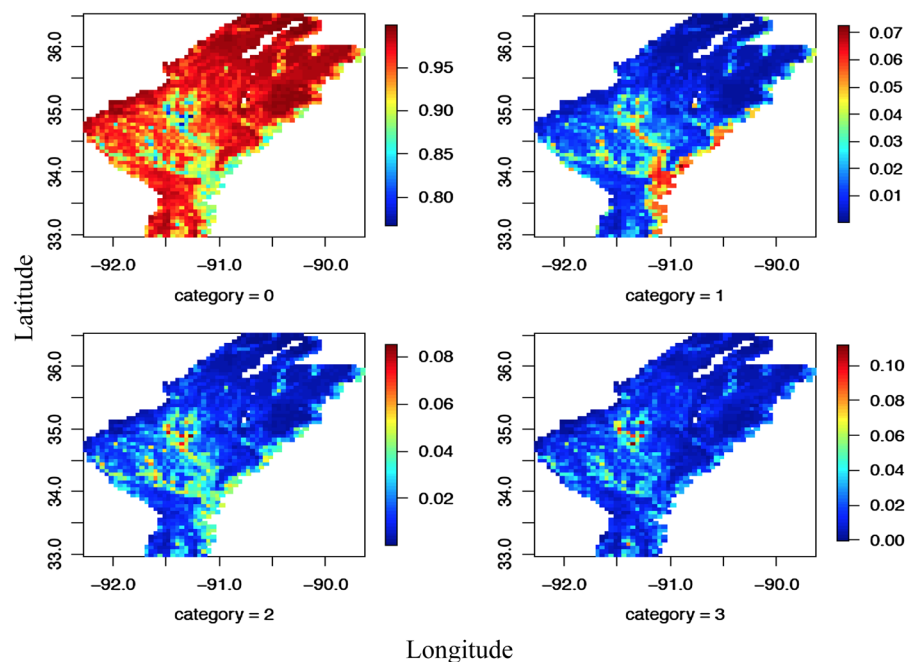
of -91.0° and north of 34.5° (Fig. 3 and supplementary figures). The probability for 1–10 mallards present was highest along the Mississippi River south of 34.5° , and in a block of managed lands (Bald Knob National Wildlife Refuge and Henry Gray Hurricane Lake, Rex

Hancock Black Swamp, and Steve N. Wilson Raft Creek Bottoms Wildlife Management Areas) adjacent to the northwestern ARMAV bluff line. The probability for 10–100 and over 100 mallards present was highest around the same region that 1–10 mallards were located, as well as in a group of cells in the Grand Prairie Ecoregion near Stuttgart, AR (Fig. 3 and supplemental figures). In addition to visualizing spatial patterns and distributions, the model allows for a regional examination of covariate performance, which can be extended to all covariates and surveys. As surface water and WSI were both strong predictors of mallard presence and abundance, their distributions can be compared to the distribution of mallards and the distribution of the spatial random effect. Further, models without important ecological variables (i.e. surface water, WSI), as in our agriculture model, can be visualized to see the poor predictive nature of the model (Fig. 4).

Discussion

We modeled dynamic and ephemeral resources in a heterogeneous landscape using a biologically meaningful scale to predict the distribution of a wetland-dependent migratory bird (Holland et al. 2009;

Fig. 3 Probability surfaces for mallard abundances to occur within the ARMAV during early-January 2014, predicted by the full model. Category 0 = no mallards present, Category 1 = 0–10 mallards present, Category 2 = 11–100 mallards present, Category 3 = 100+ mallards present. The probability of all categories equals to 1.0 for each cell



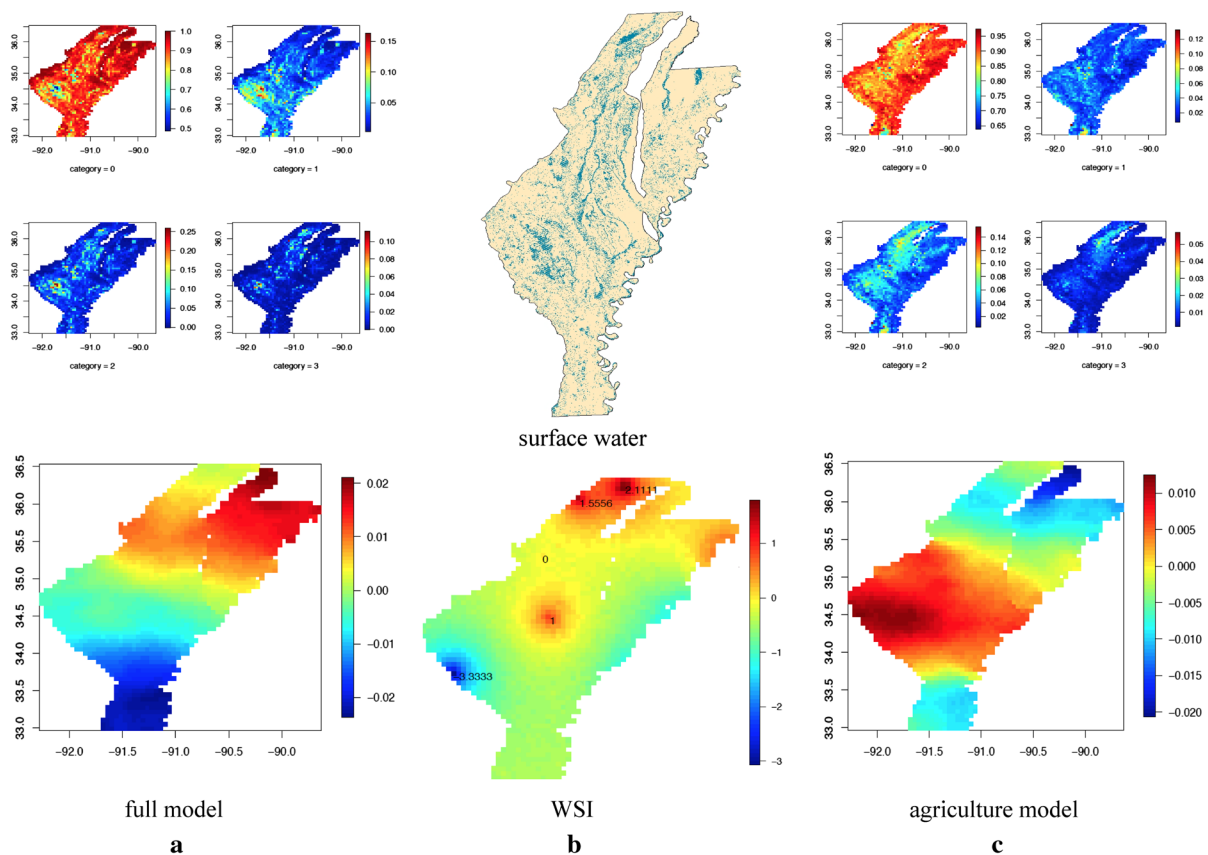


Fig. 4 Effects of covariates on the predictive capability of the spatio-temporal model for mallard distribution and abundance. Figure represents mallard observations of the late-January survey, which is one of 25 surveys used in the study. Part **a** results of the spatial random effects (bottom) and predicted categorical abundance (top) from the full model, which was the best performing model. Part **b** distribution of significant covariates surface water (top) and WSI (bottom) during the late-January 2013 survey. Part **c** results of the spatial random effects (bottom) and predicted categorical abundance (top) from the agriculture model, which was the worst performing model.

Leblond et al. 2011; McGarigal et al. 2016). Extent and distribution of surface water associated with selected land cover had the most influence on mallard presence (wetlands, rice fields, and fallow fields) and abundance (rice fields), supporting past research on mallard space use. Although previous research has identified surface water as an important factor driving mallard abundance (Allen 1987; Reinecke et al. 1988; Davis et al. 2011), we included temporal variation in surface water to improve the predictive ability of our species distribution model (Pickens and King 2014; Yackulic and Ginsberg 2016). Additionally, the

Surface water and WSI were not included in the agriculture model. The full model predicted more mallards to be present the southwestern portion of the ARMV (part-a top), coinciding with higher amounts of surface water and less severe weather (negative WSI values). Additionally, the covariates fully explained mallard presence in the southwestern portion of the ARMV (part-a bottom). Whereas the agriculture model did not predict mallards to be in the southwestern portion of the ARMV (part-c top) and the covariates did not fully explain the presence of mallards in the same region (part c-bottom)

visualization of ecological patterns at the landscape levels are improved by incorporating covariates into hierarchical models (e.g. surface water, WSI) at the smallest scale, especially when many land cover covariates are static at the macro habitat level (Bastos et al. 2016). Indeed, recent waterfowl research has relied on static land cover datasets (e.g. National Land Cover Dataset) that have a limited capacity to detect surface water (Beatty et al. 2014a). The land cover covariates used from the cropland data layer were static within season, but changed among season, and our extensive multi-year dataset allowed for reliable

predictions of mallard distributions (USDA-NASS 2015; Yackulic and Ginsberg 2016).

We found mallards were clumped among wetlands farther south in the ARMAV. The spatial random effect found our covariates over-predicted mallard presence in a span of wetlands in the northern ARMAV. The spatial random effect illustrated patterns that were not fully explained by the model, so future research can investigate other ecological characteristics that may structure mallard space use patterns (Banerjee and Fuentes 2012; Allen et al. 2013). For example, our model expected more mallards to use the northern ARMAV than we observed, and researchers could investigate possible regional factors such as hunting pressure that could be driving mallards to under-utilize the area (Johnson 2007; St. James et al. 2013). Furthermore, restoration of lower MAV wetlands has fallen short of goals, illustrating the importance of elucidating regional factors that drive mallard distribution to understand processes at larger spatial scales, such as the entire ARMAV (Kross et al. 2008; Faulkner et al. 2011; Leach et al. 2012).

Publicly managed lands provide a small proportion of overall wildlife habitat in the USA (Runge et al. 2016). Consequently, private lands contain the vast majority of potential wildlife habitat, and identification of private lands with quality habitat allows management planners to consider the capacity of these areas to support wildlife populations (Leblond et al. 2011). Our models suggested agricultural land was consistently more important for mallards than managed land, which was unexpected because these managed lands provide higher quality wetland habitat (Reinecke et al. 1989; King and Keeland 1999). However, we consistently found that mallard distributions predicted to be on agriculture fields were part of wetland systems that had publicly managed wetlands, specifically within two to ten kilometers of managed land (Fig. 1 and supplemental figures). Our observations were entirely diurnal, and mallards can make daily movements between diurnal and nocturnal locations (Davis et al. 2011; Beatty et al. 2014b). Diurnal location decisions are thought to be driven in large part by hunting pressure, and considerable diurnal hunting pressure occurs within publicly managed lands in the ARMAV. We emphasize our analyses of diurnal locations are appropriate because

diurnal habitat meet critical resource needs, for example, as sanctuary habitat during the hunting season (St. James et al. 2013).

Cultivated crops can provide spatially and temporally predictable and concentrated sources of food for wildlife (Allen 1987; Stafford et al. 2010). As expected, we found that rice fields had the strongest influence on mallard abundance of any agriculture habitat in the ARMAV. The attraction to rice fields most likely resulted from the valuable nutrients provided by waste rice that are needed in the winter months and the physical structure more often present in rice fields than soybean fields (Kross et al. 2007; Stafford et al. 2010). However, rice fields must be inundated with surface water for mallards to feed on waste rice, and without regular inundation of rice fields, waste rice and waste soybean can equally contribute to total food intake (Delnicki and Reinecke 1986). We did find soybean fields were a predictor of mallard distributions, but they were never the most important covariate, most likely because soybeans degrade faster and provide fewer nutrients than rice (Nelms and Twedt 1996). Therefore, due to spatio-temporal variations in seasonal flooding of rice fields, we suggest that mallards were simply using soybean fields due to their high abundance (31–34% of total extent), compared to the lower abundance of rice fields (10–17% total extent). The consistently strong influence of rice fields on mallard abundance indicates preference for this less-available habitat (Kross et al. 2007, 2008). Additionally, our measurement of waste grain was an attempt to test if crop yields can serve as a proxy for waste grains in landscape scale studies, and we found evidence that a measurement of landscape level waste grain can be useful when describing mallard presence. However, Stafford et al. (2006) did find that waste grain measurements can vary among single fields. Consequently, we caution against relying solely on crop yields for waterfowl distribution models. Also, management recommendations have suggested the availability of agriculture habitat rather than waste grain is more reliable predictor of waterfowl abundance, which more aligns with our overall results (Hagy et al. 2014).

Notably, our analysis advances modeling by incorporating an abiotic weather variable (WSI) along with biotic factors to predict species spatio-temporal distributions (Albanese et al. 2012; Anderson 2013;

Notaro et al. 2014). Current climate models predict changes in waterfowl migration and non-breeding distributions, so a need exists for climate to be incorporated in species distribution models (Guillemin et al. 2013; Beatty et al. 2017). Whereas Schummer et al. (2010) analyzed the relationship between weather and waterfowl at waterfowl management areas within Missouri, as we are aware, this was the first study to use the WSI in distribution models at a large extent (ARMAV). Although localized weather does not represent climate, we found that within the ARMAV, the weather affected mallard abundance and distribution, and mallards moved within the ARMAV towards less severe weather conditions. Mallards sought the same habitat type throughout the winter regardless of the time of year, and we found mallard distributions moved south as the winter progressed, coinciding with more severe weather. Consequently, our results emphasize a temporally dynamic management strategy within the winter season, which could allocate management resources appropriately throughout the MAV as a function of time of year. This emphasizes the need to incorporate time of year in management strategies so enough resources are available in the southern ARMAV later in the winter, when less mallards will be in the northern ARMAV and more will be in the southern ARMAV. Mallards will make regional movements in response to weather conditions and we found this to occur within one ecoregion (Nichols et al. 1983). Although WSI was developed to quantify weather conditions for waterfowl, similar indices could be developed and included in species distributions for other taxa.

Considerable research on mallard habitat use in the MAV suggests many factors influence mallard abundance distributions (Fredrickson and Heitmeyer 1988; Kross et al. 2007; Davis et al. 2011). However, a spatio-temporal analysis of mallard distributions from a multi-year dataset at the landscape scale has been lacking and is necessary to assess factors affecting waterfowl abundance (Almaraz and Amat 2004). We found that mallards use a mosaic of habitats, and extensive surface water is necessary to sustain large populations of mallards. By documenting temporal variation in habitat conditions from remotely sensed data and accounting for spatio-temporal variation in the model, we have

improved the understanding of waterfowl ecology in the MAV (Albanese et al. 2012; Pickens and King 2014). Our results provide managers with additional information on how dynamic variation in ecological variables (i.e. weather, surface water) affect the spatio-temporal distribution of mallards. Further, we showed that agriculture land is important over a large landscape, so management strategies can use our results to work with private land owners to improve the private management of land for waterfowl conservation. Additionally, our predictive models may prove to be critical if the extent of winter habitats continues to be reduced, thus altering the hydrology of the ARMAV. Using long-term data sets to model migratory bird distribution and abundance is becoming increasingly prevalent, and we suggest our approach to model species distributions should be further refined and applied to other migratory animals (Pacifi et al. 2016).

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