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RESEARCH ARTICLE

Influences of landscape composition on hunter-harvested mallard body mass and condition in eastern Arkansas

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Abstract

Waterfowl with more body mass and a greater body condition during the non-breeding season are thought to be more likely to survive and have increased productivity during the following breeding season. Body mass and body condition in waterfowl should reflect the resources available to them locally. We analyzed the relationship of landscape composition on mallard (*Anas platyrhynchos*) body mass and body condition (mass-wing length index) among age and sex groups. We calculated these variables from hunter-harvested mallards during the 2019–2020 and 2020–2021 duck hunting seasons in the Lower Mississippi Alluvial Valley of Arkansas, USA. We used linear mixed-effects models to analyze changes in body mass and body condition with changes in the percent landscape composition of water cover, woody wetlands, herbaceous wetlands, rice, soybeans, and disturbance. We found that body mass and condition of harvested mallards were positively associated with greater proportions of water cover and woody wetlands but negatively associated with greater proportions of herbaceous wetlands and human disturbance from human infrastructure. Management actions focused on providing flooded and woody wetland areas on the landscape that allow waterfowl to access food resources, while decreasing the

[†]Retired

disturbance around wetlands in the form of road density and human infrastructure, should increase body mass and body condition in mallards spending the non-breeding season in the Lower Mississippi Alluvial Valley.

KEYWORDS

Anas platyrhynchos, bottomland hardwood forest, foraging ecology, morphology, waterfowl, woody wetlands

Some migratory North American waterfowl, such as mallards (*Anas platyrhynchos*), spend the non-breeding season in the Lower Mississippi Alluvial Valley (LMAV) before migrating back to breeding areas in the Prairie Pothole Region of the United States and Canada (Bellrose 1976). Waterfowl, like many other birds, must maintain or mediate changes in their body mass during the non-breeding season. Although the breeding season also presents challenges in the maintenance of body mass by birds (Hepp et al. 1990, Sjöberg et al. 2000), the non-breeding winter period can be especially challenging due to lower temperatures, a dwindling food supply, frozen water limiting access to food resources, and the pressure of hunting (Loesch et al. 1992, Schummer et al. 2010). Individuals that can meet their energetic needs should have better body condition than conspecifics that struggle to meet energetic needs (Owen and Cook 1977; Delnicki and Reinecke 1986; Reinecke et al. 1988, 1989). During the non-breeding season, ducks must find and occupy areas that provide sufficient resources in the form of abundant and nutritious food and avoid human or other wildlife predators (Reinecke et al. 1989, Madsen and Fox 1995). Likewise, body condition or body mass can be directly tied to an individual's fitness (Klimas et al. 2020).

Body condition, as a function of mass and structural components, has been related to numerous facets of waterfowl fitness. For example, during the non-breeding season in early winter, better body condition can increase survival rates (Bergan and Smith 1993), whereas waterfowl in poorer body condition are more likely to be infected by parasites (Shutler et al. 1999, Meixell et al. 2016). Individuals with lower body mass (which may result in a lower body condition) may have delayed courtship and breeding pair formation (Miller 1985, Hepp 1986). In contrast, better non-breeding body condition in some waterfowl species increases the chances of survival and level of productivity during the following breeding season (Heitmeyer and Fredrickson 1981, Devries et al. 2008, Warren et al. 2014, Fowler et al. 2020). Better body condition can also decrease time spent in spring migration (Dujins et al. 2017), allowing migrants to reach the breeding grounds sooner, potentially increasing reproductive success (Rohwer 1992, Elmberg et al. 2005, Devries et al. 2008).

One of the fundamental strategies of waterfowl management is manipulating land cover to maximize the amount of available food on the landscape (Edwards et al. 2012), while regulating human activity (e.g., providing sanctuaries) to reduce unnecessary energy use (Reinecke et al. 1989, Fredrickson and Taylor 2007). Therefore, conservation agencies spend substantial time and financial resources to manage waterfowl habitat to ensure adequate foraging and resting locations. Waterfowl using areas with adequate foraging and resting locations should assimilate more energy, resulting in higher body mass and greater body condition index values.

The LMAV is one of the largest non-breeding areas for waterfowl in North America (Bellrose 1976, Reinecke et al. 1989). Non-breeding ducks in this region forage and rest in woody wetlands such as flooded bottomland hardwood forests, herbaceous wetlands such as moist-soil impoundments, flooded agricultural crops, and waterfowl sanctuaries with low levels of human disturbance (Reinecke et al. 1989, Pearse et al. 2012). Waterfowl meet their dietary requirements by foraging for combinations of seeds, acorns, and macroinvertebrates in wetlands such as woody wetlands (Fredrickson and Heitmeyer 1988, Heitmeyer and Fredrickson 1990, Krapu and Reinecke 1992, Miller et al. 2003, Foth et al. 2014), herbaceous wetlands (Fredrickson and Taylor 1982, Anderson and Smith 1999, Gray et al. 1999, Checkett et al. 2002, Hagy and Kaminski 2012), or flooded agricultural fields (Loesch and Kaminski 1989, Ringelman 1990, Checkett et al. 2002, Kaminski et al. 2003). Waterfowl must also use a variety of habitat characteristics to avoid hunting pressure or other human disturbances, reduce predation risks, rest, and loaf (Reinecke et al. 1989; Davis et al. 2009; Hagy et al. 2017; Herbert et al. 2018, 2021). Areas that contain much human disturbance can cause waterfowl to alter their behavior (Riddington et al. 1996, Burger and Gochfeld 1998, Pease et al. 2005, St. James et al. 2013), thus expending energy (Knapton et al. 2000, Taylor 2010). For this reason, conservation agencies also manage waterfowl sanctuaries, which are areas closed to human access during the hunting season (Bellrose 1954, Madsen 1998). Waterfowl spending the non-breeding season in the LMAV use a combination of wetland types to meet nutritional demands required by different life cycle events (e.g., pair formation, molting; Pearse et al. 2012).

The mallard is the most harvested waterfowl species during the non-breeding season in the LMAV (Raftovich et al. 2021). Aside from being popular among recreational hunters, mallards serve as a focal species of waterfowl management because their response to management is likely indicative of how other dabbling duck species respond (Reinecke et al. 1989, Nichols et al. 2007, Herbert et al. 2021). The Lower Mississippi Valley Joint Venture has a target objective for Arkansas, USA, to provide approximately 219.4 million duck energy days (DEDs) to support a population of 1,863,311 waterfowl during the 110-day nonbreeding season (Lower Mississippi Valley Joint Venture 2015). Current bioenergetic models indicate that the LMAV of Arkansas only provides 54–58% of the target DED objective (Lower Mississippi Valley Joint Venture 2015). In addition, food resources for mallards are unevenly distributed across the LMAV (Hagy et al. 2014). Thus, we hypothesize the body condition and body mass of mallards in the LMAV are likely influenced by the landscape composition of their chosen non-breeding areas.

We assessed the relationship between body mass and body condition of hunter-harvested mallards with landscape composition in the LMAV of Arkansas during 2 winters. Our overall goal was to explore relationships in landscape cover in the vicinity of each mallard's harvest location with body mass and condition and to use this relationship to identify areas within the Arkansas LMAV likely to promote greater body mass and better body condition. We predicted that body mass and body condition of harvested mallards would be greatest in areas with more woody wetlands (i.e., areas where forest and shrubland account for >20% of vegetative cover and soil is periodically flooded or covered with water), herbaceous wetlands (i.e., areas where perennial herbaceous vegetation account for >80% of vegetative cover and soil is periodically flooded or covered with water), flooded rice fields, and overall water cover because these wetlands provide mallard foraging resources and constitute targets for habitat management (Fredrickson and Taylor 1982, Fredrickson and Heitmeyer 1988, Pearse et al. 2012). We also predicted that a greater proportion of flooded soybean fields or areas with high levels of human disturbance (in the form of road density and human infrastructure) would result in mallards with lower body mass and body condition (Ringelman 1990, Madsen 1998, Pearse et al. 2012).

STUDY AREA

We conducted the study during the Arkansas duck hunting seasons of 2019–2020 (23 Nov 2019–8 Feb 2020) and 2020–2021 (21 Nov 2020–6 Feb 2021). Our study area spanned the entirety of the LMAV of Arkansas, which makes up approximately 34% of the entire MAV floodplain (Oswalt 2013) and hosts some of the greatest densities of waterfowl in the world during the winter (Raftovich et al. 2021; Figure 1). The LMAV spans 10 million ha from mid-latitude to southern portions of the Mississippi Flyway (Reinecke et al. 1989). The LMAV is also within a humid subtropical climate region that consists of mild winters (late Dec to late Mar) and hot summers (late Jun to late Sep) and is subject to experiencing droughts and floods (Bruns and Abbas 2005, Potter and Xu 2022). The elevation ranged from 28–131 m above sea level (Google Earth Pro 7.3; Google, Mountain View, CA, USA) and average rainfall was 49.67 cm (SE = 2.89) in 2019–2020 and 29.62 cm (SE = 1.42) in 2020–2021. Average daily temperature ranged from −1.11 to 18.62°C in 2019–2020 and −1.67 to 16.39°C in 2020–2021. The LMAV of Arkansas contains

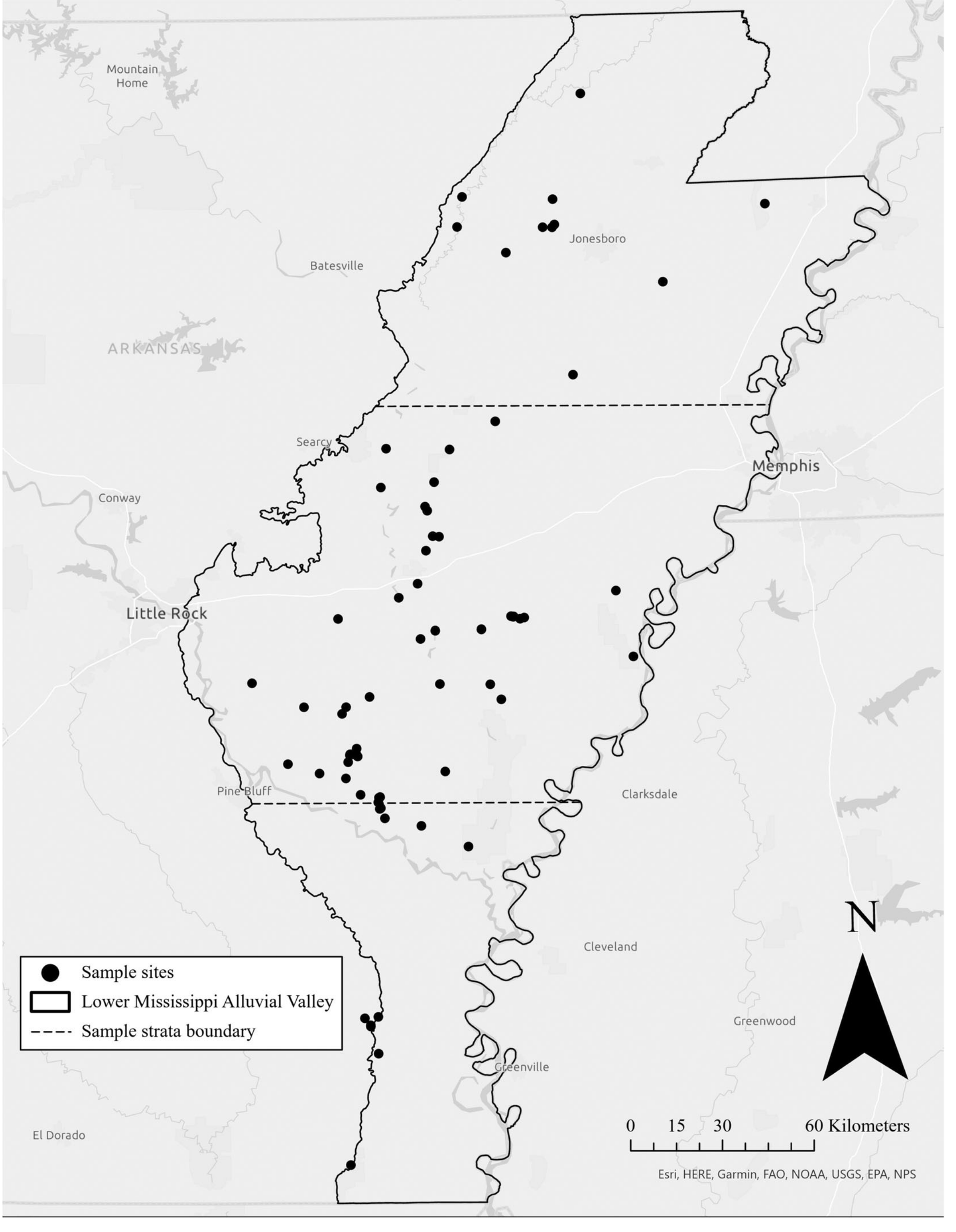

FIGURE 1 Harvest locations and sample strata (north [top third], central [middle third], and south [bottom third] separated by dashed lines) of mallards across the Lower Mississippi Alluvial Valley of Arkansas, USA, during duck hunting seasons 2019–2020 and 2020–2021.

TABLE 1 Average percent water cover, rice, soybean, woody wetlands, herbaceous wetlands, and disturbance (±SE) within 30-km buffers surrounding all mallard harvest locations (*n* = 73) and within the Arkansas, USA, portion of the Lower Mississippi Alluvial Valley (LMAV) during duck hunting seasons 2019–2020 and 2020–2021 (averaged among years).

	30-km buffer		LMAV	
Variable	$\bar{x}$	SE	$\bar{x}$	SE
% water cover	24.618	0.144	26.452	0.531
% rice	4.947	0.385	5.112	0.142
% soybean	4.041	0.168	6.767	0.337
% woody wetlands	7.020	0.657	6.130	0.500
% herbaceous wetlands	0.266	0.003	0.273	0.002
% disturbance	0.522	0.034	0.589	0.000

several land cover types that waterfowl use for food resources and other important life cycle events (Reinecke et al. 1989), including on agricultural wetlands (bottomland hardwood forests and herbaceous wetlands), soybean fields, rice fields, other agricultural crops (in lower densities), and developed areas such as towns and cities (U.S. Department of Agriculture [USDA] 2020; Table 1). In Arkansas wetlands, the dominant vegetation consists of grasses (barnyard grasses [*Echinochloa* spp.], sprangletops [*Leptochloa* spp.], panicgrass [*Panicum* spp.]), sedges (true sedges [*Carex* spp.], nutsedges [*Cyperus* spp.]), forbs (beggarticks [*Bidens* spp.], knotweeds [*Polygonum* spp.], common cocklebur [*Xanthium strumarium*]), vines (trumpet vine [*Campsis radicans*], redvine [*Brunnichia ovata*]), and woody plants (willow [*Salix* spp.], buttonbush [*Cephalanthus occidentalis*]; Kross 2006, Veon and McClung 2023). In some tracts of Arkansas wetlands, oaks (*Quercus* spp.) and cypress (*Taxodium* spp.) can be important trees that provide food and cover for wetland-dependent species (Reinecke et al. 1989).

METHODS

Body mass and body condition measurements

We used mallards harvested from hunters at private duck hunting clubs and public hunting areas using a stratified sampling design. We divided the Arkansas LMAV into North, Central, and South and focused on collecting body measurements from harvested ducks across as wide of a geographic range as available within each of the 3 strata (Figure 1). For each bird, we assigned a sex class using plumage dimorphism and an age class using adult or immature feather morphology characteristics among the scapulars, proximal underwing coverts, greater tertial coverts, tertials, middle and lesser coverts, and primary coverts (Carney 1992). We measured body mass (±1 g) using an electronic scale and wing length (±1 mm; measured from the notch of the bend of the wing to the end of the longest primary feather; Carney 1992). As described in Veon et al. (2023), the amount of food in the esophagus was estimated according to 3 categories (none [0 g], small [0–20 g], or large [>20 g]) through palpation. We excluded individuals that contained more than 20 g of food in their esophagus.

We calculated a standardized body condition for each bird using the residuals from mass by wing length regressions specific to each age-sex class to account for age-sex differences and used this as one of our response variables. Because body condition indices have received much criticism for not being representative of energetic stores in waterfowl (Green 2001, Schamber et al. 2009, Labocha and Hayes 2012, Klimas et al. 2020) and because we did not validate our body condition index through lipid metabolite analyses, we also chose to perform analyses on body mass that was not corrected by a structural component (Sparling et al. 1992, Schamber et al. 2009). Because body mass can vary by age and sex (Hohman and Weller 1994, Gunnarsson et al. 2011), we first standardized body mass by each age-sex group by centering each group on their means separately, then scaling each group by their standard deviation (Quinn and Keough 2002, Bell et al. 2007). We then combined these measurements into one centered and scaled body mass response variable (hereafter referred to as standardized body mass).

Landscape composition

We extracted landscape composition and human disturbance variables within a 30-km radius of each mallard's nearest known harvest location. To obtain nearest known harvest location, we consulted with hunters and had them point out harvest locations on a map. In some instances, hunters did not want to divulge the exact location of harvest and we instead used a general location within approximately 3 km of the actual harvest location. Because we did not collect radio-telemetry data, we relied upon informed (Beatty et al. 2014) assumptions of mallard space use. We assumed the 30-km buffer captured most mallard daily movements and conservatively encompassed the local foraging and resting areas that ducks had recently been using (Beatty et al. 2014). An *a priori* analysis of satellite telemetry from Beatty et al. (2014) indicated that 98% of movements (720 out of 735 movements; derived from steps ≤24 hours a part) for mallards during winter in Arkansas were <30 km in a span of 8.11 hours on average. Therefore, we had a high degree of certainty that most mallards in our study had used the land cover within their respective 30-km buffers immediately preceding harvest. Mallards can have non-breeding home ranges considerably smaller than the 30-km buffers we used (e.g., 8–20-km radii [27–67% the size of our buffer]; Jorde et al. 1983, Allen 1987). Therefore, our 30-km buffers were more conservative. Finally, because most waterfowl require around 4–72 hours to assimilate energy (i.e., lipids) from the food they ingest, we assumed that mallards had assimilated energy from the vicinity of their harvest site at the time of collection; thus, their body mass and condition would reflect recent energy assimilation (Krapu 1981, Charalambidou et al. 2005). Our approach assumed that mallards were using all resources within a 30-km radius of the harvest location and this resource use reflected recent changes in body mass and condition. We also assumed that mallards did not forage outside of the buffer and that birds were not new arrivals to the buffer area. We recognize these assumptions may be erroneous in some cases and explore the implications of assumption violations in our results in the Discussion.

We evaluated 7 land cover variables that have been shown or predicted to influence waterfowl body mass or body condition (Reinecke et al. 1989, Heitmeyer and Fredrickson 1990, Ringelman 1990, Taylor 2010) and that were related to mallard foraging, resting, or human disturbance. For each nearest known harvest location, we calculated the percentage of water cover, woody wetlands, herbaceous wetlands, flooded rice fields, flooded soybean fields, area of human disturbance, and area of lands managed by state or federal management agencies.

To determine the amount of water cover within a harvest location buffer, we used a Google Earth Engine (GEE) water layer (Donnelly 2021). We generated a separate water layer for each year of the study. The first water layer represents the entire area of the LMAV inundated in water (raster cells containing ≥10% water cover) during 1 November 2019 through 8 February 2020. The second water layer represents the entire area of the LMAV inundated in water (raster cells containing ≥10% water cover) during 1 November 2020 through 6 February 2021. We determined the area of woody wetlands and herbaceous wetlands using the woody wetland and emergent herbaceous wetland classifications in the National Land Cover Database (2019). The woody wetlands classification is defined as land cover cells that contained >20% forest or shrubland vegetative cover that could have been saturated or covered with water. The emergent herbaceous wetlands classification is defined as cells that contained >80% perennial herbaceous vegetative cover that could have been saturated or covered with water. We defined percent human disturbance as the combination of road density and development using medium disturbance cells from a human impact avoidance database (U.S. Geological Survey Gap Analysis Project 2011). To calculate the percent area of rice fields and soybean fields within each buffer, we used the USDA Cropland Data Layer (USDA 2020). We chose to focus on rice and soybeans because they occur in large quantities within the LMAV of Arkansas (USDA 2021) and are used as food resources by waterfowl. We also calculated the percent of area composed of managed lands (e.g., state and federally managed) within each buffer using the Protected Areas Database of the United States (U.S. Geological Survey Gap Analysis Project 2020). We first overlayed each GEE water layer (2019–2020 and 2020–2021) separately with the National Land Cover Database, USDA Cropland Data Layer, and the Protected Areas Database of the United States before we extracted variables from those layers to ensure we only included land cover types accessible to foraging ducks. After we acquired all landscape layers, we used the zonal statistics tool in ArcGIS Pro 2.8 (Esri, Redlands, CA, USA) to calculate the total area of each landscape cover variable (km^2) within each harvest location buffer, which we then used to calculate the proportion of each landscape variable within each buffer.

Analyses

To explore how landscape composition influenced mallard body mass and body condition, we used linear mixed-effects models in R (R Core Team 2020) using the lme4 package (Bates et al. 2015). We first checked for collinearity using Pearson's correlation coefficient. Managed lands were strongly correlated with woody wetlands ($r = 0.78$), so we excluded managed lands from our models. No other variables were highly correlated (i.e., $|r| \geq 0.7$; Dormann et al. 2013); thus, we retained all other variables for analyses. We used both standardized body mass and body condition index as response variables. We analyzed each age-sex cohort together because we had first standardized their values. To control for variation across harvest locations and because sometimes multiple birds were harvested from the same location, we used nearest known harvest location as the random effect. We used percent water cover (log transformed), percent rice, percent soybeans (log transformed), percent woody wetlands, percent herbaceous wetlands (log transformed), and percent disturbance (log transformed) as fixed factors. We did not log transform percent rice or percent woody wetlands because these variables met model assumptions of linearity among residuals. We centered fixed effects on their means and scaled them by their standard deviation for standardization of covariates (Schielzeth 2010). Finally, we fit harvested mallard body mass and condition global models (i.e., full additive models) using maximum likelihood. During the fitting process, we ensured model convergence occurred and no singularity issues were present among all models. We further assessed model fit of the global models using residual plots (Figures S1–S16, available in Supporting Information; Pinheiro and Bates 2000, Bolker et al. 2009, Bates et al. 2015).

We used a model selection framework to assess the relationship of landscape variables with mallard body mass and body condition. We developed 10 *a priori* models made up of combinations of landscape variables predicted to influence mallard body mass and body condition (Tables S1–S2, available in Supporting Information). We conducted model selection using Akaike's Information Criterion (AIC) approach (Burnham and Anderson 2002) where we assumed lower AIC is more predictive. Because models within AIC < 7 have been shown to have some explanatory support, we considered models within this range to be competitive (Burnham and Anderson 2002, Burnham et al. 2011). Similarly, when applicable, we obtained parameter estimates by model-averaging all models within 7 ΔAIC of the top model (Burnham and Anderson 2002). We calculated AIC weights for each model to help assess which models held the most weight of evidence (Anderson and Burnham 2002, Burnham and Anderson 2004). Additionally, because our results among models for body mass and body condition were very closely aligned and body mass and body condition were highly correlated ($r = 0.92$), we only present figures for and spatially model results from the body mass analyses. After analyses, we back-transformed axes of figures for variables shown to be related to mallard body mass for interpretation on the original scale.

To spatially model our results, we generated a 500-m × 500-m grid across the LMAV of Arkansas. We chose a 500-m × 500-m grid area because developing maps with higher resolutions can be computationally intensive (Zhang and

Roy 2017). Additionally, most land cover classifications at higher resolutions (e.g., 30-m × 30-m resolution) appear geographically plausible and, at the synoptic scale, are similar to the 500-m × 500-m scale captured by the Moderate Resolution Imaging Spectroradiometer (MODIS) from which land cover datasets (e.g., National Land Cover Database, Cropland Data Layer) are derived (where higher resolutions data layers are achieved using training datasets; Zhang and Roy 2017). Using methods adapted from Lassiter et al. (2021), we then calculated the percent landscape composition variable for each grid cell. We reclassified each grid cell's percent landscape composition to corresponding predictions of mallard body mass from the linear mixed-effects model analysis. We completed these steps individually for each statistically significant variable (i.e., model-averaged estimates with confidence intervals that did not overlap zero) that influenced mallard body mass. Because independent variables were centered and scaled before analysis, we used the absolute value of model-averaged estimates to develop a total average of importance among variables (Gelman and Hill 2006) included in top models with confidence intervals that did not overlap zero (equation 1). We then divided the absolute value of each variable model-averaged estimate by the total average variable importance to derive the proportion of average variable importance for each fixed effect that held a relationship with mallard body mass (equation 2). We then used each of these proportions of importance as the weight (*w*) for each variable when combining each mallard body mass prediction map using the weighted sum tool within ArcGIS Pro 2.8.

$$|\beta_{water\ cover}| + |\beta_{woody\ wetlands}| + |\beta_{herbaceous\ wetlands}| + |\beta_{disturbance}| = \text{total average variable importance } (\beta_{TotAvgImp}) \quad (1)$$

$$|\beta_{water\ cover}|/\beta_{TotAvgImp} = \text{proportion of average variable importance for water cover among top models.} \quad (2)$$

RESULTS

During the 2019–2020 duck hunting season, we measured 1,101 mallards composed of 383 adult males, 450 juvenile males, 51 adult females, and 217 juvenile females from 36 private land locations and 14 public land locations. The first date a mallard was harvested was 23 November 2019, while the last date of harvest was 8 February 2020. The mean date of harvest was 4 January 2020. During the 2020–2021 duck hunting season, we measured 1,176 mallards including 424 adult males, 452 juvenile males, 56 adult females, and 244 juvenile females at 20 private land locations and 20 public land locations. The first date a mallard was harvested was 21 November 2020, while the last date of harvest was 6 February 2021. The mean date of harvest was 4 January 2021. Overall, we collected samples from 47 unique hunting clubs or private locations, and 26 different public hunting areas (Figure 1). Standardized body mass, and body condition, on average varied based on sample years, sampling strata, age, and sex (Tables 2–3).

The proportion of land cover within harvest buffers aligned with proportion of overall coverage of these land covers across the LMAV. Among our variables, percent water cover spanned the most area among harvest site buffers ($\bar{x}$ = 24.62%, SE = 0.14) and the LMAV ($\bar{x}$ = 26.45%, SE = 0.53). The minimum coverage by a variable within our harvest site buffers ($\bar{x}$ = 0.27%, SE = 0.003) and the LMAV ($\bar{x}$ = 0.27%, SE = 0.002) was percent herbaceous wetlands (Table 1). Additionally, among global models for both body mass and condition analyses, residual plots indicate that assumptions of linearity and homogeneity of variances were met (Figures S1–S16). Model convergence was achieved in all models, no singularity was detected in any model, and both global models ranked higher than the null model, further indicating model fit was achieved.

Changes in standardized mallard body mass were best explained by the proportion of water cover, woody wetlands, herbaceous wetlands, and disturbance and all except disturbance appeared in each of the top 3 competitive models. Cumulatively, the 3 top models accounted for 97% of the weight of evidence. Disturbance appeared within the top 2 models, which cumulatively accounted for 91% of the weight of evidence (Table 4). In all models, water cover and woody wetlands were positively associated with waterfowl body mass, indicating that harvested mallards were heavier in locations containing higher proportions of water and woody wetlands. Among

TABLE 2 Average standardized (centered and scaled) body mass (± SE) and sample size (n), and average body mass (g; ± SE), for each age and sex class of harvested mallards within the north, central, and south portions of the Lower Mississippi Alluvial Valley (LMAV) in Arkansas, USA, during duck hunting seasons 2019–2020 and 2020–2021.

		Males						Females					
		Adults			Juveniles			Adults			Juveniles		
Year	Strata	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Standardized body mass													
2019–2020	North	−0.073	0.227	39	−0.195	0.172	52	−1.064	0.472	5	−0.073	0.278	21
	Central	−0.147	0.055	290	−0.156	0.052	312	−0.082	0.126	43	−0.219	0.073	160
	South	−0.328	0.140	54	−0.265	0.106	86	−0.018	1.100	3	−0.333	0.152	36
2020–2021	North	0.295	0.112	63	0.279	0.142	62	0.653	0.578	8	0.380	0.158	46
	Central	0.076	0.063	236	0.058	0.062	252	0.187	0.141	34	−0.015	0.078	135
	South	0.214	0.091	125	0.360	0.080	138	−0.193	0.273	14	0.526	0.128	63
Body mass													
2019–2020	North	1,308.282	23.456		1,250.404	18.110		1,074.000	41.987		1,110.381	30.353	
	Central	1,300.617	5.690		1,254.516	5.471		1,161.349	11.160		1,094.456	8.008	
	South	1,281.907	14.454		1,243.058	11.150		1,167.000	97.767		1,082.028	16.621	
2020–2021	North	1,346.381	11.585		1,300.339	14.959		1,226.625	51.413		1,159.761	17.199	
	Central	1,323.720	6.521		1,277.056	6.543		1,185.235	12.573		1,116.637	8.518	
	South	1,337.952	9.382		1,308.935	8.440		1,151.429	24.275		1,175.667	13.923	

TABLE 3 Average body condition (±SE) and sample size (n) for each age and sex class of harvested mallards within the north, central, and south portions of the Lower Mississippi Alluvial Valley (LMAV) in Arkansas, USA, during duck hunting seasons 2019–2020 and 2020–2021.

		Males						Females					
		Adults			Juveniles			Adults			Juveniles		
Year	Strata	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
2019–2020	North	−0.049	0.220	39	−0.199	0.182	52	−1.189	0.378	5	−0.030	0.278	21
	Central	−0.162	0.053	290	−0.165	0.052	312	−0.056	0.127	43	−0.197	0.073	160
	South	−0.241	0.146	54	−0.246	0.095	86	−0.081	0.893	3	−0.309	0.134	36
2020–2021	North	0.206	0.112	63	0.414	0.130	62	0.704	0.527	8	0.462	0.171	46
	Central	0.071	0.064	236	0.011	0.061	252	0.193	0.153	34	−0.063	0.078	135
	South	0.282	0.091	125	0.377	0.083	138	−0.257	0.288	14	0.484	0.129	63

TABLE 4 Akaike's Information Criterion (AIC) model selection statistics for linear mixed-effects models (ΔAIC < 7) evaluating the influence of percent water cover (water), rice, soybean, woody wetlands (wood), herbaceous wetlands (herb), and disturbance on standardized (centered and scaled) body mass of harvested mallards during duck hunting seasons 2019–2020 and 2020–2021 in the Lower Mississippi Alluvial Valley of Arkansas, USA. We also present the number of parameters (K), Akaike weight (AICwt), and log likelihood (LL) for each model.

Model	K	AIC	ΔAIC	AICwt	LL
Water + wood + herb + disturbance	7	6,360.73	0.00	0.64	−3,173.36
Global model	9	6,362.44	1.72	0.27	−3,172.22
Water + wood + herb	6	6,365.52	4.80	0.06	−3,176.76

TABLE 5 Akaike's Information Criterion (AIC) model-averaged estimates (with 95% CI) of variables contained within top models (ΔAIC < 7), which evaluated the influence of percent water cover, rice, soybean, woody wetlands, herbaceous wetlands, and disturbance on standardized (centered and scaled) body mass of harvested mallards during duck hunting seasons 2019–2020 and 2020–2021 in the Lower Mississippi Alluvial Valley of Arkansas, USA.

Variable	Estimate	SE	95% CI
Water cover	0.20	0.07	0.07–0.33
Woody wetlands	0.23	0.06	0.12–0.34
Herbaceous wetlands	−0.19	0.06	−0.31–−0.07
Disturbance	−0.14	0.05	−0.24–−0.04
Rice	−0.02	0.05	−0.13–0.08
Soybeans	−0.12	0.08	−0.28–0.04

the top model set, herbaceous wetlands and disturbance were negatively associated with body mass, indicating that harvested mallards weighed less in locations containing higher proportions of herbaceous wetlands and disturbance by human development. Model estimates indicate that rice and soybeans were unrelated to mallard body mass (Table 5; Figure 2).

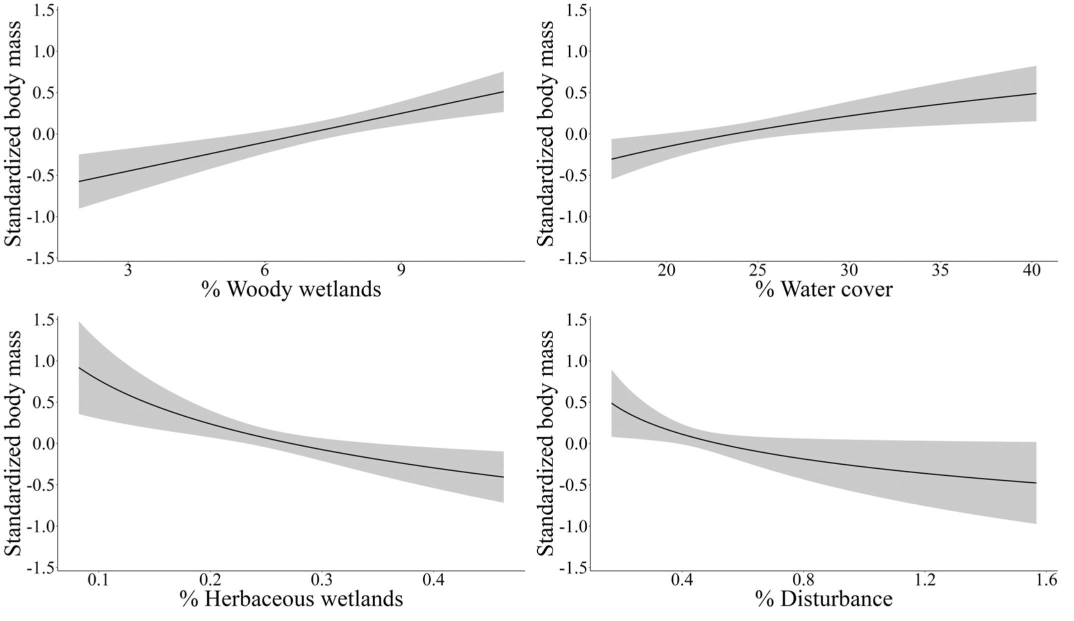

FIGURE 2 Predicted relationship of harvested mallard standardized (centered and scaled) body mass with percent woody wetlands, water cover, herbaceous wetlands, and disturbance within the Lower Mississippi Alluvial Valley of Arkansas, USA, during duck hunting seasons 2019–2020 and 2020–2021 (−1.5 standardized body mass is approximately 1,156 g in an adult male mallard, 1,111 g in a juvenile male mallard, 1,040 g in an adult female mallard, and 951 g in a juvenile female mallard; 0 standardized body mass is approximately 1,310 g in an adult male mallard, 1,269 g in a juvenile male mallard, 1,174 g in an adult female mallard, and 1,114 g in a juvenile female mallard; and 1.5 standardized body mass is approximately 1,465 g in an adult male mallard, 1,427 g in a juvenile male mallard, 1,308 g in an adult female mallard, and 1,277 g in a juvenile female mallard). Solid black lines refer to estimated mean standardized body mass and gray bands are upper and lower limits (using 95% CIs).

TABLE 6 Akaike's Information Criterion (AIC) model selection statistics for linear mixed-effects models (ΔAIC < 7) evaluating the influence of percent water cover (water), rice (rice), soybean (soy), woody wetlands (wood), herbaceous wetlands (herb), and disturbance (disturbance) on residual body condition index of harvested mallards during duck hunting seasons 2019–2020 and 2020–2021 in the Lower Mississippi Alluvial Valley of Arkansas, USA. We also present the number of parameters (*K*), Akaike weight (AICwt), and log likelihood (LL) for each model.

Model	*K*	AIC	ΔAIC	AICwt	LL
Water + wood + herb + disturbance	7	6,327.07	0.00	0.52	−3,156.53
Global model	9	6,327.74	0.67	0.37	−3,154.87
Water + wood + herb	6	6,332.31	5.24	0.04	−3,160.16
Water + rice + soy + wood + herb	8	6,333.60	6.54	0.02	−3,158.80

Changes in mallard body condition were best explained by the proportion of water cover, woody wetlands, herbaceous wetlands, and disturbance and all except disturbance appeared in the top 4 competitive models. Cumulatively, the 4 top models accounted for 95% of the weight of evidence. Disturbance appeared within the top 2 models, which cumulatively accounted for 89% of the weight of evidence (Table 6). In all models, water cover and

TABLE 7 Akaike's Information Criterion (AIC) model-averaged estimates (with 95% CI) of variables contained within top models (ΔAIC < 7), which evaluated the influence of percent water cover, rice, soybean, woody wetlands, herbaceous wetlands, and disturbance on residual body condition index of harvested mallards during duck hunting seasons 2019–2020 and 2020–2021 in the Lower Mississippi Alluvial Valley of Arkansas, USA.

Variable	Estimate	SE	95% CI
Water cover	0.21	0.08	0.05–0.36
Woody wetlands	0.20	0.07	0.07–0.33
Herbaceous wetlands	−0.19	0.07	−0.32–−0.06
Disturbance	−0.15	0.05	−0.26–−0.04
Rice	−0.06	0.06	−0.17–0.05
Soybeans	−0.12	0.09	−0.29–0.05

woody wetlands were positively associated with waterfowl body condition, indicating that harvested mallards were in better condition in locations containing higher proportions of water and woody wetlands. Among the top model set, herbaceous wetlands and disturbance were negatively associated with body condition, indicating that harvested mallards were of a lower condition in locations containing higher proportions of herbaceous wetlands and disturbance by human development. Model averaged estimates indicate that rice and soybeans were also unrelated to mallard body condition (Table 7).

Among the top models within the body mass analyses, woody wetlands averaged the highest variable importance value ($w = 0.30$), followed by water cover ($w = 0.26$), herbaceous wetlands ($w = 0.25$), and disturbance ($w = 0.18$). Mallards with predicted higher body mass were found to be in areas with higher proportions of woody wetlands and water cover but low proportions of herbaceous wetlands and human disturbance in the form of human infrastructure (Figure 3).

DISCUSSION

We found that the body mass and body condition of hunter-harvested mallards were greatest in areas with more water cover and woody wetlands, and least in areas with higher proportions of herbaceous wetlands and human disturbance. Contrary to our predictions, mallard body mass and condition were unrelated to the proportional coverage of flooded rice or soybeans. These results indicate the importance of increased water cover and woody wetlands, and the mitigation of human disturbance from human development, to body mass and condition in mallards (Reinecke et al. 1988, Chabreck et al. 1989, Reinecke et al. 1989, Pease et al. 2005).

Support for the use of body condition indices in waterfowl are mixed (Schamber et al. 2009, Labocha and Hayes 2012, Klimas et al. 2020, Palumbo and Shirkey 2022, Vanausdall et al. 2022). Because we were unable to validate our measure of body condition with a measure of lipid content, we also analyzed a measure of standardized body mass uncorrected for a structural component (Schamber et al. 2009, Klimas et al. 2020). We found standardized body mass and body condition to be highly correlated and the results from both model sets using standardized body mass and body condition indices held similar model averaged estimates, providing us a high degree of reliability in our findings.

Although we have confidence that most harvested mallards sampled within our study had used resources within the respective 30-km buffers before harvest based on an *a priori* analysis of data from Beatty et al. (2014), we acknowledge uncertainty in the precise space use patterns for our samples because we did not have accompanying telemetry data. Indeed, birds likely do not use the same area throughout the winter but may move across the MAV in response to changing environmental conditions and food availability (Nichols et al. 1983,

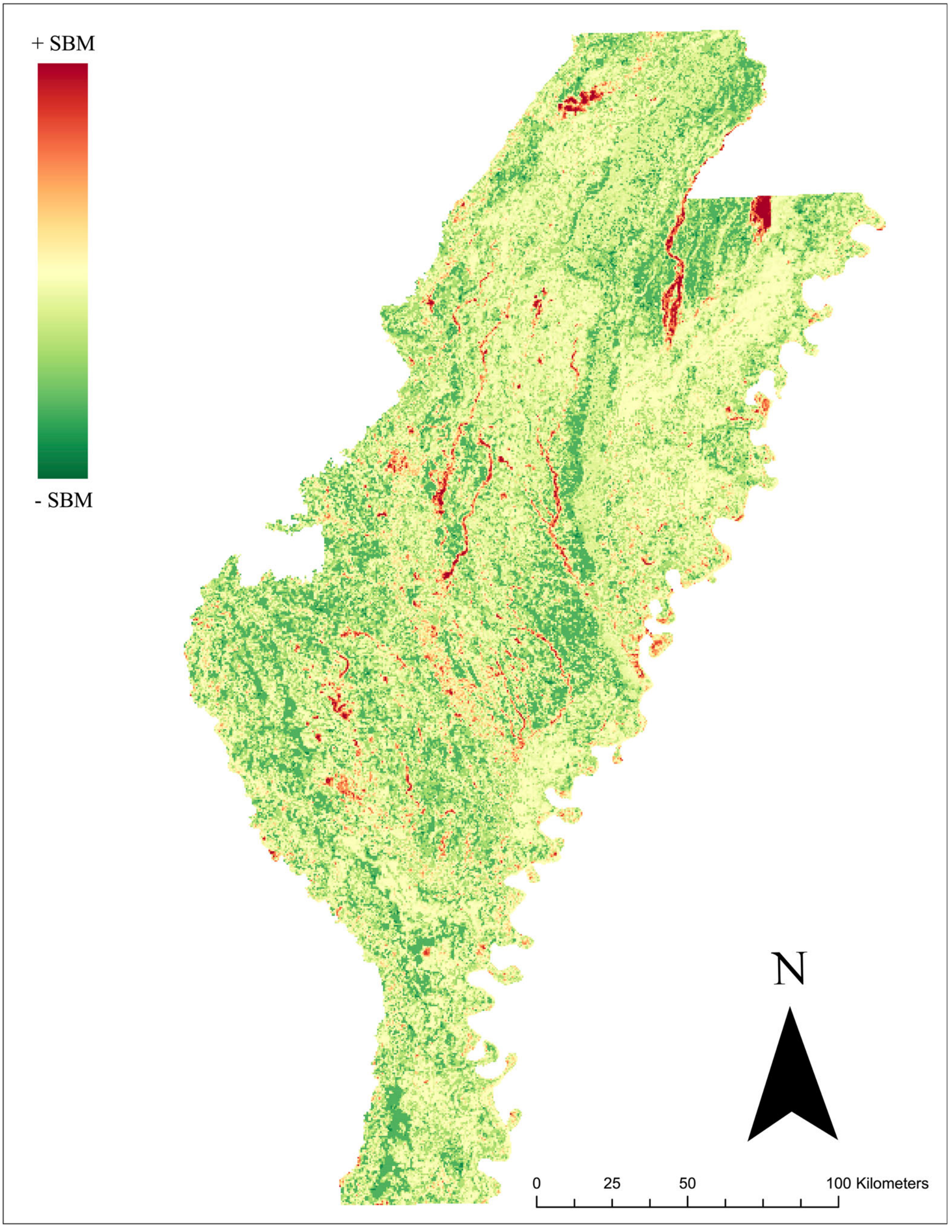

FIGURE 3 Predicted harvested mallard standardized (centered and scaled) body mass (SBM) within the Lower Mississippi Alluvial Valley of Arkansas, USA, based on relationships with percent woody wetlands, water cover, herbaceous wetlands, and disturbance from hunting seasons 2019–2020 and 2020–2021. This map consists of a continuous color scale where more red areas refer to locations that are predicted to have mallards with higher body mass (+SBM [4.58 SBM; approximately 1,782 g in an adult male mallard, 1,751 g in a juvenile male mallard, 1,583 g in an adult female mallard, and 1,612 g in a juvenile female mallard]) and more green areas indicate areas with predicted lower body mass (−SBM [−2.37 SBM; approximately 1,066 g in an adult male mallard, 1,019 g in a juvenile male mallard, 962 g in an adult female mallard, and 857 g in a juvenile female mallard]).

Allen 1987, Herbert et al. 2018, Palumbo and Shirkey 2022). Thus, it is certain that some of our birds likely moved into the area in which they were harvested, and their body mass and condition is reflective of conditions elsewhere. In a similar context, mallards could have been using a much smaller home range than 30 km (Jorde et al. 1983, Allen 1987) and this could have increased the level of randomness explaining model variation. However, we do not believe use of a larger or smaller buffer area occurred often because our null model in both body mass and condition analyses was the worst ranking model. Additionally, habitat composition is usually most accurate when applied to large areas and most likely better able to capture landscape trends (Allen 1987). This can be observed with how well the average proportional values of land cover variables within our harvest location buffers represented proportional availability across the entirety of the LMAV (Table 1).

We also acknowledge that if the body mass or condition of harvested mallards did not respond within 72 hours of energetic assimilation, the mass and condition of mallards could be reflective of food that was ingested >72 hours before harvest (which could potentially be reflective of resources outside of a mallard's harvest location buffer). We believe that this was not the case for several reasons. First, we removed birds with large amounts of undigested esophageal contents from our analysis, so largely undigested foods (i.e., unassimilated diet contents) would not greatly influence results. Second, studies have shown that mallards have a highly responsive gastrointestinal (GI) system (Miller 1975). Mallards have the capacity to quickly digest and store energy from even the most low-quality diets by rapidly lengthening and shortening the size of the GI tract (Miller 1976). Because mallards rapidly assimilate energy in the form of lipids, and lipids are highly correlated to changes in mass in mallards (Krapu 1981, Schamber et al. 2009), we believe that food resources ingested >72 hours before harvest likely introduced little variation into body mass and condition measurements. Likewise, we did not observe large uncertainty around predictions of body mass and condition in relation to landscape cover ranges found within the vicinity of harvest location buffers. Finally, because our buffer size of 30 km was likely conservative and was informed by an *a priori* analysis of satellite telemetry from Beatty et al. (2014), we believe that if body mass was reflective of food ingested >72 hours before harvest, it was likely reflective of the food resources used within the harvest location buffer. Therefore, because we chose a large, conservative 30-km radius, we believe that harvested mallards had likely spent most of their preceding time in the area encompassed by the buffer, and the land cover variables within the buffer are reflective of those used by harvested mallards. Nevertheless, studies using telemetry to understand exactly where mallards were foraging and resting before their body mass and condition are measured should provide valuable insight.

Additionally, there is a potential bias whereby mallards that have recently settled in an area might be more susceptible to harvest, and this susceptibility is likely the result of increased foraging behaviors by harvested mallards needing to increase their mass (compared to live captured mallards that tend to be heavier on average; Heitmeyer et al. 1993). If this occurred in our sample, it could have biased our results because these mallards could have been using a landscape outside of the defined buffers in this study. However, it is still possible that a mallard that is new to a fine-scale location from which it was harvested had spent time residing elsewhere within our large conservative buffers. Further, despite there being a possibility of mallards new to an area having a greater harvest susceptibility, direct evidence for this potential bias is absent from the peer-reviewed literature and warrants future research.

Mallards are dabbling ducks that forage in shallow water where they eat seeds, hard and soft mast, agricultural waste grain, and invertebrates. As available water on the landscape increases (due to rain or flooding), foraging areas become available to mallards because additional areas begin to hold standing water and the footprints of wetlands expand. Numerous studies support our results that mallard body mass and condition increases with increasing water availability (Reinecke et al. 1988, Guillemain et al. 2000, Fredrickson and Taylor 2007). For instance, Delnicki and Reinecke (1986) found that mallards spending the non-breeding season in the LMAV were heavier (i.e., better condition) during wetter years than drier years. Similarly, Veon et al. (2023) found that mallards spending the non-breeding season in the LMAV were heavier after periods of rainfall and river flooding, and like Delnicki and Reinecke (1986), mass increases were most likely the result of increased access to food resources.

Heitmeyer and Fredrickson (1981) found that winter precipitation was also positively correlated with mallard productivity the following spring, indicating that mallards were arriving in a better condition to engage in breeding behaviors. Therefore, as more water cover is available within a mallard's home range during the nonbreeding season, it is likely they spend less time in search of resources and they will maintain a larger body mass or better condition (Fleskes et al. 2016).

Arkansas historically had more expansive bottomland hardwood forests than exist today that contributed to meeting the resource needs and life cycle requirements of mallards during the non-breeding season and could potentially play a large role in why large numbers of mallards spend the non-breeding season in this region (Fredrickson and Heitmeyer 1988). Flooded bottomland hardwood forests provide both foraging and resting opportunities for mallards. They provide waterfowl with high energy mast in the form of acorns (Allen 1980, Reinecke et al. 1989, Heitmeyer and Fredrickson 1990, Dabbert and Martin 2000, Miller et al. 2003) and valuable proteins and amino acids from macroinvertebrates harbored in the leaf litter and soil (Fredrickson and Heitmeyer 1988, Fredrickson and Batema 1992, Krapu and Reinecke 1992, Kaminski et al. 2003, Foth et al. 2014). Woody wetland complexes are also important to waterfowl during life cycle events beyond foraging. For example, woody wetlands offer mating pairs a place to avoid stress caused by courting parties that could occur on more open areas (Heitmeyer 1985). Woody wetlands also offer waterfowl a place to roost and avoid predators (Fredrickson and Batema 1992). Thus, waterfowl occupying woody wetlands may be less likely to engage in energetically costly behaviors (e.g., excessively flying to avoid disturbance, predators, or to search for food), which may result in better body mass and condition. Based on spatial projections from our model, mallard body mass is greater in areas with more bottomland hardwood forests. Most notably, many of these bottomland hardwood forests are owned and managed by state and federal conservation agencies or exist as part of hunting clubs (Figure 3). Because many of these areas are public hunting areas, bottomland hardwood forests can, at times, be heavily disturbed via hunting. These disturbances could potentially decrease mallard body mass and condition. We suggest 2 possible reasons why mallards residing in or near these heavily hunted areas may have better body mass and condition. First, forested systems offer more cover, thus making it easier for ducks to avoid predators (including human predators) and lowering energetically costly vigilant behaviors (e.g., flying, swimming; Reinecke et al. 1989, Fredrickson and Batema 1992, Knapton et al. 2000, Taylor 2010). Second, ducks could be maintaining energy levels by day roosting away from these compounds when hunting pressure is high (typically in the morning) and returning to use wooded wetlands in the afternoon, evening, or nighttime (Lancaster et al. 2015, Shirkey et al. 2020). Better understanding how woody wetlands may mitigate disturbances that would otherwise reduce mallard body mass and condition warrants future research.

Although we did not investigate the effects of hunting disturbance on mallard body mass and condition, our results did indicate that human disturbance in the form of road density and human infrastructure was negatively associated with mallard body mass and condition. Likewise, our prediction map shows that ducks harvested from or near areas of development will likely have reduced body mass (Figure 3). This could result from visual or auditory cues from human anthropogenic disturbances (Knittle and Porter 1988, Madsen and Fox 1995, Zimmer et al. 2010). For example, recent studies found that road traffic noise (isolated from visual cues) can cause waterfowl to distance themselves from the noise source (Veon and McClung 2023) and waterfowl heart rates (i.e., indicator of energetic burn) can increase amidst firework shows (Wascher et al. 2022). More information is needed on how waterfowl body mass and condition may change in the face of different disturbances and how they adapt and habituate to these disturbances over time. However, at least in the short term, disturbances generated from human development could lead to unnecessary energy use by waterfowl and lower body mass and condition (Knapton et al. 2000, Taylor 2010, Veon and McClung 2023).

Herbaceous wetlands, some of which are intensively managed moist-soil units, can offer waterfowl a wide variety of seeds and vegetative matter, and a variety of aquatic invertebrates that are valuable as a food resource (Fredrickson and Taylor 1982, Anderson and Smith 1999, Gray et al. 1999, Checkett et al. 2002, Hagy and Kaminski 2012). However, our results did not support our hypothesis that mallard body mass and condition would increase as herbaceous wetland land cover increased. It is possible that our results are biased towards unmanaged herbaceous wetlands, as most (~ 82%) of the herbaceous wetlands in the region are not intensively managed for waterfowl food resources (Reinecke et al. 1989, Lower Mississippi Valley Joint Venture 2020). Herbaceous wetlands that are not heavily managed by water manipulation and other management techniques have reduced productivity for waterfowl food resources (Allen 1987, Reinecke et al. 1989, Kross et al. 2008, Fleming et al. 2015, Tapp et al. 2018), thus potentially resulting in lower body mass and condition among nearby mallards. Additionally, most herbaceous wetlands are relatively small as compared to tracts of woody wetlands, which could contribute to a greater degree of disturbance from hunters or other visitors (Fredrickson and Taylor 1982, Reinecke et al. 1989, Madsen 1998, Pease et al. 2005).

We did not see changes in mallard body mass and condition with changes in percent buffer of rice or soybeans, despite our hypothesis that rice would be positively associated with body mass and condition because of its high energetic value and that soybeans would be negatively associated with body mass and condition because of its low nutritional value (Loesch and Kaminski 1989, Ringelman 1990, Checkett et al. 2002). The lack of a relationship between body mass and condition and percent buffer of rice fields can most likely be explained by changing agricultural practices such as planting earlier maturing rice variants, stripper-header harvesting, and fall tillage, all of which reduce the amount of actual waste rice present on the ground for ducks upon arrival to the non-breeding grounds (Anders et al. 2008). Thus, the high-energy seed resources available to foraging waterfowl in rice fields is much lower than in the past (Stafford et al. 2006, Kross et al. 2008). Once this reduced remaining waste rice is inundated with water, ducks and other waterfowl may continue to reduce this resource over time. Crops like soybeans also degrade quickly compared to other natural seeds, further reducing availability. For example, soybeans have been found to degrade the quickest among common agricultural grains, losing 1% of energy a day while flooded (Fredrickson and Reid 1988). Therefore, there may be an uneven distribution or availability of rice and soybeans among agricultural fields within our harvest site buffers. Although we selected rice and soybean cells that had at least 10% water cover, our water layer considers the presence of all water on the landscape during the winter (early Nov–early Feb). However, the degree of flooding among crop fields could be highly variable across time (e.g., fields lose all water during periods of drought, or become completely inundated by controlled or natural flooding events). Thus, compared to woody and herbaceous wetlands, agricultural fields likely provide more variable food resources that rapidly decline across the winter period. Additionally, rice and soybeans are some of the most planted agricultural crops within the Arkansas LMAV (USDA 2021, 2022). Therefore, the amount of land cover in rice and soybeans among harvest locations may not have varied much; thus, our models failed to detect any relationship.

Our spatial projections of model results are not the distribution of where heavier, harvested mallards resided within our samples. Rather, our model (Figure 3) represents where harvested mallard body mass is predicted to be heavier or lighter based on estimated trends with proportions of land cover types. We emphasize that resources (foraging and resting) likely vary within wetlands made up of similar land cover types because of a multitude of factors we were unable to measure on the ground (e.g., differences in management techniques, timing of hydrological regimes, biogeochemistry).

MANAGEMENT IMPLICATIONS

Our results could help in identifying areas for restoration and management in an effort to promote landscapes containing features associated with increased mallard body mass and condition. Management actions focused on providing flooded and woody wetlands on the landscape that allow waterfowl to access food resources, while decreasing the disturbance around wetlands in the form of road density and human infrastructure, should increase body mass and body condition in mallards spending the non-breeding season in the Lower Mississippi Alluvial Valley, which is ultimately related to their fitness.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

ETHICS STATEMENT

Because waterfowl were being harvested by hunters regardless of project protocols, we did not need institutional animal care and use committee approval to obtain waterfowl measurements. We were required to have a state collection permit (permit number 031620201) to retain wings from waterfowl for aging at later dates.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on GitHub at https://github.com/jonvon16/Veonetal_BodyMassCondition_CH2_Dat.git.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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