Annual variation in food densities and factors affecting wetland use by waterfowl in the Mississippi Alluvial Valley

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Abstract

Spatial and temporal heterogeneity in habitat quantity and quality, weather and other variables influence the production of food and the distribution of waterfowl, making it difficult to predict carrying capacity accurately. Food densities for waterfowl, which are key parameters of energetic carrying capacity models, were examined in managed moist-soil wetlands and bottomland hardwood forests in or near the Mississippi Alluvial Valley (MAV) of the southern United States of America, to determine variation in those densities across wetlands and years. Secondly, the relationship between migratory waterfowl density in managed wetlands and local and mid-latitude factors north of the study area was examined to identify mechanisms influencing waterfowl density at latitudes used during winter. At individual wetlands and within years, food densities were highly variable, but coefficients of variation (CV) at the scale of the MAV and nearby areas across years were relatively low (moist-soil CV = 21%, bottomland hardwood forest CV = 11%). Local precipitation was inversely related to waterfowl density in managed moist-soil wetlands, and this relationship was stronger than other local and mid-latitude factors including weather severity and temperature. Our data suggest that simplistic daily ration models may reasonably incorporate fixed estimates of food density for managed moist-soil wetlands and bottomland hardwood forests to predict energetic carrying capacity of waterfowl habitat at the scale of the MAV across multiple years. However, substantial variation in food densities among locations and time periods likely limits the utility and accuracy of these models when scaled down temporally or spatially. Therefore, the challenge in predicting annual carrying capacity for waterfowl in the MAV likely depends less on precisely estimating food densities at the scale of individual wetlands and more on determining spatial and temporal availability of habitats that contain food resources for waterfowl.

Key words: bottomland hardwood forest, conservation planning, dabbling duck, daily ration model, migration, moist-soil, weather severity.

Waterfowl ecologists use predictive models to develop habitat conservation objectives sufficient to meet the energy demands of migrating and wintering waterfowl populations in North America and elsewhere (Soulliere *et al.* 2007; Reinecke *et al.* 1989). These models require estimates of food density and foraging demand, with the latter reflecting the number and duration of stay of individuals foraging in a given area (Williams *et al.* 2014). Many previous studies have aimed to measure the density and availability of food in habitats used by waterfowl, but few researchers have examined variability in food densities at multiple temporal and spatial scales (*cf.* Lovvorn & Gillingham 1996). Moreover, variation or changes in regional and habitat use by waterfowl can have significant effects on carrying capacity model predictions of habitat requirements (Hagy *et al.* 2014).

Food availability for waterfowl can be influenced by a range of factors including annual production and seasonal decomposition of plant and animal foods, depletion of food resources by wildlife other than waterfowl, diet selectivity by foragers, ice and snow cover, duration and depth of flooding, disturbance by humans and natural predators and photoperiodic cues triggering migration (Rees 1981; Newton 1998; Schummer *et al.* 2010; Hagy & Kaminski 2012a,b). Moreover, even if available in some parts of the migratory range, foods may not be encountered by waterfowl because of variation within and between years in the timing of migration and regional movements by waterfowl (Bellrose *et al.* 1979; Schummer *et al.* 2010; Krementz *et al.* 2011, 2012; O'Neal *et al.* 2012; Hagy *et al.* 2014). Currently, energetic carrying capacity models used by some Joint Ventures of the North American Waterfowl Management Plan and other conservation partners include fixed parameters (*i.e.* constants) which may not account for spatio-temporal variation in food density or other factors that result in a mismatch of foods becoming available and waterfowl being present to access those foods (Soulliere *et al.* 2007; Williams *et al.* 2014). In order to develop habitat conservation objectives effectively, conservation planners require an understanding of variation in carrying capacity estimates resulting from variable parameter estimates and the mechanisms underlying waterfowl habitat use to determine priority habitats for conservation (Schummer *et al.* 2010; Hagy & Kaminski 2012b; Beatty *et al.* 2014b; Hagy *et al.* 2014; Williams *et al.* 2014).

Recently, information has become

available to help explain waterfowl movements and habitat use during winter in relation to landscape composition (Pearse *et al.* 2012; Beatty *et al.* 2014b). In addition to landscape-scale factors measured close to wintering and stopover sites used by large numbers of waterfowl, factors north of wintering areas could affect the southward movement of individuals and these may be useful in further explaining and predicting wetland use (Schummer *et al.* 2010). For migratory species such as waterfowl, habitat selection is likely a hierarchical process and factors affecting selection may vary temporally and interact spatially (Beatty *et al.* 2014a,b). For example, the cumulative effects of decreasing temperatures, freezing of wetlands and snow cover can cause regional decreases in abundance of waterfowl at autumn staging areas (Schummer *et al.* 2010), but once birds reach their southern wintering grounds where harsh weather conditions are less common, other factors such as precipitation (which influences wetland availability), food availability and intrinsic wetland factors may influence habitat use (Davis *et al.* 2009; Hagy & Kaminski 2012b; Dalby *et al.* 2013). Factors related to migratory movements from mid-latitude areas to more southerly wintering grounds may influence the abundance of birds within southern areas and allow comparison of the relative influence of local and mid-latitude factors on site use by the birds.

Although a number of studies have examined waterfowl movements and abundance in relation to food, habitat juxtaposition and other factors influencing movements along the migration route, there is a need for studies that simultaneously consider factors within wintering areas and those occurring at latitudes north of wintering areas, which may cause movements of birds into wintering areas and influence their access to foods, subsequent fitness and conservation planning (Lovvorn & Baldwin 1996; Haig *et al.* 1998; Pearse *et al.* 2012). The annual variation in food density in managed moist-soil wetlands and bottomland hardwood forests in and near the Mississippi Alluvial Valley (MAV), an important wintering area for North American waterfowl at the continental level (Reinecke *et al.* 1989), was examined to determine variation in parameter estimates used in energetic carrying capacity models at two spatial scales (within and across study wetlands in the MAV) and across years. Secondly, the relative influence of factors measured not only locally but also at a mid-latitude location on migratory waterfowl densities in managed wetlands was investigated. Our objectives were to: 1) describe variation in food densities across wintering areas used by migrating waterfowl during autumn and winter in the MAV, and 2) determine factors that influence waterfowl densities on managed wetlands to better inform the conservation planning process.

Methods

Variation in food abundance

Waterfowl density and associated food densities were estimated in moist-soil wetlands and food density was also estimated in bottomland hardwood forests in or near the MAV (Reinecke *et al.* 1989;

Hagy & Kaminski 2012a,b). Data presented here and related sample collection methods have previously been described in detail by Hagy and Kaminski (2012b) and Straub (2012), but different analyses were conducted to address our novel objectives. Moist-soil and bottomland forest wetlands are used extensively by many species of waterfowl, especially dabbling ducks (*Anas* sp.), for provision of food resources and other life-history needs (Reinecke *et al.* 1989). Moist-soil wetlands provide abundant natural seeds and tubers after they are flooded, which typically occurs in late autumn or early winter, and bottomland hardwood wetlands provide hard mast (*e.g.* acorns) throughout winter which typically become available during periodic bottomland flooding events (Reinecke *et al.* 1989; Hagy & Kaminski 2012b; Straub 2012). To estimate annual densities of sound red oak *Quercus* sp. acorns, we installed and checked 1-m^2 seed traps monthly from November through February 2009–2013 at five study wetlands across the MAV (Straub 2012). Additionally, to estimate moist-soil seed and tuber densities, we collected 10 benthic core subsamples during November or December (*i.e.* before most wintering waterfowl accessed wetlands and depleted foods) in 2006–2008 at each of three wetland plots immediately following flooding that had been either: 1) mown, 2) disced, or 3) not manipulated during the autumn prior to flooding, for 22 wetlands in or near the MAV (2006 = 6 wetlands, 2007 = 9 wetlands, 2008 = 7 wetlands). Laboratory processing followed Hagy and Kaminski (2012b) and Straub (2012); seed and tuber densities were adjusted for seeds lost, missed or destroyed during processing (Hagy *et al.* 2011), seeds and tubers of plant taxa thought to be avoided or infrequently consumed by waterfowl were removed from density estimates (Hagy & Kaminski 2012a) and coefficients of variation (CV) were estimated for each wetland (CV = s.d./mean density for all foods combined in non-manipulated wetland plots), across wetlands for each year, and across years for both moist-soil wetlands and bottomland hardwood forests.

Local and mid-latitude factors affecting waterfowl density

Waterfowl were enumerated by species from elevated hides during crepuscular periods 2–3 times weekly at each wetland plot from first flooding (*i.e.* November–December) through to waterfowl leaving the wetlands and surrounding area (*i.e.* late February), during winters 2006–2009 (Hagy & Kaminski 2012b). We combined densities of all dabbling duck species observed and analysed only this variable as dabbling ducks comprised >90% of observations and their densities were positively correlated with densities of all waterbirds combined (Hagy & Kaminski 2012b).

To accomplish our goal of investigating factors affecting waterfowl densities in wetlands in the study area, we examined the influence of weather and habitat variables measured within or near wetlands in the MAV (*i.e.* local) and weather variables measured *c.* 200 km north of our study area (*i.e.* mid-latitude) where large concentrations of waterfowl may winter if they are not encouraged to migrate further south by weather or other factors (Schummer *et al.*

2010). Concurrent assessment of local wintering area and mid-latitude variables addresses the hypothesis that waterfowl densities might be influenced by extrinsic factors (*e.g.* a weather severity index (WSI); Schummer *et al.* 2010), and these events may exert a greater influence than local conditions in southerly areas (*i.e.* factors near and within the southerly wetlands) to which the birds migrate. Weather data from central Missouri, which is in the northern part of the typical wintering range for Mallard *Anas platyrhynchos* following the Mississippi Flyway, were assumed to provide a reasonable representation of the effects of weather on duck movements from northern staging and wintering areas into the MAV, including our study wetlands. Weather data (*i.e.* WSI, cumulative precipitation during winter (October 1 to observation date), and mean daily temperature) from the closest weather station and water depth gauge readings from within each wetland were used to evaluate local influences on waterfowl densities. Water depths and weather data were recorded on the same day as waterfowl densities. For more northern (mid-latitude) parts of the wintering range, the same weather variables were acquired. Data were acquired from the Historical Climatology Network National Oceanographic Atmospheric Service weather stations at Farmington, Missouri (mid-latitude) and also from weather stations closest to (≤ 50 km from) study wetlands (at Batesville, Corinth, Greenwood, Starkville and Yazoo City in Mississippi; Covington, Jackson and Union City in Tennessee).

Linear mixed models were used in R (nlme; Pinheiro *et al.* 2014) to assess variation in dabbling duck density across managed moist-soil wetlands in relation to various explanatory variables. A set of candidate models (Table 1), each representing a unique biologically-plausible scenario, was built and models were compared for explanatory support using Akaike's information criterion adjusted for small sample size (AIC_c; Burnham & Anderson 2002). Because study wetlands were repeatedly sampled within a season, observation date was included as a repeated effect in the model. Additionally, the management category for each wetland plot (*i.e.* mow, disc or no manipulation) nested within wetland was designated as a random effect because evidence (*i.e.* lowest AIC_c) suggested that this increased the explanatory power of our global model (Zuur *et al.* 2009). Models were developed to assess support for mid-latitude factors, local factors, a combination of both local and mid-latitude factors, the effects of year and date of surveys, and finally a null model containing only the intercept. Inspection of residual plots and histograms indicated that dabbling duck density (*i.e.* the response variable) was not normally distributed and had heterogeneous variance when plotted against independent variables. Dabbling duck density therefore was natural log transformed prior to analysis. Parameter estimates from the most parsimonious model were back-transformed to describe the size of each effect. We provide marginal and conditional R^2 statistics as a means to assess the fit of each candidate model (Nakagawa & Schielzeth 2013). Marginal R^2 describes the proportion of variance

Table 1. Results of linear mixed models predicting dabbling duck density in managed moist-soil wetlands in or near the Mississippi Alluvial Valley during late autumn and winter 2006–2009, with the difference between each model-specific Akaike Information Criteria adjusted for small sample size (ΔAIC_c) and that of the top model. Model variables include local (LO) and mid-latitude (MO) estimates of cumulative winter precipitation (PrecipW), water depth (Depth), a weather severity index (WSI), temperature (Temp), year, management practice (autumn mowing, discing, or no management; Treat) and Julian day.

Model	**AIC_c**	**ΔAIC_c**	**R^2_{marg}**	**R^2_{cond}**
LOPrecipW+LODepth	2248.3	0	0.04	0.34
LOPrecipW + LODepth + MOPrecipW	2254.6	6.3	0.05	0.34
LOTemp+LODepth+LOPrecipW	2257.4	9.1	0.04	0.35
LOPrecipW + LODepth + MOWSI	2257.5	9.2	0.04	0.35
LODepth + MOPrecipW	2262.4	14.1	0.00	0.44
LOPrecipW + LOTemp + LODepth + MOWSI	2263.5	15.2	0.04	0.36
LOPrecipW + LOTemp + LODepth + MOPrecipW	2263.6	15.3	0.05	0.34
LOPrecipW + LODepth + MOWSI + MOPrecipW	2263.7	15.4	0.05	0.34
LOTemp + LOPrecipW + LODepth + MOWSI + MOPrecipW	2269.3	21.0	0.05	0.35
LODepth + MOWSI + MOPrecipW	2271.8	23.5	0.00	0.45
LOTemp + LODepth + MOWSI + MOPrecipW	2276.1	27.8	0.00	0.44
LODepth	2286.9	38.6	0.00	0.44
LOTemp+LODepth	2294.9	46.6	0.00	0.41
LODepth + MOWSI	2297.2	48.9	0.00	0.45
LOPrecipW	2407.0	158.7	0.03	0.36
LOPrecipW+LOTemp	2415.7	167.4	0.03	0.36
LOPrecipW + MOWSI	2416.6	168.3	0.03	0.36
MOPrecipW	2417.9	169.6	0.00	0.44
LOPrecipW + MOWSI + MOPrecipW	2420.8	172.5	0.04	0.35
MOPrecipW + MOTemp	2427.3	179.0	0.00	0.45
MOPrecipW + MOWSI	2427.5	179.2	0.00	0.45
Treat	2449.7	201.4	0.07	0.29
Null (Intercept)	2462.0	213.7	0.00	0.43
Year	2468.9	220.6	0.01	0.39
Julian day	2469.9	221.6	0.02	0.36
LOTemp	2470.5	222.2	0.00	0.42
MOTemp	2472.7	224.4	0.00	0.44
MOWSI	2472.8	224.5	0.00	0.45

explained by the fixed factor(s) while conditional R^2 describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2013).

Additionally, a general linear mixed model was used in SAS 9.3 to evaluate the effects of year and wetland on food density in managed moist-soil wetlands in late autumn (*i.e.* approximately early November, before waterfowl used wetlands) by performing a different analysis of data presented by Hagy and Kaminski (2012b). Year and wetland were included as fixed effects and wetland management practice (*i.e.* discing, mowing or no manipulation of robust moist-soil vegetation; see Hagy & Kaminski 2012b) within each wetland plot was included as a random effect. The response variable (food density) was natural log transformed to normalize residuals and homogeneity of variances among years and wetlands. Results were considered significant at $P < 0.05$.

Results

For managed moist-soil, CVs for seed and tuber densities ranged from 9–77% within wetlands ($\bar{x}$ = 31%, n = 22) and from 32–115% across years ($\bar{x}$ = 69%, n = 3). Overall, the CV of the annual mean seed density across years and wetlands was less (CV = 21%) than within years or most wetlands (Fig. 1). For bottomland hardwood forests, CVs for red Oak acorn densities ranged from 16–60% within wetlands ($\bar{x}$ = 33% n = 5) and from 11–29% across wetlands ($\bar{x}$ = 18%, n = 4). Overall, the CV of the annual mean acorn density across

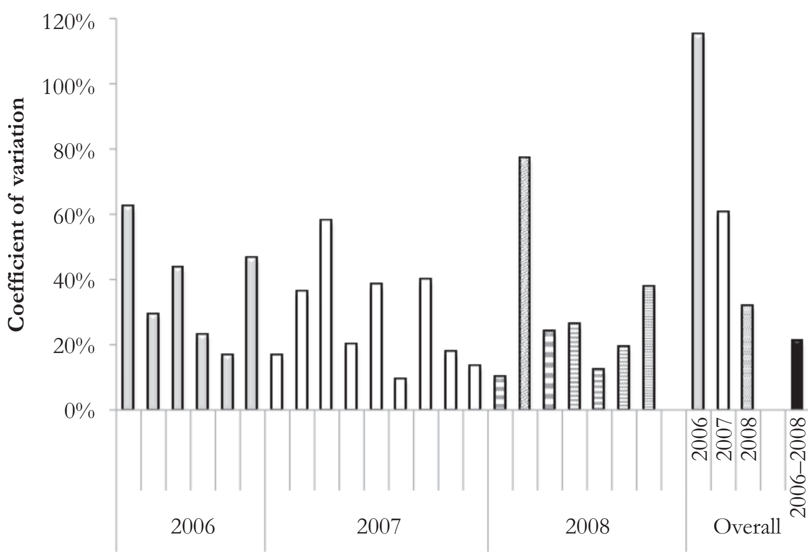

Figure 1. Coefficients of variation (%) for means of seed and tuber density for individual wetland plots, across wetland plots within years, and across wetland plots and years (overall) during late autumn 2006–2008 in managed moist-soil wetlands (n = 22 unmanipulated moist-soil wetland plots) in or near the Mississippi Alluvial Valley.

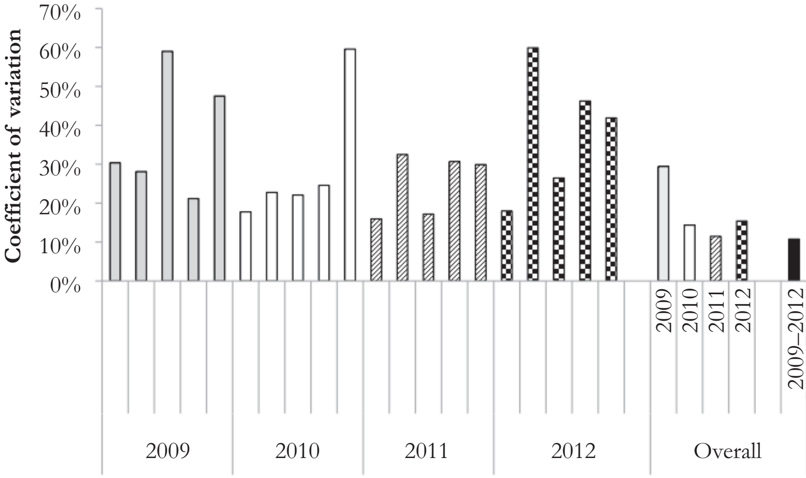

Figure 2. Coefficients of variation (%) for means of red Oak acorn production density for individual wetlands, across wetlands within years, and across wetlands and years (overall) during late autumn and winter 2009–2012 in bottomland hardwood forests (*n* = 5 wetlands surveyed repeatedly) in or near the Mississippi Alluvial Valley.

years and wetlands was less (CV = 11%) than individual years or most wetlands (Fig. 2). Food densities in managed moist-soil wetlands in late autumn varied by wetland ($F_{16,32}$ = 6.56, P < 0.001) but did not differ among years ($F_{2,13}$ = 2.01, P = 0.174) (Fig. 3).

On evaluating the explanatory variables thought to influence dabbling duck density, the top model contained factors measured only at the local scale (Table 1). Dabbling duck densities in managed moist-soil wetlands were negatively associated with local winter precipitation (*i.e.* an assumed correlate of local wetland availability) and positively associated with mean water depth of wetland plots, although confidence intervals associated with the beta estimate overlapped zero for water depth and thus we did not explore that relationship further (Fig. 4). A 9.6 cm increase in local precipitation during winter decreased predicted numbers of dabbling ducks in managed moist-soil wetlands by 1 duck/ha. Models containing only mid-latitude or mid-latitude plus local factors were not competitive (ΔAIC_c > 6.3). Although we had low model uncertainty, the proportion of the variance explained by depth and local winter precipitation (R^2 = 0.04) was less than the variance explained by the combination of fixed effects and random variables (R^2 = 0.34).

Discussion

Small-scale spatial or temporal estimates of food density (*e.g.* among wetlands or years) in managed moist-soil wetlands and bottomland hardwood forests were highly variable and means from these estimates were relatively imprecise, which is consistent with other studies in similar habitats

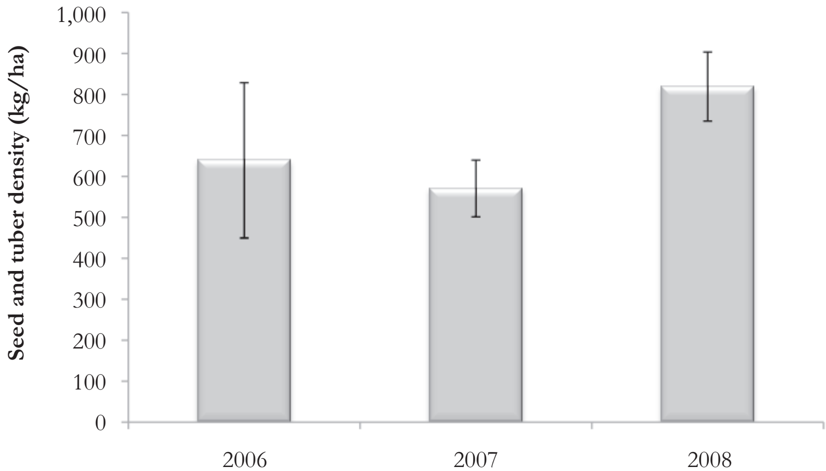

Figure 3. Seed and tuber density (dry weight, in kg/ha ± s.e.) during late autumn 2006–2008 in managed moist-soil wetlands (n = 64 wetland plots) in or near the Mississippi Alluvial Valley (data from Hagy & Kaminski 2012b).

(Stafford *et al.* 2006; Kross *et al.* 2008; Evans-Peters *et al.* 2012; Straub 2012; Olmstead *et al.* 2013). However, coefficients of variation were relatively low and means were similar when estimated across wetlands and years. Thus, use of fixed food densities in simplistic daily ration models for conservation planning purposes at a large spatial scale appears to be a reasonable practice. At the MAV scale and across the years of the study, food densities in managed moist-soil wetlands and bottomland hardwood forests were relatively constant; however, the spatial distribution of that food within the region varied annually. Because waterfowl are highly mobile and respond to changing habitat conditions, they are likely able to move within the landscape and respond to changing distributions of food and habitat availability. In fact, many factors other than food density likely influence habitat use, and direct relationships between food resources and waterfowl distribution seem to be difficult to detect without incorporating additional local environmental conditions into habitat models (Fleming 2010; Tapp 2013; Weegman 2013).

Hagy and Kaminski (2012b) presented data indicating that early winter food densities varied with management practice in moist-soil wetlands; they considered year and wetland as random effects relative to their research questions, but did not test them explicitly. Herein, re-examination of their data across years indicated that while waterfowl food densities varied by wetland, there was not an apparent annual difference in their study area (Fig. 3). The variation between individual wetlands was much greater than across years. Similarly, Straub (2012) reported that acorn densities in bottomland hardwood forests fluctuated greatly across years for individual wetlands;

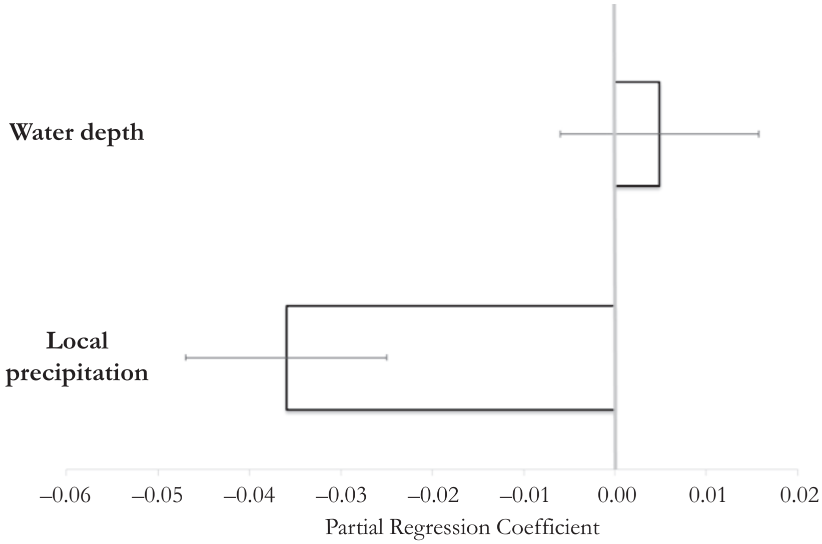

Figure 4. Direction and relative effect size (partial regression coefficient with 95% confidence intervals) for variables in the top model predicting dabbling duck densities during late autumn 2006–2008 in managed moist-soil wetlands (*n* = 64 wetland plots) in or near the Mississippi Alluvial Valley.

however, at the scale of the MAV, annual estimates were similar. Although some bottomland hardwood forests produced few acorns in some years, low yield never occurred at all wetlands in the same year. Across years, MAV-wide estimates of red Oak acorn abundance were precise (CV = 11%), but variability across wetlands was great (Fig. 2). Stafford *et al.* (2006) and Kross *et al.* (2008) both reached similar conclusions for seeds in rice fields and moist-soil wetlands, respectively, in the MAV. Thus, while daily ration models incorporating fixed food densities may reasonably predict carrying capacity at large spatial scales, with all other parameters being equal, substantial variation among locations and time periods likely limits the predictive accuracy of these models when scaled down spatially.

In managed moist-soil wetlands (Kross *et al.* 2008), bottomland hardwood forests and agricultural rice fields (Stafford *et al.* 2006), food production for waterfowl has been shown to be highly variable between sites but much less variable across years and large regions, such as the MAV. Variation at individual wetlands may be influenced by management practices (Hagy & Kaminski 2012b), management frequency and intensity (Brasher *et al.* 2007; Olmstead *et al.* 2013), and other environmental factors that are difficult to predict accurately. Therefore, the challenge in predicting annual carrying capacity in the managed wetlands and bottomland hardwood forests of the MAV likely depends less on accounting for annual differences in site-specific food densities and more on availability of those wetlands as habitats suitable for waterfowl. However, flooding of foods at the appropriate time

(Greer *et al.* 2007) and to the appropriate depth (Hagy & Kaminski 2012b) may be a challenge in some years. To date, we are aware of few attempts to quantify functionally available habitats at a scale such as a joint venture region (but see Soulliere *et al.* 2007), despite the clear need to determine and quantify food availability.

We examined the relative influences of mid-latitude and local factors on waterfowl densities in managed wetlands in and near the MAV and determined that local precipitation, an assumed surrogate of wetland availability, was most influential in explaining variation in dabbling duck density. Managed wetlands with extensive water control capabilities, such as the wetlands included in our study (see Hagy & Kaminski 2012b), are often flooded before many passively or non-managed wetlands and are available when waterfowl first arrive in the late autumn and early winter. Thus, waterfowl are likely attracted to these managed wetlands initially but may later colonise passively filled or temporary wetlands following periods of sufficient rainfall (Beatty *et al.* 2014a). Given the rapid declines in waterfowl food densities in managed wetlands documented by Hagy and Kaminski (2012b), our results suggest that waterfowl may move to alternative locations, such as agricultural fields (Pearse *et al.* 2012), following precipitation events to acquire newly-available food on flooded farmland.

Interestingly, evidence is accumulating that suggests local habitat availability may be a better predictor of duck density in managed wetlands than food density (Hagy 2010; Tapp 2013) or weather and precipitation in more northerly portions of the Mallard's wintering range (Krementz *et al.* 2012; Beatty *et al.* 2014b). Distributions and duration of stay of waterfowl at autumn staging areas can vary with wetland area, disturbance (Stafford *et al.* 2010), wetland forage quality (O'Neal *et al.* 2012), precipitation (Krementz *et al.* 2011, 2012) and vegetation characteristics (Moon & Haukos 2008), but others have failed to show a relationship between food abundance and waterfowl use of wetlands (Percival *et al.* 1998; Straub 2008; Brasher 2010; Fleming 2010). Weather has been shown to influence regional abundance of ducks (Schummer *et al.* 2010), but Krementz *et al.* (2012) reported that temperature and the onset of freezing conditions were not significant determinants of departure date during autumn migration. Cumulative research suggests that there is a significant degree of plasticity in the autumn migration of duck species to the wintering grounds (Bellrose *et al.* 1979; Krementz *et al.* 2012). We posit that a suite of factors including photoperiod, the location and timing of severe weather events and habitat availability and quality interact with considerable inter- and intraspecific variation to determine migratory patterns, but continued research is necessary to differentiate their relative contribution to the timing of waterfowl migration and habitat use.

At a continental or flyway scale, a suite of factors influences waterfowl habitat selection, including wetland availability (Beatty *et al.* 2014b). Krementz *et al.* (2011) and Hagy *et al.* (2014) anecdotally noted that, during spring- and autumn-migration, Mallard stopover use and duration of stay may have been related to precipitation and the availability of local wetlands, respectively. Interestingly, we identified a relationship between local precipitation and duck densities in the wintering region of the MAV, which might also suggest that once ducks migrate to latitudes where influences of photoperiod, weather severity and other factors decrease (*i.e.* wintering areas; Schummer *et al.* 2010), wetland habitat availability is also an important driver of habitat selection (Webb *et al.* 2010; Pearse *et al.* 2012). Thus, conservation planning models can benefit from considering timing and extent of flooding (*i.e.* wetland inundation) when determining habitat objectives at large spatial scales (*e.g.* Joint Ventures).

Although challenging to build and parameterise, spatially explicit models that incorporate variables (*e.g.* precipitation) that account for spatial and temporal variability in habitat availability may be needed for more accurate predictions of food availability and site use by ducks. However, relatively simplistic daily ration models that incorporate fixed estimates of food density are likely adequate for predicting energetic carrying capacity at the MAV scale for waterfowl that are highly mobile and can respond rapidly to changing habitat conditions and availability. A critical next step in improving the accuracy of energetic carrying capacity models is estimating the spatial and temporal extent and variability of habitats by modelling the wetland areas suitable for exploitation of food resources by waterfowl (Williams *et al.* 2014). Future modelling attempts could incorporate the spatial arrangement of patches (*i.e.* costs of food acquisition), temporal availability of patches within and among years and individual patch value rather than aggregate food availability to improve accuracy and utility at smaller scales. In reality, extensive inter- and intraspecific variation in migration timing and life-history strategies add considerable uncertainty to energetic models (Hagy *et al.* 2014) and efforts aimed at reducing these uncertainties or quantifying the relative effects on energetic carrying capacity models at annual and longer-term timescales would be beneficial (see Notaro *et al.* 2014; Schummer *et al.* 2014).

In summary, our data indicate that annual food densities in managed wetlands and bottomland hardwood forests were generally stable across the 3-year study at a regional scale used by a Joint Venture for conservation planning. It may be beneficial for conservation planners to quantify longer-term variability in food resources and examine factors influencing the availability of these resources to waterfowl in other regions used by wintering waterfowl. Furthermore, if the results are extended to other wintering areas and habitat types, quantifying and facilitating habitat availability within the landscape for waterfowl, in sufficient quantities to meet their energetic demands at the appropriate time and location, is a challenge worthy of additional exploration.

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