RESEARCH ARTICLE

# Landscape effects on mallard habitat selection at multiple spatial scales during the non-breeding period

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**Abstract** Previous studies that evaluated effects of landscape-scale habitat heterogeneity on migratory waterbird distributions were spatially limited and temporally restricted to one major life-history phase. However, effects of landscape-scale habitat heterogeneity on long-distance migratory waterbirds can be studied across the annual cycle using new technologies, including global positioning system satellite transmitters. We used Bayesian discrete choice models to examine the influence of local habitats and landscape composition on habitat selection by a generalist dabbling duck, the mallard (*Anas platyrhynchos*), in the midcontinent of North America during the non-breeding period. Using a previously published empirical movement metric, we separated the non-breeding period into three seasons, including autumn migration, winter, and spring migration. We defined spatial scales based on movement patterns such that movements >0.25 and <30.00 km were classified as local scale and movements >30.00 km were classified as relocation scale. Habitat selection at the local scale was generally influenced by local and landscape-level variables across all seasons. Variables in top models at the local scale included proximities to cropland, emergent wetland, open water, and woody wetland. Similarly, variables associated with area of cropland, emergent wetland, open water, and woody wetland were also included at the local scale. At the relocation scale, mallards selected resource units based on more generalized variables, including proximity to wetlands and total wetland area. Our results emphasize the role of landscape composition in waterbird habitat selection and provide further support for local wetland landscapes to be considered functional units of waterbird conservation and management.

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## Introduction

Land use changes have altered the structure and composition of ecosystems on a global scale, yet studies evaluating the influence of broad-scale habitat heterogeneity on vertebrate space use and movement are relatively rare (Turner 2005; Cornell and Donovan 2010). Habitat heterogeneity is especially prominent in landscapes that contain abundant wetland habitat due to the highly variable hydrologic patterns of many wetland ecosystems (Herfindal et al. 2012). Landscapes with relatively high proportions of wetland habitat and a diverse array of wetland types, also referred to as wetland complexes, exhibit variation in structure as a result of natural and anthropogenic forces, including precipitation, development, conservation programs, and water control (Dwyer et al. 1979; Weller 1988). Consequently, wetland landscape composition may influence habitat use and movements of migratory waterbirds, which have temporally dynamic energetic and habitat requirements throughout the annual cycle (Riffell et al. 2003; Taft and Haig 2006).

Previous studies that quantified effects of landscape composition on migratory waterbirds were generally restricted to local analyses and a single life-history period, such as migration, wintering, or breeding (Naugle et al. 1999; Webb et al. 2010; Pearse et al. 2012). Thus, a broader spatial and temporal approach to evaluate the influence of landscape composition on waterbird habitat use has potential to provide additional insight into cumulative effects of resource utilization decisions throughout the annual cycle (Arzel et al. 2006). Additionally, the influence of spatial heterogeneity on waterbird habitat use has broad conservation implications for managing migratory birds that use ecologically and geographically disparate resources throughout the annual cycle (Webster et al. 2002). In particular, the non-breeding period of the annual cycle for migratory birds is of interest to conservation planners because of its potential to influence subsequent breeding activities and recruitment (Marra et al. 1998; Devries et al. 2008).

Isolated wetlands rarely contain sufficient resources for individual waterbirds to meet daily, weekly, and seasonal energetic requirements within a dynamic annual cycle (Dwyer et al. 1979; Reinecke et al. 1989; Webb et al. 2010). Consequently, wetland landscapes are energetically advantageous for migratory waterbirds because they include a variety of wetland types within close geographic proximity to provide access to a diverse array of food types (Tidwell et al. 2013) and allow birds to minimize flight distances among wetlands (Farmer and Parent 1997). Although researchers have hypothesized that landscape composition may influence migratory waterbird habitat selection during the non-breeding portion of the annual cycle, quantitative evidence to support this prediction is lacking (Farmer and Parent 1997; Naugle et al. 1999; Webb et al. 2010; Pearse et al. 2012).

Resource and habitat selection studies often used the spatial extent or resolution at which habitat availability is measured to define spatial scales (Boyce 2006). However, an individual's behavioral state likely impacts habitat selection patterns (Schick et al. 2008). For example, long distance migrants may respond to broad patterns in the spatial distribution of habitats, whereas individuals engaged in intermediate foraging flights might respond to habitat heterogeneity at finer spatial scales (Morales and Ellner 2002; Patterson et al. 2008; Schick et al. 2008). Empirical movement data can be used to provide insight into the behavior state of an individual, and this information can be used to accurately define appropriate spatial and temporal scales for habitat selection studies (Schick et al. 2008).

Recent efforts to model associations between landscape composition and bird counts have implicitly assumed increased population densities and/or abundances indicated superior habitat (e.g., Taft and Haig 2006). However, animal population density and abundance can be misleading indicators of wildlife-habitat relationships (Van Horne 1983; Bock and Jones 2004; Johnson 2007) and previous waterbird habitat use studies have rarely accounted for spatial variation in habitat availability. As a result, there is a need to evaluate the effects of landscape composition on waterbirds with an approach that accounts for spatial habitat availability. Habitat selection models compare used resource units to available resource units to account for temporal and spatial variance in availability (Manly et al. 2002). Thus, our objective was to assess the effects of landscape composition on habitat selection by a generalist dabbling duck, the mallard (*Anas platyrhynchos*), during the non-breeding portions of the annual life cycle, including autumn migration, winter, and spring migration. We used data

from individual birds marked with global positioning system (GPS) satellite transmitters in the midcontinent region and employed a use—availability design to evaluate the influence of landscape composition on space use. Further, we used a Bayesian hierarchical approach to model this relationship at two spatial scales.

## Methods

### Capture and GPS telemetry

We captured adult mallard hens in two separate cohorts in 2010 and 2011. Marking, handling, and telemetry procedures were described previously (Beatty et al. 2013; Kesler et al. 2014). Briefly, the first cohort included 20 individuals captured in Yorkton, Saskatchewan, Canada (51°13′N 102°28′E) in September 2010, and the second cohort included 20 birds captured in February 2011 at several locations in Arkansas, USA (5-Oaks Duck Lodge at 34°20′N 91°36′E, Bayou Meto Wildlife Management Area at 34°13′N 91°31′E, Black River Wildlife Management Area at 36°03′N, 91°09′E). We outfitted captured individuals with solar-powered GPS (accuracy ±18 m) satellite transmitters (Model PTT-100, Microwave Telemetry, Inc., Columbia, MD, USA) attached with a Teflon ribbon harness (Malecki et al. 2001; Miller et al. 2005; Beatty et al. 2013). Transmitters were programmed to obtain four GPS fixes (i.e., locations) each day. Consequently, we assumed that GPS fixes encompassed the range of mallard diurnal and nocturnal behaviors (Webb et al. 2011, Kesler et al. 2014). Birds were monitored until the transmitter failed or until we observed consecutive GPS fixes ≤100 m from the last recorded fix for an individual bird (Beatty et al. 2013). Thus, consecutive GPS fixes ≤100 m apart were retained if the bird moved >100 m at some point in the future. In addition, we did not evaluate GPS fixes outside of the USA where standardized geospatial habitat data were not available.

Mallard habitat use may vary as a result of differing nutritional requirements, energetic expenditures, and behaviors exhibited across the annual cycle (Drilling et al. 2002). Consequently, we separated the non-breeding portion of the life cycle into three separate seasons based on individual movements: autumn migration, winter, and spring migration (see Beatty et al. 2013). Briefly, net displacement was modeled to obtain individual estimates for the timing and duration of autumn and spring migrations (Beatty et al. 2013). Fourteen ducks were excluded from migration analysis and, thus, did not have individual migration estimates but had sufficient observations for inclusion in habitat selection analysis. For these birds we assigned mean season dates according to year (Supplementary Material, Appendix 1) (Beatty et al. 2013).

### Spatial scales

Habitat selection analyses that include multiple spatial scales can improve understanding of wildlife-habitat relationships (Johnson 1980; McDonald et al. 2012). To define geographically, ecologically, and behaviorally relevant spatial scales, we examined movement patterns of individuals during the three previously identified seasons. For each interval between GPS fixes, we calculated the natural log of distance moved (km) to obtain an empirical distribution of step lengths. We excluded intervals that were >24 h apart to minimize the effects of movement that occurred when the transmitter signal was inadequate. We fit a Gaussian fixed kernel density estimator with biased-cross validation to the natural log transformed empirical distribution (density function in R; R Development Core Team 2013).

Based on the smoothed data, we visually identified two approximate breaks in the distribution and classified each GPS fix $i$ as one of three spatial scales based on the Euclidean distance moved from the previous fix $i$–1. First, step lengths that were <0.25 km were interpreted to be within-wetland movements in response to the distribution of resources at fine spatial scales. We excluded these movements from further analysis due to the limited resolution of our habitat data (National Land Cover Database 2006; Fry et al. 2011). Second, local movements ranged from 0.25 to 30.00 km and were considered daily foraging flights in response to variation in habitats and resources at intermediate spatial scales. Although the minimum value for the local scale (0.25 km) was larger than recently published estimates for dabbling ducks (e.g. 0.02 km; Pearse et al. 2011), we specifically identified the break in the distribution at 0.25 km as the local scale cut-off value to obtain a conservative estimate for foraging flights. The maximum step length value
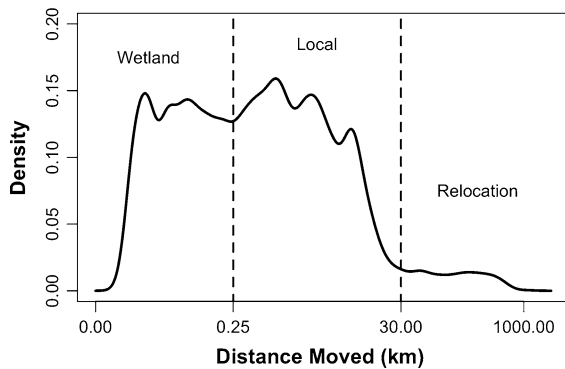
**Fig. 1** Probability density function and associated spatial scales based on natural log transformed step lengths for mallards during the non-breeding period of the annual cycle. Distance moved represents the natural log of the distance between GPS fix $i$ and fix $i–1$ for focal fix $i$. Labels on the $x$ axis have been back-transformed to display units in km

for local scale (30.00 km) flights corresponded to observed maximums for previously published estimates for dabbling ducks engaged in foraging flights (Link et al. 2011; Pearse et al. 2011). For example, Davis and Afton (2010) documented a maximum distance for foraging flights of 25.80 km for wintering female mallards in the lower Mississippi Alluvial Valley. Finally, relocation movements were identified as step lengths that were >30.00 km regardless of the season (autumn migration, winter, spring migration) in which they occurred (Fig. 1).

### Defining availability

We used discrete choice models to examine habitat selection separately at local (movements 0.25–30.00 km) and relocation (movements >30.00 km) scales (Cooper and Millspaugh 1999; Thomas et al. 2006). Discrete choice models frame habitat selection as a series of experiments whereby individuals make decisions on habitat use from a set of alternatives within a defined choice set (Cooper and Millspaugh 1999; Pardoe and Simonton 2008). In our discrete choice models, the number of choice sets was equal to the total sample size in the model, and one choice set included one used resource unit matched to a suite of available resource units. We considered GPS fixes to represent used resource units whereas available resource units were generated with random points in a geographic information system (GIS). Thus, availability (i.e., random points)

was defined separately for each used resource unit (i.e., GPS fix) and varied across choice sets to reflect spatial changes in available habitats (Cooper and Millspaugh 1999).

At the local scale, we defined availability separately for each used resource unit with a 30-km buffer centered on the used resource unit in ArcGIS 10.0 (ESRI, Redlands, CA, USA). To discretely represent available resource units, we generated 19 random points within the buffer to produce a choice set of 20 alternatives at the local scale (1 used resource unit/19 available resource units). We then measured a series of habitat covariates for each used and available resource unit (see below). Although as few as five available alternatives are sufficient to obtain consistent parameter estimates in discrete choice models (McFadden 1978), we used 19 alternatives to account for spatial variation in habitat covariates at the local scale (sensu Bonnot et al. 2011).

We defined availability at a broader spatial scale for relocation flights. For each used resource unit classified as a relocation flight, we identified the previous GPS fix and connected the two points with a straight line in ArcGIS 10.0. A 30-km availability buffer was applied to the line, which denoted the straight-line distance between GPS fix $i$ and $i–1$ for the focal used resource unit $i$. To discretely represent available resource units, we generated 24 random points within the buffer to yield a choice set of 25 alternatives at the relocation scale (1 used resource unit/24 available resource units). We then measured a series of habitat covariates for each used and available resource unit (see below). We used 24 available alternatives to account for the increased spatial variation in habitat covariates at the relocation scale compared to the local scale (sensu Bonnot et al. 2011). We characterized availability using a straight line between the focal GPS fix and previous GPS fix because we wanted to restrict availability to those areas most likely to be visually surveyed by migrating ducks.

### Habitat covariates

We measured a series of covariates to characterize habitat proximate to each used and available resource unit. All covariates were based on the 2006 National Land Cover Database (NLCD 2006), which seamlessly classified land cover across the conterminous United States at a spatial resolution of 30 m (Fry et al.

2011; Wickham et al. 2013). We chose NLCD 2006 due to its consistent methodology, extensive spatial coverage, and relatively restricted image capture dates (Fry et al. 2011; Wickham et al. 2013).

Although NLCD 2006 contained 16 land cover classes, we focused our analyses on cultivated agricultural crops, emergent herbaceous wetlands, open water, and woody wetlands, which are the four habitat types most likely to influence mallard habitat selection (Drilling et al. 2002; Wickham et al. 2013). Cultivated crops included annual crops such as corn, soybeans, rice or cotton as well as perennial crops like orchards and vineyards (Wickham et al. 2013). Emergent herbaceous wetlands were intermittently flooded areas that had >20 % herbaceous vegetative cover (Wickham et al. 2013). Open water habitat was characterized as permanently flooded with <25 % vegetative or soil cover (Wickham et al. 2013). Woody wetlands included intermittently flooded areas with trees or woody shrubs comprising >20 % cover (Wickham et al. 2013). For each used and available resource unit, we measured the proximity to the nearest feature (km) for the four aforementioned habitats (proximity to cultivated crops, proximity to emergent herbaceous wetland, proximity to open water, proximity to woody wetland). 'Proximity to' values equaled zero if the resource unit was in the specified habitat and were negative (in km) when the resource unit was not in the specific habitat. To obtain a thorough characterization of resource units, availability and landscape variable buffers did not restrict proximity-to variables.

In addition, we evaluated the importance of general wetland habitat with a variable that measured proximity to the nearest wetland habitat, regardless of wetland type. As a result, this metric was equal to the maximum value among the three wetland habitats: proximity to emergent wetland, proximity to open water, proximity to woody wetland (Table 1). We specifically used proximity metrics to characterize habitat near each used and available resource unit because they are less sensitive to spatial error compared to indicator variables (Conner et al. 2003).

Emerging evidence indicates migrating and wintering dabbling duck habitat use is influenced by landscape composition (Webb et al. 2010; Pearse et al. 2012). Consequently, in addition to proximity variables, we measured a series of covariates that quantified landscape composition at a relatively broad spatial scale for each used and available resource unit.

**Table 1** Habitat covariates included in discrete choice models to examine midcontinent mallard habitat selection during autumn migration, winter, and spring migration from 2010–2012

| Variable | Description |
| --- | --- |
| CrpPrx | Proximity to cultivated crops (km) |
| EmgPrx | Proximity to emergent herbaceous wetland (km) |
| OwtrPrx | Proximity to open water (km) |
| WodyPrx | Proximity to woody wetland (km) |
| WetPrx | Proximity to wetland habitat (km), equal to the maximum value among EmgPrx, OwtrPrx, WodyPrx |
| CrpAr | Cultivated crop area (ha) |
| EmgAr | Emergent herbaceous wetland area (ha) |
| OwtrAr | Open water area (ha) |
| WodyAr | Woody wetlands area (ha) |
| WetAr | Wetland habitat area (ha), equal to the sum of EmgAr, OwtrAr, WodyAr |

Proximity variables equaled 0 if the resource unit was in the habitat and were negative (km) if the resource unit was not in the specified habitat

Area variables were measured within a 3.46 km buffer centered on each resource unit

To calculate landscape composition metrics, we placed a 3.46 km buffer centered on each used and available resource unit and estimated area (ha) of cultivated cropland, open water, woody wetlands, and emergent wetlands within the buffer through a workflow that included processes in ArcGIS 10, Geospatial Modelling Environment (Beyer 2012), R, Python, and FragStats 4.1 (McGarigal et al. 2012). We also created an additional landscape composition variable that represented the total area of wetland habitat within the 3.46 km buffer, which was equal to the sum of open water, woody wetland and emergent wetland areas (Table 1). We used a 3.46 km buffer because this value represented the mean step length for foraging flights at the local scale and closely corresponded with previously published values for mean foraging flight distance (e.g., 4.8 km; Link et al. 2011). We did not include metrics for wetland density, diversity, or connectivity in our models due to relatively coarse spatial scale of the data and limited ability to identify specific wetland types beyond the three categories. Further, landscape composition likely has a primary and constraining effect on ecological processes whereas landscape configuration has a secondary effect (Turner 2005).

Statistical analysis

We modeled resource selection with Bayesian random-effects multinomial logit models, also referred to as mixed logit discrete choice models, to account for correlation of observations from individual ducks (Thomas et al. 2006). The number of alternatives within a choice set varied across spatial scales: the local scale had a choice set size of 20 resource units and the relocation scale had a choice set size of 25 resource units.

We modeled the probability of choosing alternative $j$ in choice set $i$ by animal $a$ based on $k$ predictors:

$$P_{aij} = \frac{\exp\left(\beta_{1a}x_{1ij} + \beta_{2a}x_{2ij} + \ldots \beta_{ka}x_{kij}\right)}{\sum_{j=1}^{J} \exp\left(\beta_{1a}x_{1ij} + \beta_{2a}x_{2ij} + \ldots \beta_{ka}x_{kij}\right)} \quad (1)$$

where $j$ indexes alternatives within a choice set (ranges from 1 to 20 at local scale, 1 to 25 at relocation scale), $J$ represents the total number of alternatives within a choice set ($J = 20$ at local scale, $J = 25$ at relocation scale), $i$ indexes choice sets and represents the sample size ($i = 1\ldots N$), $a$ indexes individual-level coefficients to account for variance in selection patterns among individual ducks, and $\sum_{j=1}^{J} P_{aij} = 1$. To obtain population-level coefficients, we assumed individual-level coefficients for all predictors were normally distributed with population mean $\mu_k$ and standard deviation $\sigma_k$. We assumed vague normal distributions for all population-level hyper-parameters where $\mu_k \sim Normal(0, 100)$ and $\sigma_k \sim Uniform(0, 100)$ (Supplementary Material, Appendix 2).

Mallard habitat selection patterns may vary as a result of a shift in behavior between day and night (LaGrange and Dinsmore 1989; Stafford et al. 2007). Additionally, waterfowl may alter habitat use patterns during the day as a result of anthropogenic disturbance (Arzel et al. 2006; Dooley et al. 2010; Dinges 2013). Thus, at the local scale we fit separate models for diurnal and nocturnal periods within each season (Supplementary Material, Appendix 3). However, at the relocation scale we did not separate data according to season or diel period because of low sample sizes. We developed a set of five candidate models to evaluate alternative hypotheses on the factors influencing mallard habitat selection (Supplementary Material, Appendix 4).

At the local scale, we fit the five candidate models according to season (autumn migration, winter, spring migration) and diel period (day, night) for a total of 30 models (3 seasons × 2 diel periods × 5 candidate models = 30). Additionally, we fit the five aforementioned models to the relocation scale without regard to season or diel period. We combined GPS locations from different years to enhance sample sizes. All models with the exception of the null contained random coefficients associated with individuals to account for variance in selection patterns among ducks. We ranked the five candidate models according to deviance information criterion (DIC), which is a Bayesian alternative to Akaike's information criterion (Spiegelhalter et al. 2002). We calculated ΔDIC values based on the top model and considered >5 ΔDIC units to be a substantial improvement in model fit (Thomas et al. 2006). We inferred that all variables in top models influenced habitat selection. However, because we were specifically interested in population-level selection, we based further inferences on habitat selection on the posterior distribution of the population-level mean $\mu_k$ and its associated 95 % credible intervals. Specifically, we interpreted those predictors with 95 % credible intervals that did not overlap zero as relatively important variables in habitat selection models.

We fit candidate discrete choice models in WinBUGS v1.4.3 (Lunn et al. 2000) using the R package R2WinBUGS (Sturtz et al. 2005). Although the number of iterations, thinning and burn-in varied according to season and candidate model, we ran three separate chains for all candidate models (Supplementary Material, Appendix 5, Table S1). We assessed convergence using the Brooks–Gelman–Rubin statistic (Brooks and Gelman 1998) where values <1.1 were considered indicative of convergence to the posterior distribution (Gelman and Hill 2007). To speed convergence, we centered and standardized all predictor variables using two standard deviations $\left(\frac{x-\bar{x}}{2s}\right)$ (Gelman and Hill 2007).

Habitat selection studies assume that habitats used disproportionately to their availability confer a fitness advantage to individuals (Manly et al. 2002). As a result, habitat selection analyses essentially monitor individuals to indirectly assess habitat quality (Johnson 2007). In addition to this implicit assumption, we made several assumptions specific to this study. First, we assumed all wetlands within 30-km availability buffers were available, thus, we did not account for hydrologic condition, water depth, or hunting disturbance in estimates of wetland availability. We also did

not account for variation in within-wetland food availability within habitat classes (sensu Straub et al. 2012). Third, we assumed a relatively static landscape from 2006 to 2010–2012, the time lapse between NLCD 2006 data collection and the present study. Although hydrology, water depth, disturbance, food availability, and land use changes likely affect mallard habitat use, we did not consider these factors in analyses due to limitations of the geospatial habitat data and the broad spatial scale of the study (Reinecke et al. 1989; Drilling et al. 2002; Greer et al. 2009; Dooley et al. 2010). However, we utilized relatively coarse habitat covariates in our analyses, including proximity-to and area variables, to minimize the effects of any geospatial data inaccuracies.

# Results

## Capture, GPS telemetry and spatial scales

Five transmitters from the first cohort failed before autumn migration (2010), and two transmitters from the second cohort failed before spring migration (2011). Thus, our sample was reduced to 33 individuals. Fourteen individuals were not monitored for a sufficient period of time to be included in migration models (Beatty et al. 2013). Thus, Beatty et al. (2013) fit individual migration chronology models to 19 of 33 ducks, which were used to assign mean dates for autumn migration, winter, and spring migration to the remaining 14 individuals.

A total of 20,784 GPS locations were recorded over the duration of the study. We removed 10,731 breeding season observations and an additional 4,149 observations that occurred at the wetland scale

during the non-breeding season. In addition, we removed 427 observations that occurred outside the USA due to limitations of geospatial data. Thus, our final sample was comprised of 5,477 locations. The number of individuals according to spatial scale, season and, diel period varied from 19 to 33 and the total number of fixes ranged from 220 to 1317 (Table 2). Birds were often tracked for more than 1 year and all GPS location data were collected between 25 September 2010 and 17 September 2012.
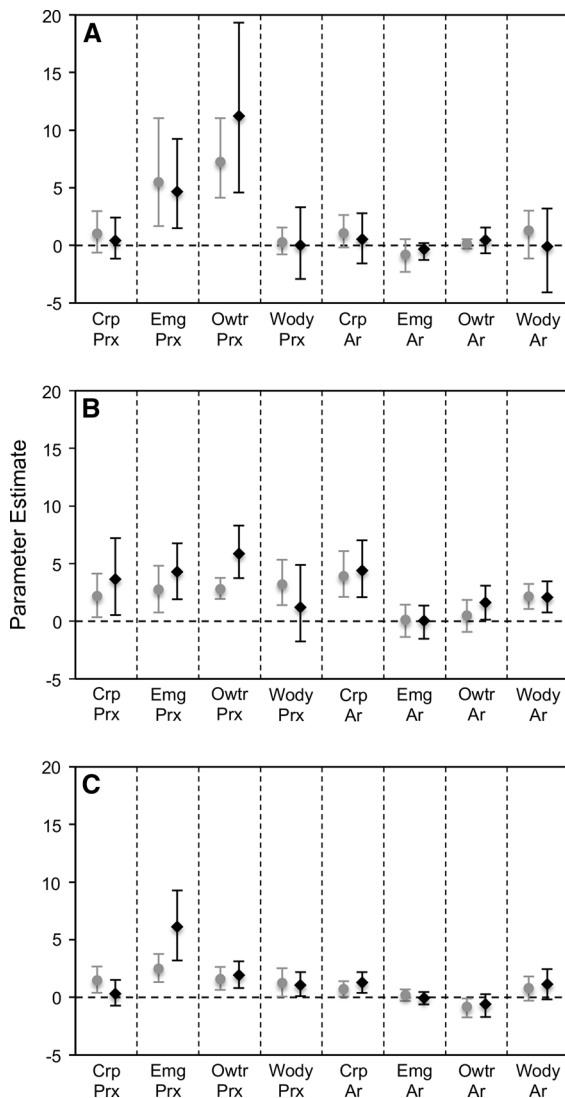
## Habitat selection

The top model for autumn migration at the local scale was the full model for diurnal and nocturnal periods (model 5) (Supplementary Material, Appendix 5, Table S2). During autumn migration, ducks selected resource units proximate to emergent wetlands and open water, but posterior distributions for all landscape composition variables overlapped zero (Fig. 2a). Mean parameter estimates were similar between diel periods for all covariates.

The full model was also the top winter model for both day and night (Supplementary Material, Appendix 5, Table S2). During winter, ducks selected resource units proximate to crops, emergent wetlands, and open water during both diel periods, and resource units near woody wetlands were selected during the day but not at night (Fig. 2b). Posterior distributions for proximity to open water did not overlap between diurnal and nocturnal periods, indicating increased selection of open water areas at night. Landscape composition variables played a prominent role in habitat selection during the winter compared to autumn migration. Areas of cropland and woody wetland positively influenced selection during day and

**Table 2** Discrete choice sample statistics to examine midcontinent mallard habitat selection during the non-breeding period from 2010–2012, including spatial scale, season, diel period, number of individual ducks (A), total number of GPS fixes (N), mean number of fixes per individual ($\bar{x}$), standard deviation (SD), and range of fixes per individual duck (range)

| Scale | Season | Diel period | A | N | $\bar{x}$ | SD | Range |
|---|---|---|---|---|---|---|---|
| Local | Autumn Migration | Diurnal | 19 | 323 | 17.00 | 19.01 | 1–85 |
| | | Nocturnal | 20 | 220 | 11.00 | 14.17 | 1–65 |
| | Winter | Diurnal | 30 | 1317 | 43.90 | 39.25 | 3–149 |
| | | Nocturnal | 30 | 1033 | 34.43 | 30.41 | 2–120 |
| | Spring migration | Diurnal | 23 | 1188 | 51.65 | 19.00 | 17–101 |
| | | Nocturnal | 23 | 1045 | 45.43 | 18.30 | 9–77 |
| Relocation | – | – | 33 | 351 | 10.64 | 7.21 | 1–30 |

**Fig. 2** Parameter estimates and associated 95 % credible intervals for the top discrete choice models according to deviance information criterion that examined habitat selection patterns for mallards during **a** autumn migration, **b** winter, and **c** spring migration at the local scale (movements 0.25–30.00 km). For each season, parameter estimates and 95 % credible intervals are displayed for diurnal (*gray circles*) and nocturnal (*black triangles*) models

night, and open water area positively influenced selection at night (Fig. 2b).

The top model for spring migration at the local scale was the full model for both diel periods (Supplementary Material, Appendix 5, Table S2). Ducks selected resource units proximate to emergent wetlands, open water, and woody wetlands during both diel periods, and resource units near crops were

selected during the day but not at night (Fig. 2c). Posterior distributions for landscape composition variables overlapped zero with the exception of cropland area (Fig. 2c).

The top model for the relocation scale was the general landscape composition model (model 3) (Supplementary Material, Appendix 5, Table S3). At the relocation scale, ducks selected resource units proximate to general wetland habitat ($\hat{\beta}_{Wetprx} = 1.45$; 95 % Credible Interval = 1.05–1.91) as well as landscapes with high wetland area ($\hat{\beta}_{WetAr} = 0.46$; 95 % Credible Interval = 0.15–0.75). Thus, a reduced, generalized model was the top model at the relocation scale whereas the full model was universally the top model at the local scale.

Resource units proximate to emergent wetlands and open water were consistently selected across all three seasons at the local scale (Fig. 2). In contrast, selection for resource units proximate to woody wetlands varied across seasons, with high levels in the spring and low values in autumn (Fig. 2). Although NLCD 2006 included shrub/scrub and mature bottomland hardwood wetlands within the woody wetlands classification, our results indicate increased selection of woody wetlands during spring migration compared to autumn migration and winter. In addition, results indicated seasonal variation in selection patterns for resource units proximate to cropland, with greatest values observed in the winter and lowest values observed in autumn.

## Discussion

One of the primary goals of ecology is to elucidate the effects of spatially heterogeneous environments on movement, dispersal, reproduction, and survival of wildlife populations in dynamic landscapes (Wu and Hobbs 2002; Turner 2005; Wu 2013). In addition, emerging trends in ecology have advocated for a behavioral link to spatial scaling (Lima and Zollner 1996; Schick et al. 2008). Waterbirds are ideal for examining the effects of landscape mosaics and spatial scales on habitat selection patterns due to their dynamic annual cycle and ability to thoroughly survey the landscape. Consequently, we investigated the effects of landscape composition on habitat selection of midcontinent mallards across the non-breeding

period using NLCD 2006 at two spatial scales defined by behavioral state. Mallard habitat selection after long-distance relocation scale flights focused on the limiting habitat (wetlands) at the continental scale during the non-breeding period rather than on cultivated crops, which are ubiquitous in the midcontinent region. In contrast, habitat selection after flights between roosting and foraging areas at the local scale focused on habitat diversity at intermediate spatial scales (Davis and Afton 2010; Webb et al. 2010). We demonstrated that wetland landscape composition influenced mallard habitat selection at both spatial scales, although local variables were more important predictors of habitat selection than landscape factors.

Many waterbird species shift diets from seeds and grains in the autumn and early winter to natural wetland food resources in the late winter and spring (Fredrickson and Heitmeyer 1988; Arzel et al. 2006; Tidwell et al. 2013). Natural foods within forested wetlands decompose at decreased rates compared to flooded cultivated crops, and forested wetlands contain persistent invertebrate communities through late winter (Fredrickson and Heitmeyer 1988; Greer et al. 2009; Foster et al. 2010). We observed an increase in woody wetland selection during winter and spring migration compared to autumn migration, which may be associated with increased invertebrate and protein intake by females to prepare for breeding (Heitmeyer 2006; Tidwell et al. 2013). In addition, woody wetlands also provide suitable cover for increased pairing activities that occur during late winter and spring migration (LaGrange and Dinsmore 1989; Reid et al. 1989; Arzel et al. 2006).

Emergent herbaceous wetlands provide important foraging and resting areas for waterbirds due to the abundance of natural foods and vegetative cover (Stafford et al. 2007; Pearse et al. 2011, 2012). In addition, open and deep-water areas provide essential resources throughout the non-breeding portion of the life cycle for many waterbird species. For example, open water habitats are used as foraging areas when shallow wetlands dry or freeze and large impoundments provide areas for birds to roost, preen, and court while minimizing the risk of predation from terrestrial predators (Reid et al. 1989; Heitmeyer 2006). Indeed, we found proximity to open water and emergent wetland were important predictors of mallard habitat selection across all three seasons. However, some waterbird species are diet generalists capable of exploiting anthropogenic foods, and, as a result, flooded crops have also been advocated as a vital resource for migrating and wintering dabbling ducks (Reid et al. 1989; Reinecke et al. 1989; Pearse et al. 2012). In our study, cultivated crops were important predictors of habitat selection after foraging flights at the local scale in the winter, but were not important variables during autumn or spring migration.

Wetland landscapes represent an essential component of staging, stopover, and wintering areas for migratory waterbirds (Reinecke et al. 1989; Webb et al. 2010; Pearse et al. 2012; this study). Sites with greater wetland area are more likely to include diverse wetland habitats that facilitate the acquisition of nutrients according to the needs of a dynamic annual cycle (LaGrange and Dinsmore 1989). Indeed, wetland landscapes allow birds to shift foraging patterns and/or diets in response to environmental conditions, life history requirements, or disturbance (Heitmeyer 2006; Tidwell et al. 2013). In addition, conservation easements and sites with limited anthropogenic disturbance such as waterfowl sanctuaries, may influence waterbird space use within a wetland landscape during the non-breeding season (Beatty et al. in review). As a result, wetland landscapes allow migratory birds to exploit multiple wetland habitats to meet the needs of annual cycle events while minimizing energetically costly flights among foraging, roosting, and resting areas (Farmer and Parent 1997; Taft and Haig 2006).

Recent trends in ecology have attempted to link animal behavior with landscape structure to synthesize disparate fields in ecology (Lima and Zollner 1996; Schick et al. 2008). One of the central themes of landscape ecology involves identifying the scale of effect, which is defined as the scale at which an ecological response is best predicted by landscape structure (Ethier and Fahrig 2011; Jackson and Fahrig 2012). In behavioral ecology, models that predict within-patch foraging movements have not successfully 'scaled-up' to between-patch movement processes within heterogeneous landscapes, indicating additional models are needed to elucidate patterns at broader spatial scales (Morales and Ellner 2002). Thus, the scale of effect should not only consider the focal species but individual behavioral mode and local landscape structure (Ethier and Fahrig 2011; Jackson and Fahrig 2012; Albanese et al. 2012). For example, foraging flight distances in waterbirds are dependent upon the distribution of food and roosting habitat at intermediate spatial scales, and, as

a result, foraging flight distances are often the product of local landscape structure (Farmer and Parent 1997; Pearse et al. 2011). In contrast, migratory flight distance and stopover site selection are the result of a complex interaction of climate, weather, body condition, molt status, and landscape structure (Arzel et al. 2006; Albanese et al. 2012). In this study, we demonstrated that individuals responded to different habitat cues at different spatial scales linked to behavioral state. Birds engaged in daily foraging flights at the local scale focused on the distribution of specific wetland types. In contrast, landscapes with abundant wetland habitat provided an initial cue to migrating individuals at the relocation scale. Thus, our results provide further evidence that wetland landscapes deserve consideration as a functional unit of waterbird management and conservation (Taft and Haig 2006; Albanese et al. 2012).

## References

Albanese G, Davis CA, Compton BW (2012) Spatiotemporal scaling of North American continental interior wetlands: implications for shorebird conservation. Landsc Ecol 27:1465–1479

Arzel C, Elmberg J, Guillemain M (2006) Ecology of spring-migrating Anatidae: a review. J Ornithol 147:167–184

Beatty WS, Kesler DC, Webb EB, Raedeke AH, Naylor LW, Humburg DD (2013) Quantitative and qualitative approaches to identifying migration chronology in a continental migrant. PLoS ONE 8:e75673

Beatty WS, Kesler DC, Webb EB, Raedeke AH, Naylor LW, Humburg DD (in review) The role of protected area wetlands in waterfowl habitat conservation: implications for protected area network design

Beyer HL (2012) Geospatial Modelling Environment (Version 0.7.2.0) (Software). Available at http://www.spatialecology.com/gme

Bock CE, Jones ZF (2004) Avian habitat evaluation: should counting birds count? Front Ecol Environ 2:403–410

Bonnot TW, Wildhaber ML, Millspaugh JJ, DeLonay AJ, Jacobson RB, Bryan JL (2011) Discrete choice modeling of shovelnose sturgeon habitat selection in the lower Missouri River. J Appl Ichthyol 27:291–300

Boyce MS (2006) Scale for resource selection functions. Divers Distrib 12:269–276

Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. J Comput Graph Stat 7:434–455

Conner LM, Smith MD, Burger LW (2003) A comparison of distance-based and classification-based analyses of habitat use. Ecology 84:526–531

Cooper AB, Millspaugh JJ (1999) The application of discrete choice models to wildlife resource selection studies. Ecology 80:566–575

Cornell KL, Donovan TM (2010) Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird. Landscape Ecol 25:109–122

Davis BE, Afton AD (2010) Movement distances and habitat switching by female mallards wintering in the lower Mississippi Alluvial Valley. Waterbirds 33:349–356

Devries JH, Brook RW, Howerter DW, Anderson MG (2008) Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618–628

Dinges AJ (2013) Participation in the Light Goose Conservation Order and effects on behavior and distribution of waterfowl in the Rainwater Basin of Nebraska. MS Thesis, University of Missouri-Columbia

Dooley JL, Sanders TA, Doherty PF Jr (2010) Mallard response to experimental walk-in and shooting disturbance. J Wildl Manag 74:1815–1824

Drilling N, Titman R, McKinney F (2002) Mallard (*Anas platyrhychos*). In: Pool A, Gill F (eds) Birds North America. Academy of Natural Sciences; American Ornithologists' Union, Philadelphia

Dwyer TJ, Krapu GL, Janke DM (1979) Use of prairie pothole habitat by breeding mallards. J Wildl Manag 43:526–531

Ethier K, Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. Landscape Ecol 26:865–876

Farmer AH, Parent AH (1997) Effects of the landscape on shorebird movements at spring migration stopovers. Condor 99:698–707

Foster MA, Gray MJ, Harper CA, Walls JG (2010) Comparison of agricultural seed loss in flooded and unflooded fields on the Tennessee National Wildlife Refuge. J Fish Wildl Manag 1:43–46

Fredrickson LH, Heitmeyer ME (1988) Waterfowl use of forested wetlands of the southern United States: an overview. In: Weller MW (ed) Waterfowl in winter. University of Minnesota Press, Minneapolis, pp 307–323

Fry JA, Xian G, Jin S, Dewitz JA, Homer CG, Yang L, Barnes CA, Herold ND, Wickham JD (2011) Completion of the 2006 national land cover database for the conterminous United States. Photogramm Eng Remote Sensing 77:858–864

Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York

Greer DM, Dugger BD, Reinecke KJ, Petrie MJ (2009) Depletion of rice as food of waterfowl wintering in the Mississippi Alluvial Valley. J Wildl Manag 73:1125–1133

Heitmeyer ME (2006) The importance of winter floods to mallards in the Mississippi Alluvial Valley. J Wildl Manag 70:101–110

Herfindal I, Drever MC, Høgda K-A, Podruzny KM, Nudds TD, Grøtan V, Sæther B-E (2012) Landscape heterogeneity and the effect of environmental conditions on prairie wetlands. Landscape Ecol 27:1435–1450

Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? Landscape Ecol 27:929–941

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Johnson MD (2007) Measuring habitat quality: a review. Condor 109:489–504

Kesler DC, Raedeke AH, Foggia J, Beatty WS, Webb EB, Humburg DD, Naylor LW (2014) Effects of satellite transmitters on captive and wild mallards. Wildl Soc Bul 38

LaGrange TG, Dinsmore JJ (1989) Habitat use by mallards during spring migration through central Iowa. J Wildl Manag 53:1076–1081

Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. Trends Ecol Evol 11:131–135

Link PT, Afton AD, Cox RR Jr, Davis BE (2011) Daily movements of female mallards wintering in southwestern Louisiana. Waterbirds 34:422–428

Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Stat Comput 10:325–337

Malecki RA, Batt BDJ, Sheaffer SE (2001) Spatial and temporal distribution of Atlantic population Canada geese. J Wildl Manag 65:242–247

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals, 2nd edn. Kluwer Academic Publishers, The Netherlands

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886

McDonald LL, Erickson WP, Boyce MS, Alldredge JR (2012) Modeling vertebrate use of terrestrial resources. In: Silvy NJ (ed) The wildlife techniques manual: research, 7th edn. The Johns Hopkins University Press, Baltimore, pp 410–428

McFadden D (1978) Modeling the choice of residential location. In: Karlqvist A, Lundqvist L, Snickars F, Weibull J (eds) Spatial interaction theory and planning models. North Holland Publishing Company, Amsterdam, pp 75–96

McGarigal K, Cushman SA, Ene E (2012) FragStats (Version 4.1) (software). Available from http://www.umass.edu/landeco/research/fragstats/fragstats.html

Miller MR, Takekawa JY, Fleskes JP, Orthmeyer DL, Casazza ML, Perry WM (2005) Spring migration of northern pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. Can J Zool 83:1314–1332

Morales JM, Ellner SP (2002) Scaling up animal movements in heterogeneous landscapes: the importance of movement behavior. Ecology 83:2240–2247

Naugle DE, Higgins KF, Nusser SM, Johnson WC (1999) Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecol 14:267–276

Pardoe I, Simonton DK (2008) Applying discrete choice models to predict Academy Award winners. J R Stat Soc Ser A 171:375–394

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models of individual animal movement. Trends Ecol Evol 23:87–94

Pearse AT, Krapu GL, Cox RR Jr, Davis BE (2011) Spring-migration ecology of northern pintails in south-central Nebraska. Waterbirds 34:10–18

Pearse AT, Kaminski RM, Reinecke KJ, Dinsmore SJ (2012) Local and landscape associations between wintering dabbling ducks and wetland complexes in Mississippi. Wetlands 32:859–869

R Development Core Team (2013). R: a language and environment for statistical computing (software). R Foundation for Statistical Computing, Vienna. Available at http://www.R-project.org

Reid FA, Kelley JR Jr, Taylor TS, Fredrickson LH (1989) Upper Mississippi Valley wetlands—refuges and moist-soil impoundments. In: Smith LM, Pederson RL, Kaminski RM (eds) Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, pp 181–202

Reinecke KJ, Kaminski RM, Moorhead DJ, Hodges JD, Nassar JR (1989) Mississippi alluvial valley. In: Smith LM, Pederson RL, Kaminski RM (eds) Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, pp 203–247

Riffell SK, Keas BE, Burton TM (2003) Birds in North American Great Lakes coastal wet meadows: is landscape context important? Landscape Ecol 18:95–111

Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, Conde DA, Halpin PN, Joppa LN, McClellan CM, Clark JS (2008) Understanding movement data and movement processes: current and emerging directions. Ecol Lett 11:1338–1350

Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit. J R Stat Soc Ser B 64:583–639

Stafford JD, Horath MM, Yetter AP, Hine CS, Havera SP (2007) Wetland use by mallards during spring and fall in the Illinois and central Mississippi River valleys. Waterbirds 30:394–402

Straub JN, Gates RJ, Schultheis RD, Yerkes T, Coluccy J, Stafford JD (2012) Wetland food resources for spring-migrating ducks in the Upper Mississippi River and Great Lakes Region. J Wildl Manag 76:768–777

Sturtz S, Ligges U, Gelman A (2005) R2WinBUGS: a package for running WinBUGS from R. J Stat Softw 12:1–16

Taft OW, Haig SM (2006) Importance of wetland landscape structure to shorebirds wintering in an agricultural valley. Landscape Ecol 21:169–184

Thomas DL, Johnson D, Griffith B (2006) A Bayesian random effects discrete-choice model for resource selection: population-level selection inference. J Wildl Manag 70:404–412

Tidwell PR, Webb EB, Vrtiska MP, Bishop AA (2013) Diets and food selection of female mallards and blue-winged teal during spring migration. J Fish Wildl Manag 4:63–74

Turner M (2005) Landscape ecology: what is the state of the science? Annu Rev Ecol Evol Syst 36:319–344

Van Horne B (1983) Density as a misleading indicator of habitat quality. J Wildl Manag 47:893–901

Webb EB, Smith LM, Vrtiska MP, LaGrange TG (2010) Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. J Wildl Manag 74:109–119

Webb EB, Smith LM, Vrtiska MP, Lagrange TG (2011) Factors influencing behavior of wetland birds in the Rainwater Basin during spring migration. Waterbirds 34:457–467

Webster MS, Peter PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17:76–83

Weller MW (1988) Issues and approaches in assessing cumulative impacts on waterbird habitat in wetlands. Environ Manag 12:695–701

Wickham JD, Stehman SV, Gass L, Dewitz J, Fry JA, Wade TG (2013) Accuracy assessment of NLCD 2006 land cover and impervious surface. Remote Sens Environ 130:294–304

Wu J (2013) Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. Landscape Ecol 28:1–11

Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecol 4:355–365