



The role of protected area wetlands in waterfowl habitat conservation: Implications for protected area network design



William S. Beatty ^{a,*}, Dylan C. Kesler ^a, Elisabeth B. Webb ^b, Andrew H. Raedeke ^c, Luke W. Naylor ^d, Dale D. Humburg ^e

^a Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA

^b U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA

^c Missouri Department of Conservation, 3500 East Gans Road, Columbia, MO 65201, USA

^d Arkansas Game and Fish Commission, 2 Natural Resources Drive, Little Rock, AR 72205, USA

^e Ducks Unlimited, 1 Waterfowl Way, Memphis, TN 38120, USA

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ABSTRACT

The principal goal of protected area networks is biodiversity preservation, but efficacy of such networks is directly linked to animal movement within and outside area boundaries. We examined wetland selection patterns of mallards (*Anas platyrhynchos*) during non-breeding periods from 2010 to 2012 to evaluate the utility of protected areas to migratory waterfowl in North America. We tracked 33 adult females using global positioning system (GPS) satellite transmitters and implemented a use-availability resource selection design to examine mallard use of wetlands under varying degrees of protection. Specifically, we examined effects of proximities to National Wildlife Refuges, private land, state wildlife management areas, Wetland Reserve Program easements (WRP), and waterfowl sanctuaries on mallard wetland selection. In addition, we included landscape-level variables that measured areas of sanctuary and WRP within the surrounding landscape of each used and available wetland. We developed 8 wetland selection models according to season (autumn migration, winter, spring migration), hunting season (present, absent), and time period (diurnal, nocturnal). Model averaged parameter estimates indicated wetland selection patterns varied across seasons and time periods, but ducks consistently selected wetlands with greater areas of sanctuary and WRP in the surrounding landscape. Consequently, WRP has the potential to supplement protected area networks in the midcontinent region. Additionally, seasonal variation in wetland selection patterns indicated considering the effects of habitat management and anthropogenic disturbances on migratory waterfowl during the non-breeding period is essential in designing protected area networks.

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1. Introduction

Conservation practitioners use protected areas as primary and effective tools to preserve biodiversity, and a diverse array of ecosystem types is included in the global protected area network (Rodrigues et al., 2004; Scott et al., 2001). However, global, regional, and local environmental drivers such as climate change, land use change, and anthropogenic disturbance have the potential to drastically alter surrounding landscapes (Faleiro et al., 2013; Groom et al., 2006; Hannah et al., 2007; Mantyka-Pringle et al., 2012). As a result, the effectiveness of protected areas can be

limited if sites are isolated and/or if the surrounding landscape is not considered in area design (Margules and Pressey, 2000; Newmark, 1996).

To mitigate effects of protected area isolation, conservationists develop networks of protected areas that collectively account for landscape composition, structure, and function to spatially distribute risk and address life history needs of highly mobile organisms (Margules and Pressey, 2000). Protected areas and protected area networks also often encompass properties owned by multiple conservation groups with disparate goals. Consequently, many protected area networks balance biodiversity preservation with other working economic uses. For example, conservation planners may have to address conflicts among publicly owned protected areas and other conservation areas managed by private individuals or organizations (Hannah, 2010; Knight, 1999; Rissman et al., 2007).

* Corresponding author. Tel.: +1 573 884 5245; fax: +1 573 884 5070.

E-mail addresses: w_beatty@hotmail.com (W.S. Beatty), keslerd@missouri.edu (D.C. Kesler), webbli@missouri.edu (E.B. Webb), Andrew.Raedeke@mdc.mo.gov (A.H. Raedeke), lwnaylor@agfc.state.ar.us (L.W. Naylor), dhumburg@ducks.org (D.D. Humburg).

In mid-continent North America, protected wetlands provide an excellent example of a functional protected area network. Wetlands provide a variety of cultural, economic, and ecological benefits, including flood control, pollution mitigation, recreation opportunities, and wildlife habitat (Costanza et al., 1997; Zedler and Kercher, 2005). However, wetlands have declined in the contiguous United States by approximately 53% since European settlement, and wetlands currently exist within a fragmented patchwork landscape, often with reduced capacities to provide vital ecosystem services (Dahl, 2011; Mitsch and Gosselink, 2007; Zedler and Kercher, 2005). To mitigate effects of wetland loss and degradation, federal and state agencies in the United States have opportunistically acquired and protected wetlands through various conservation initiatives (Curtin, 1993; Scott et al., 2004). The U.S. Fish and Wildlife National Wildlife Refuge (NWR) System and state wildlife management areas (WMA) were among the first functional protected area networks in the world, establishing protected areas beginning in 1903, although these areas are often managed independently of one another (Curtin, 1993).

In recent years, public conservation agencies and non-governmental organizations (NGOs) have emphasized the importance of incorporating private and working lands into wetland protected area networks in the midcontinent region (King et al., 2006; Knight, 1999; North American Waterfowl Management Plan Committee, 2012). Conservation easement programs are one mechanism used by conservation planners to preserve biodiversity on privately owned lands (King et al., 2006; Schoenholtz et al., 2001). The largest public conservation easement program specifically targeted to conserving wetland habitat for wildlife is the Natural Resources Conservation Service Wetlands Reserve Program (WRP), which was first authorized in the Food, Agriculture, Conservation, and Trade Act of 1990 (i.e. Farm Bill) (United States Congress, 1990). Along with other conservation easements held by land trusts (e.g. Wetlands America Trust), WRP has significantly contributed to wetland habitat and conservation goals throughout North America (Kaminski et al., 2006; King et al., 2006; Schoenholtz et al., 2001). However, WRP and other conservation easement programs may provide limited benefits to wildlife due to minimal management and/or anthropogenic activities.

Waterfowl populations are among the fauna that may benefit from the network of protected wetlands in North America. In the midcontinent region, waterfowl hunting is a prominent and traditional recreational activity, and as such, protected wetlands have been managed by numerous conservation entities with a broad range of interests (Jenkins et al., 2010). However, the relative role of various types of protected areas in migratory waterfowl conservation remains unclear (Olmstead et al., 2013; Rissman et al., 2007; Waddle et al., 2013). Although recent research has evaluated waterfowl abundance on private conservation easements and WMAs, abundance studies often do not account for wetland availability (Evans-Peters et al., 2012; Kaminski et al., 2006; Lancaster, 2013; Olmstead et al., 2013; Tapp, 2013). Research on wetland selection accounts for wetland availability and assumes that waterfowl are choosing from a suite of wetlands within a defined area (McDonald et al., 2012). Relatively few studies have compared waterfowl wetland selection patterns among private conservation easements, federally managed wetlands, state managed wetlands, or wetlands on working lands. Thus, our objective was to examine the utility of protected area wetlands to migratory waterfowl during the non-breeding period within the framework of a use-availability resource selection design. To meet this objective, we tracked adult female mallards (*Anas platyrhynchos*) using global positioning system (GPS) satellite transmitters and developed multinomial discrete choice models that accounted for variance in wetland type. We used the mallard because it is a generalist waterfowl species that is the focus of extensive wetland protection,

restoration, and management throughout North America (Drilling et al., 2002; Johnson et al., 1997). Under the Federal Water Pollution Control Act of 1972 (33 USC 1251), many wetlands on private land have some measure of jurisdictional protection in the United States. However, we did not consider wetlands on private land (except those enrolled in conservation easement programs) to be within the protected area network because these wetlands have greater potential to be influenced by changing land use trends, variation in regulation and enforcement measures, and fluctuating economic conditions (Dahl, 2011).

2. Materials and methods

2.1. Capture and GPS telemetry

Adult female mallards (after hatch year) were captured in two separate groups in 2010 and 2011 (Beatty et al., 2013). The first group was captured near Yorkton, Saskatchewan, Canada (51°13'N 102°28'E) in late September 2010 whereas the second group was captured at multiple locations in Arkansas, USA in February 2011 under federal banding permit 06569 (Five 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) (Beatty et al., 2013). Reasonable efforts were made by Arkansas Game and Fish Commission and Ducks Unlimited Canada field personnel to minimize animal stress, and capture and handling procedures were initially described in Beatty et al. (2013). Briefly, we captured adult female mallards with rocket nets or swim-in traps and fit captured birds with a Teflon-ribbon harness equipped with a solar-powered global positioning system (GPS) satellite transmitter (Argos/GPS PTT 100, Microwave Telemetry, Inc., Columbia, Maryland, USA; ±18 m accuracy) programmed to obtain four GPS fixes (i.e. locations) per day. We attached transmitters with a harness design based on Malecki et al. (2001). For all birds captured in Arkansas, combined transmitter and harness accounted for <4% of body mass, and <3% of body mass in 18 of 20 individuals. Marked birds were monitored until transmitters failed or were immobile for at least one day (Beatty et al., 2013). Because waterfowl spend relatively small proportions of time in flight, we assumed all GPS locations were obtained when birds were on the ground (Pearse et al., 2011).

2.2. Delineating seasons and spatial scale

Public wildlife management areas, private lands, and conservation easements spatially and temporally vary in habitat condition (i.e. flooding) and food availability (De Steven and Gramling, 2012; Evans-Peters et al., 2012; Olmstead et al., 2013). In addition, mallard wetland use may differ across the non-breeding period in accordance with nutritional and energetic requirements of annual cycle events (Drilling et al., 2002). We separated the non-breeding portion of the annual cycle into three seasons (autumn migration, winter, spring migration) according to methods outlined in Beatty et al. (2013). Briefly, we modeled an empirical movement metric (net displacement) using single and double sigmoid functions to estimate timing of autumn and spring migrations for individual birds (Beatty et al., 2013). A subset of ducks ($n = 14$) did not have sufficient data to be included in migration models; therefore we used mean migration dates according to year to delineate seasons for those individuals (Beatty et al., 2013, 2014).

Resource selection patterns may vary due to differences in the distribution of resources across spatial scales (Johnson, 1980; McDonald et al., 2012). To specifically identify a behaviorally relevant spatial scale for wetland selection, we examined movement patterns from individual birds throughout the non-breeding

portion of the annual cycle (autumn migration, winter, spring migration). Details on delineating spatial scales have been discussed previously (Beatty et al., 2014), but in short, we calculated the natural log of distance moved (km) for each interval between GPS fixes to generate a smoothed distribution of movement distances. We identified two approximate breaks in the smoothed distribution and assigned each GPS fix (n) to one of three spatial scales based on distance moved from the previous fix ($n-1$). First, movements <0.25 km were considered within wetland movements and excluded from analyses. Second, local movements that ranged from 0.25 to 30.00 km were considered flights in response to the distribution of resources among wetlands. Finally, movements >30.00 km were interpreted to be relocation movements in response to the distribution of resources among wetland complexes and were also excluded from analyses. We excluded relocation movements (>30.00 km) from wetland selection analyses because previous research has demonstrated that dabbling ducks respond to disturbance, sanctuary, and wetland management at relatively intermediate spatial scales (Cox and Afton, 1997; Dooley et al., 2010; Stafford et al., 2007). Thus, wetland selection analyses were restricted to movements at the local scale (movements 0.25–30.00 km). Further, although we used the smoothed empirical distribution of movement distances to define spatial scales, our values correspond to previous research on waterfowl movements during the non-breeding period (Davis and Afton, 2010; Link et al., 2011; Pearse et al., 2011; Yetter et al., 2011).

2.3. Wetland availability

We used discrete choice models to examine mallard wetland selection (Cooper and Millspaugh, 1999). Discrete choice models assume that resource use is the result of a series of choices made by an individual from a matched set of available alternatives, which is defined as the choice set (Cooper and Millspaugh, 1999; Manly et al., 2002). As a result, discrete choice models allow available alternatives to vary across used resource units in accordance with spatial and temporal variation in resource availability (Bonnot et al., 2011; Cooper and Millspaugh, 1999; Manly et al., 2002).

In discrete choice models, we designated wetlands as the unit of selection; thus, choice sets included one used wetland matched to a suite of available wetlands. A used wetland was defined as a wetland that contained a mallard GPS fix during the non-breeding period (autumn migration, winter, spring migration) at the local scale. In contrast, we defined availability based on a circular buffer with a 30.00 km radius from the centroid of the used wetland in ArcGIS 10.0 (ESRI, Redlands, California, USA). We randomly selected 19 wetlands without replacement from within the 30.00 km buffer to produce a choice set of 20 wetlands, which included 19 available wetlands and 1 used wetland. Although McFadden (1978) demonstrated that as few as 5 alternatives are required to obtain consistent parameter estimates in multinomial discrete choice models, we used 19 alternatives to account for increased variance in wetland characteristics at the 30.00 km scale. We used a 30.00 km buffer to correspond to previous research on midcontinent mallard habitat selection and to reflect the distance a duck may fly on a local flight (Davis and Afton, 2010; Link et al., 2011; Pearse et al., 2011; Beatty et al., 2014). We then measured a series of covariates for each used and available wetland (see below). We obtained geospatial information on wetlands from the 2006 National Land Cover Database (NLCD 2006), which seamlessly classifies wetlands at 30-m resolution across the United States based on images captured between 2005 and 2007 (Fry et al., 2011). Overall accuracy assessment for NLCD 2006 was 78% (Wickham et al., 2013).

Although flooded cultivated crops provide an important food resource for mallards during the non-breeding period, mallards

also commonly feed in upland cultivated crop fields (Bellrose, 1980; LaGrange and Dinsmore, 1989; Pearse et al., 2012). Because we were specifically interested in wetland selection patterns and designated the wetland as the unit of selection, mallard GPS fixes that intersected non-wetland habitats (e.g. cultivated crops) according to NLCD 2006 were excluded from discrete choice models. Consequently, we examined mallard wetland selection with the most conservative classification of wetland use possible provided available geospatial data.

2.4. Wetland covariates

We characterized each used and available wetland with a series of wetland covariates calculated from numerous geospatial data sources (Online Supplementary Material, Appendix A, Table A1). NLCD 2006 classified wetlands into one of three categories (Fry et al., 2011). First, emergent herbaceous wetlands were periodically flooded areas with >80% herbaceous vegetation. Second, open water wetlands were classified as permanently flooded habitats with <25% herbaceous vegetative cover. Finally, periodically flooded areas that contained >20% coverage of trees or woody shrubs were considered woody wetlands (Fry et al., 2011). To account for variation in selection patterns among wetlands due to wetland type, we included indicator variables for emergent wetland (EMG) and woody wetland (WDY) with open water denoted as the reference category (Beatty et al., 2014). Thus, we defined wetlands as contiguous groups of wetland pixels (1 pixel = 30 × 30 m) according to NLCD 2006 and/or as WRP easements. We specifically assumed all WRP easements were inundated to overestimate WRP availability and obtain a conservative estimate of the utility of WRP easements to migratory waterfowl (Beyer et al., 2010).

We measured a series of proximity-to covariates in ArcGIS 10.0 to characterize the spatial characteristics of each wetland and its management and conservation status. We intentionally characterized wetlands with proximity-to variables because they are less sensitive to error in animal locations and geospatial covariate data than indicator variables (Conner et al., 2003). From the centroid of each wetland, we measured the proximity to the boundary of the nearest WMA (WmaPx), NWR (NwrPx), waterfowl sanctuary (SancPx), WRP easement (WrpxPx), and private land parcel (PrvPx). We defined WMAs, NWRS, sanctuaries, WRP easements, and private lands based on cadastral boundaries. Thus, proximity-to covariates equaled 0 if a wetland centroid was in the specific property boundary and were negative (km) if the wetland centroid was outside the specific property boundary. We defined sanctuary as any area that prohibited waterfowl hunting throughout duck hunting season, although all sanctuaries in our study occurred on public lands because geospatial data on private sanctuaries were not available for the midcontinent region. Thus, wetlands that exhibited SancPx values of 0 occasionally either had an NwrPx value of 0 or a WmaPx value of 0. In addition, numerous waterfowl sanctuaries occurred on public lands other than NWRS and WMAs (e.g. Army Corps of Engineers sites). We did not consider waterfowl production areas in our analysis because these areas are heavily concentrated within the breeding range of mallards (i.e. prairie pothole region). We also did not consider lands managed by the Army Corps of Engineers because these areas primarily focused on flood protection and reliable geospatial data were not available.

We combined sanctuaries on NWRS and WMAs into one variable (SancPx) because management objectives on state and federal sanctuaries were similar (i.e. provide resting areas free of anthropogenic disturbance to waterfowl). In contrast, we differentiated between WMAs and NWRS because overall patterns of anthropogenic use differ between these two types of areas. For example, in our study area, approximately 69% of NWRS contained at least

one waterfowl sanctuary compared to 8% of WMAs, and approximately 41% of NWRs were entirely closed to waterfowl hunting compared to 2% of WMAs. Similarly, approximately 52% of total NWR area in our study area was in sanctuary compared to approximately 11% of total WMA area (W. Beatty, unpublished data).

Landscape composition also has the potential to affect mallard wetland use during the non-breeding portion of the annual cycle (Cox and Afton, 1997; Webb et al., 2010; Beatty et al., 2014). To evaluate the importance of sanctuaries at the landscape scale, we included a covariate that quantified sanctuary area (SancAr) within a 3.46 km buffer around the centroid of each used and available wetland. In addition, we also measured WRP area (WrPAr) within a 3.46 km buffer around each used and available wetland. We used a 3.46 km buffer to correspond to previously published estimates on the average local flight distance for mallards (Beatty et al., 2014). All wetland covariates with the exception of EMG and WDY were centered and standardized with two standard deviations to facilitate interpretation of parameter coefficients (Gelman, 2008). We examined variance inflation factors (VIFs) for all model coefficients from a regression (proc reg, SAS) to test for collinearity among our wetland covariates (Kutner et al., 2005). We did not detect substantial collinearity in our wetland covariates as VIFs for all wetland covariates were <2.5 (Allison, 1999).

2.5. Statistical analysis

Waterfowl habitat use may vary between diurnal and nocturnal periods or as a result of hunting disturbance (Bregnballe et al., 2004; Dooley et al., 2010). We accounted for both spatial and temporal variability in duck hunting seasons using geospatial information on hunting zones and season dates from 2010 to 2011 and 2011 to 2012 (Online Supplementary Material, Appendix A). However, all GPS fixes recorded during autumn migration occurred during duck hunting season whereas all fixes recorded during spring migration occurred outside duck hunting season. Thus, for autumn and spring migrations, we analyzed data separately between diurnal and nocturnal time periods (2 time periods × 2 seasons = 4 models). In contrast, winter GPS fixes were recorded both within hunting season and after hunting season. Thus, we analyzed wetland selection patterns separately according to hunting season and time period (i.e. diurnal or nocturnal) during winter (2 time periods × 2 hunt seasons = 4 winter models). Consequently, we developed 8 different statistical models to predict wetland selection according to season (autumn migration, winter, spring migration), hunting season (present, absent), and time period (nocturnal, diurnal) using the mlogit package (Croissant, 2013) in R (R Core Team, 2013).

We used a modified all subsets approach to model selection where all candidate models contained EMG and WDY with random slopes that varied according to individual duck. We included these two indicator variables in all candidate models because previous research demonstrated that wetland type influenced mallard habitat selection (Beatty et al., 2014). As a result, we considered the null model to be the model that contained EMG and WDY with random slopes that varied according to individual. Based on this null model, we then used an all subsets approach to generate 128 candidate models for each season, time period, and hunt season combination based on 7 variables. We ranked candidate models according to Akaike's information criterion adjusted for sample size (AIC_c) and retained models with ΔAIC_c values less than or equal to 4.0 as our top model set. We conducted natural model averaging over top models ($\leq 4 \Delta AIC_c$) for each season, hunt season, and time period combination and calculated unconditional standard errors for model averaged parameters (Buckland et al., 1997; Burnham and Anderson, 2002). We used $\leq 4 \Delta AIC_c$ to identify top models because this value corresponds to the approximate

95% confidence set for the Kullback–Leibler best model (Burnham and Anderson 2002). We calculated 95% confidence intervals for model averaged parameter estimates by multiplying unconditional standard errors by 1.96. Parameters that had confidence intervals that did not overlap zero were inferred to be important variables in predicting mallard wetland selection during the non-breeding period. Although GPS transmitters collected up to four locations per day, we assumed locations obtained from the same individual were independent because we excluded GPS fixes that did not intersect wetlands and different models were developed for nocturnal and diurnal time periods.

In resource selection studies, availability is defined as resources that are accessible to an individual or population at a given spatial and temporal scale (McDonald et al., 2012). In this study, we assumed geospatial data accurately represented inundated semi-permanent and permanent wetlands. In contrast, ephemeral and seasonal wetland resolution was likely limited because NLCD 2006 classifications were based on a single date of imagery (Fry et al., 2011). Nevertheless, the capacity of NLCD 2006 to capture semi-permanent and permanent temporal inundation patterns was limited (Wickham et al., 2013). In addition, we likely overestimated WRP wetland availability because we assumed all WRP easements were flooded. WRP easements are less likely than public areas to contain infrastructure to manipulate hydrology, thereby rendering WRP easements more susceptible to natural hydrological fluctuations than public areas. In contrast, public sites (NWRs, WMAs) often contain operational water control structures, which allow area managers to minimize temporal variation in wetland hydrological condition.

3. Results

3.1. Capture and GPS telemetry

We outfitted a total of 40 adult female mallards with GPS satellite transmitters over the course of the study. Seven transmitters failed before initiation of autumn migration in 2010 so our sample was reduced to 33 birds (Beatty et al., 2013, 2014). The number of individuals included in each wetland selection model varied according to season, hunting season, and time period (Table 1).

3.2. Wetland selection

Wetland selection in midcontinent mallards during autumn migration within hunting season resulted in 14 competing models for diurnal selection and 8 competing models for nocturnal selection (Table 2). During autumn migration, mallards selected wetlands near WRP easements at night but not during the day although confidence intervals substantially overlapped between time periods (Fig. 1). Additionally, mallards selected wetlands that had greater area of sanctuary and WRP in the surrounding landscape. Confidence intervals for all other parameters evaluated for autumn migration overlapped zero.

In winter within hunting season, model selection identified 6 competing models for both diurnal and nocturnal wetland selection (Table 3). Mallards selected wetlands proximate to sanctuaries at similar levels during both day and night within hunting season (Fig. 2a). Wetlands proximate to WRP were selected at night but not during the day whereas wetlands proximate to WMAs were selected during the day but not at night. Sanctuary area and WRP area were again positive indicators of mallard wetland selection. Proximity to private land was a negative indicator of wetland selection during the day in winter within hunting season, although confidence intervals between diurnal and nocturnal models

Table 1

Sample size statistics for models to examine midcontinent mallard wetland selection patterns during the non-breeding period of the annual cycle. The number of birds (A), total number of global positioning system fixes (n), and range of the number of fixes per individual (Range) are displayed for each model.

Season	Hunt Season	Diurnal/Nocturnal	A	n	Range
Autumn migration	Yes	Diurnal	18	151	1–44
		Nocturnal	18	118	1–36
Winter	Yes	Diurnal	16	234	1–34
		Nocturnal	16	252	2–45
	No	Diurnal	21	367	2–63
		Nocturnal	22	358	1–76
Spring Migration	No	Diurnal	23	380	3–69
		Nocturnal	23	522	1–64

Table 2

Model selection results for multinomial discrete choice models that examined wetland selection for mid-continent mallards (*Anas platyrhynchos*) from 2010 to 2011 in autumn migration during hunting season. Number of parameters (K), Akaike weights (w_i) and evidence ratios (ER) are displayed along with Akaike's information criterion (AIC_c) and ΔAIC_c .

Diurnal/Nocturnal	Model	K^a	AIC_c	ΔAIC_c	w_i	ER
Diurnal	SancAr + WmaPx + WrpPx + WrpAr	8	767.18	0.00	0.19	–
	SancAr + WmaPx + WrpAr	7	767.61	0.44	0.15	1.24
	SancPx + SancAr + WmaPx + WrpPx + WrpAr	9	768.74	1.56	0.09	2.18
	SancAr + WrpPx + WrpAr	7	769.11	1.93	0.07	2.63
	SancPx + SancAr + WmaPx + WrpAr	8	769.19	2.01	0.07	2.74
	–PrvPx + SancAr + WmaPx + WrpPx + WrpAr	9	769.26	2.08	0.07	2.84
	–NwrPx + SancAr + WmaPx + WrpPx + WrpAr	9	769.43	2.25	0.06	3.08
	–PrvPx + SancAr + WmaPx + WrpAr	8	769.60	2.42	0.06	3.36
	SancAr + WrpAr	6	769.62	2.44	0.06	3.38
	NwrPx + SancAr + WmaPx + WrpAr	8	769.84	2.66	0.05	3.78
	–NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	770.60	3.42	0.03	5.54
	SancPx + SancAr + WrpPx + WrpAr	8	770.68	3.50	0.03	5.76
	–PrvPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	770.74	3.56	0.03	5.92
	–PrvPx + SancPx + SancAr + WmaPx + WrpAr	9	771.07	3.89	0.03	6.98
	–NwrPx + SancAr + WrpPx + WrpAr	8	589.30	0.00	0.30	–
	–NwrPx + SancAr + WmaPx + WrpPx + WrpAr	9	590.03	0.73	0.21	1.44
	–PrvPx – NwrPx + SancAr + WrpPx + WrpAr	9	590.91	1.61	0.13	2.23
Nocturnal	–PrvPx – NwrPx + SancAr + WmaPx + WrpPx + WrpAr	10	591.28	1.97	0.11	2.68
	–NwrPx + SancPx + SancAr + WrpPx + WrpAr	9	591.51	2.21	0.10	3.01
	–NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	592.38	3.07	0.06	4.65
	–NwrPx + SancAr + WmaPx + WrpAr	8	592.84	3.54	0.05	5.87
	–PrvPx – NwrPx + SancPx + SancAr + WrpPx + WrpAr	10	593.18	3.87	0.04	6.94

^a Number of parameters in each model includes random slopes for wetland type (EMG, WDY) with associated standard deviations.

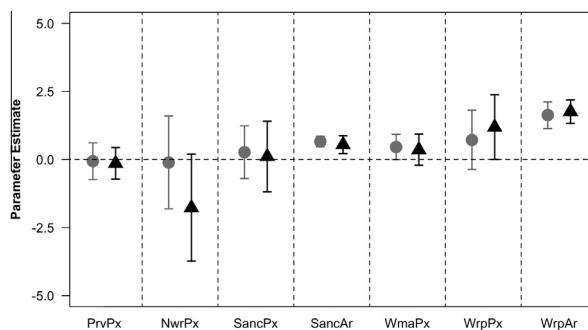


Fig. 1. Model averaged parameter estimates and 95% confidence intervals for discrete choice models that examined mallard wetland selection patterns during autumn migration within hunting season. Gray circles represent diurnal models and black triangles represent nocturnal models. PrvPx is proximity to nearest private land, NwrPx is proximity to nearest National Wildlife Refuge, SancPx is proximity to nearest waterfowl sanctuary, SancAr is waterfowl sanctuary area in surrounding landscape, WmaPx is proximity to nearest state wildlife management area, WrpPx is proximity to nearest Wetland Reserve Program easement, and WrpAr is area of Wetland Reserve Program easements in surrounding landscape.

substantially overlapped. Similar to autumn migration, mallards selected wetlands near NWRs in accordance with random expectations.

Wetland selection patterns during winter after hunting season were substantially different than selection patterns during winter

within hunting season. Model selection to examine wetland use during winter after hunting season produced 2 competing models for diurnal selection and 1 top model for nocturnal selection (Table 4). In winter after hunting season, mallards selected wetlands proximate to sanctuaries, WMAs, and WRP easements, and in contrast to within hunting season, selection patterns for proximity to WMA and WRP were similar between nocturnal and diurnal periods (Fig. 2b). In addition, sanctuary area and WRP area were positive indicators of wetland selection. However, in contrast to wetland selection patterns observed within hunting season (autumn migration and winter), mallards used wetlands proximate to NWRs less than random expectations in winter outside hunting season.

Model selection for wetland use during spring migration produced 4 competing models for diurnal selection and 3 competing models for nocturnal selection (Table 5). During both diurnal and nocturnal periods, mallards selected wetlands proximate to sanctuaries, WMAs, and WRP easements (Fig. 3). Similar to selection patterns observed during autumn migration and winter, sanctuary area and WRP area in the surrounding landscape were important predictors of mallard wetland selection in nocturnal and diurnal periods during spring migration. However, mallards used wetlands proximate to NWRs less than random expectations at night, but used them in accordance with random expectations during the day although confidence intervals partially overlapped between time periods.

Table 3

Model selection results for multinomial discrete choice models that examined wetland selection for mid-continent mallards (*Anas platyrhynchos*) from 2010 to 2012 in winter during hunting season. Number of parameters (K), Akaike weights (w_i) and evidence ratios (ER) are displayed along with Akaike's information criterion (AIC_c) and ΔAIC_c .

Diurnal/Nocturnal	Model	K^a	AIC_c	ΔAIC_c	w_i	ER
Diurnal	–PrvPx + SancPx + SancAr + WmaPx + WrpAr	9	1167.54	0.00	0.33	–
	–PrvPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	1167.70	0.16	0.30	1.08
	–PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	11	1169.55	2.01	0.12	2.74
	–PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpAr	10	1169.70	2.16	0.11	2.95
	SancPx + SancAr + WmaPx + WrpAr	8	1170.54	3.01	0.07	4.50
	SancPx + SancAr + WmaPx + WrpPx + WrpAr	9	1170.73	3.19	0.07	4.93
Nocturnal	–NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	1156.16	0.00	0.37	–
	–NwrPx + SancPx + SancAr + WrpPx + WrpAr	9	1157.04	0.88	0.24	1.55
	PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	11	1157.79	1.62	0.16	2.25
	PrvPx – NwrPx + SancPx + SancAr + WrpPx + WrpAr	10	1158.86	2.70	0.09	3.86
	SancPx + SancAr + WmaPx + WrpPx + WrpAr	9	1159.03	2.87	0.09	4.20
	SancPx + SancAr + WrpPx + WrpAr	8	1159.91	3.74	0.06	6.50

^a Number of parameters in each model includes random slopes for wetland type (EMG, WDY) with associated standard deviations.

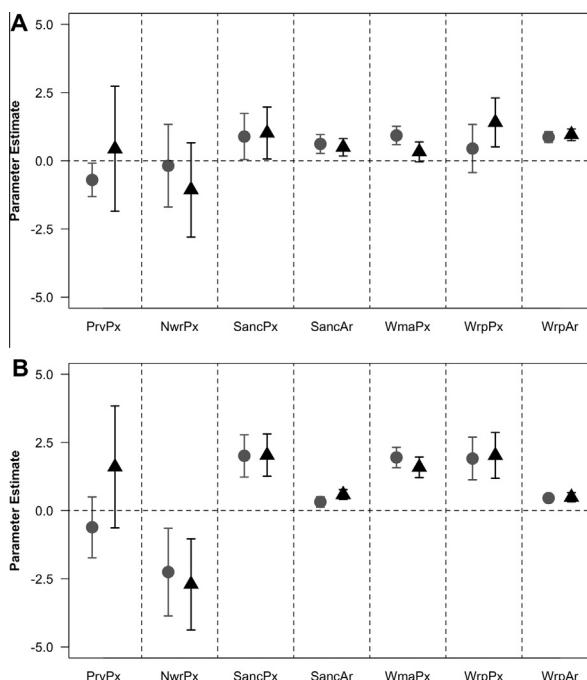


Fig. 2. Model averaged parameter estimates and 95% confidence intervals for discrete choice models that examined mallard wetland selection during winter (A) within hunting season and (B) after hunting season. Gray circles and black triangles represent diurnal and nocturnal models, respectively. PrvPx is proximity to nearest private land, NwrPx is proximity to nearest National Wildlife Refuge, SancPx is proximity to nearest waterfowl sanctuary, SancAr is waterfowl sanctuary in surrounding landscape, WmaPx is proximity to nearest state wildlife management area, WrpPx is proximity to nearest Wetland Reserve Program easement, and WrpAr is area of Wetland Reserve Program easements in surrounding landscape.

Wetland selection patterns varied among autumn migration, winter, and spring migration, but mallards consistently selected wetlands with greater areas of WRP and sanctuary in the surrounding landscape regardless of season, time period, or hunting season

status. In addition, proximities to WMA and WRP were more important predictors of wetland selection in both nocturnal and diurnal periods outside hunting season (Figs. 2b and 3) compared to within hunting season (Figs. 1 and 2a). We also observed changes in wetland selection patterns between diurnal and nocturnal periods within hunting season with regard to proximities to WMA and WRP, indicating that mallards might be altering habitat use as a result of daytime hunting pressure (Figs. 1 and 2a).

4. Discussion

Protected area networks are essential tools for conserving biodiversity in the face of rapid anthropogenic land use changes and a changing climate (Dobrovolski et al., 2011; Faleiro et al., 2013; Rodrigues et al., 2004). Consequently, recent research in conservation biology has focused on designing protected area networks that account for potential future shifts in imperiled species' geographic ranges due to spatial and temporal changes in habitat at relatively large scales (Faleiro et al., 2013; Hannah, 2010; Hannah et al., 2007). Although focus on macro-level changes in the distribution of habitats is necessary to ensure long-term protection of biodiversity, it is important for conservation planners to consider how animal movements may be affected by anthropogenic disturbances (Berger-Tal et al., 2011; Blumstein and Fernandez-Juricic, 2010; Buchholz, 2007). In this study, we examined mallard space use during the non-breeding season to evaluate utility of protected area wetlands to migratory waterfowl. Although mallards are capable of exploiting anthropogenic landscapes, we documented substantial selection of protected area wetlands, indicating protected area wetlands provide habitat resources even for an adaptable waterfowl species (Drilling et al., 2002).

Public lands have historically played a prominent role in wildlife conservation and provide habitat for a variety of species, including migratory waterfowl (Meretsky et al., 2006; Scott et al., 2004). In contrast, conservation initiatives (e.g. WRP) on working lands have only recently been recognized as potential components of landscape-level conservation strategies (King et al., 2006;

Table 4

Model selection results for multinomial discrete choice models that examined wetland selection for mid-continent mallards (*Anas platyrhynchos*) from 2010 to 2012 in winter after hunting season. Number of parameters (K), Akaike weights (w_i) and evidence ratios (ER) are displayed along with Akaike's information criterion (AIC_c) and ΔAIC_c .

Diurnal/Nocturnal	Model	K^a	AIC_c	ΔAIC_c	w_i	ER
Diurnal	–NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	1736.46	0.00	0.55	–
	–PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	11	1736.90	0.44	0.45	1.25
Nocturnal	PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	11	1507.91	0.00	1.00	–

^a Number of parameters in each model includes random slopes for wetland type (EMG, WDY) with associated standard deviations.

Table 5

Model selection results for multinomial discrete choice models that examined wetland selection for mid-continent mallards (*Anas platyrhynchos*) from 2011 to 2012 during spring migration. Number of parameters (K), Akaike weights (w_i) and evidence ratios (ER) are displayed along with Akaike's information criterion (AIC_c) and ΔAIC_c .

Diurnal/Nocturnal	Model	K^a	AIC_c	ΔAIC_c	w_i	ER
Diurnal	SancPx + SancAr + WmaPx + WrpPx + WrpAr	9	1830.05	0.00	0.48	–
	–NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	1831.54	1.49	0.23	2.11
	–PrvPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	1831.88	1.83	0.19	2.50
	–PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	11	1833.24	3.19	0.10	4.93
Nocturnal	–NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	10	2266.83	0.00	0.66	–
	–PrvPx – NwrPx + SancPx + SancAr + WmaPx + WrpPx + WrpAr	11	2268.92	2.09	0.23	2.84
	–NwrPx + SancAr + WmaPx + WrpPx + WrpAr	9	2270.35	3.52	0.11	5.82

^a Number of parameters in each model includes random slopes for wetland type (EMG, WDY) with associated standard deviation.

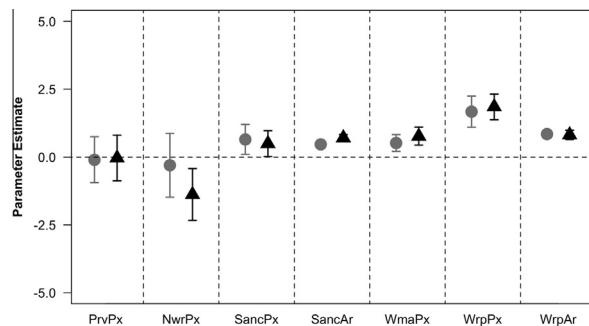


Fig. 3. Model averaged parameter estimates and 95% confidence intervals for discrete choice models that examined wetland selection patterns of mallards during spring migration outside hunting season. Diurnal models are represented with gray circles and nocturnal models are represented with black triangles. PrvPx is proximity to nearest private land, NwrPx is proximity to nearest National Wildlife Refuge, SancPx is proximity to nearest waterfowl sanctuary, SancAr is waterfowl sanctuary area in surrounding landscape, WmaPx is proximity to nearest state wildlife management area, WrpPx is proximity to nearest Wetland Reserve Program easement, and WrpAr is area of Wetland Reserve Program easements in surrounding landscape.

Knight, 1999). We demonstrated that midcontinent mallards selected wetlands near private conservation easements and with high conservation easement area in the surrounding landscape. From a landscape-level perspective, conservation easements (i.e. WRP) in our study area were not only smaller on average ($\bar{x} = 65.3$ ha, $SD = 134.4$ ha) than publicly managed parcels ($\bar{x} = 134.9$ ha, $SD = 1,265.3$ ha), but also closer to publicly managed areas ($\bar{x} = 4.0$ km, $SD = 4.8$ km) when compared to random wetlands ($\bar{x} = 7.8$ km, $SD = 6.33$ km). In addition, approximately 81% of conservation easements in our study area were under permanent contract with the remaining 19% secured with 30-year contracts. Thus, our results provide a conservative estimate of the utility of WRP easements to migratory waterfowl and demonstrate that conservation easements have the potential to provide habitat for migratory birds throughout the non-breeding period in the mid-continent region (Beyer et al., 2010). Moreover, strategically positioned easements adjacent to large public areas may provide maximum conservation return on a given economic investment, although this strategy has the potential to increase costs for conservation groups (King et al., 2006; Lennox and Armsworth, 2013; Polasky, 2006).

Areas free of anthropogenic disturbance and hunting pressure are increasingly recognized as essential to waterfowl conservation (Cox and Afton, 1997; Evans and Day, 2002; Madsen et al., 1998; McKinney et al., 2006; Stafford et al., 2007). Mallards consistently selected wetlands proximate to sanctuaries in addition to wetlands that had increased sanctuary area in the surrounding landscape, emphasizing the importance of sanctuaries to waterfowl throughout the non-breeding period. Although suitable habitat may be more important to mallards than sanctuary (Davis et al., 2009),

other studies have demonstrated the importance of sanctuaries to waterfowl outside hunting season (Madsen et al., 1998; McKinney et al., 2006). For example, in the Illinois and upper Mississippi river valleys, waterfowl sanctuary was a positive indicator of mallard wetland use outside hunting season during spring migration as well as during fall migration within hunting season (Stafford et al., 2007). In addition, our analyses likely underestimated the importance of sanctuaries to waterfowl during the non-breeding period because only geospatial data for permanent sanctuaries on publicly managed land were included. Many publicly managed areas (NWRs and WMAs) restrict waterfowl hunting to a few days each week and/or to specific times of the day, and wetlands on private land may effectively serve as sanctuary due to a lack of hunting pressure or voluntary restrictions on anthropogenic disturbance (Pearse et al., 2012). Nevertheless, sanctuaries on public areas (WMAs, NWRs) appear to be a critical component of protected area networks within the midcontinent region of North America.

The National Wildlife Refuge System is the largest functional protected area network in North America specifically designated for wildlife conservation, but many properties are managed independently from one another (Meretsky et al., 2006). Although the National Wildlife Refuge System encompasses numerous types of ecosystems, many NWRs were established to protect migratory birds and are recognized as essential breeding, migrating, and wintering habitats for waterfowl (Meretsky et al., 2006; Scott et al., 2004). In our study, mallards selected wetlands near sanctuaries throughout the non-breeding period, and waterfowl sanctuaries were heavily concentrated on NWRs in our study area (see methods). Thus, NWRs were more likely than WMAs to provide essential sanctuaries for waterfowl that contained areas free of anthropogenic disturbances (Reid et al., 1989). However, food resources on NWRs likely reached giving-up density during winter (Hagy and Kaminski, 2012), providing limited energetic benefits of foraging on NWRs compared to foraging on private wetlands (e.g. WRP) after hunting season closed (Figs. 2b and 3).

The fundamental goal of protected areas is long-term biodiversity preservation, and candidate sites are often prioritized for acquisition based on species richness or diversity (Margules and Nicholls, 1988; Margules and Pressey, 2000; Pressey et al., 2007). Consequently, protected area acquisition often reflects a temporal snapshot of site communities, which may not ensure site adequacy (Cerdeira et al., 2010; Schapaugh and Tyre, 2012). Further, the effectiveness of protected areas is directly linked to animal movement and space use patterns within and outside area boundaries (Caro, 2007; Margules and Nicholls, 1988). Although we examined wetland selection patterns of a generalist species, we demonstrated that mallards shift patterns of protected area use in response to anthropogenic disturbances. Our results indicate consideration of anthropogenic disturbance patterns and site juxtaposition can enhance protected area prioritization procedures and the effectiveness of protected areas for migratory bird conservation (Blumstein and Fernandez-Juricic, 2010; Powell and Bjork, 1995).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.05.018>.

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