Evaluating predictors of local dabbling duck abundance during migration: managing the spectrum of conditions faced by migrants

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Abstract

The development of robust modelling techniques to derive inferences from large-scale migratory bird monitoring data at appropriate scales has direct relevance to their management. The Integrated Waterbird Management and Monitoring programme (IWMM) represents one of the few attempts to monitor migrating waterbirds across entire flyways using targeted local surveys. This dataset included 13,208,785 waterfowl (eight *Anas* species) counted during 28,000 surveys at nearly 1,000 locations across the eastern United States between autumn 2010 and spring 2013 and was used to evaluate potential predictors of waterfowl abundance at the wetland scale. Mixed-effects, log-linear models of local abundance were built for the Atlantic and Mississippi flyways during spring and autumn migration to identify factors relating to habitat structure, forage availability, and migration timing that influence target dabbling duck species abundance. Results indicated that migrating dabbling ducks responded differently to environmental factors. While the factors identified demonstrated a high degree of importance, they were inconsistent across species, flyways and seasons. Furthermore, the direction and magnitude of the importance of each covariate group considered here varied across species. Given our results, actionable policy recommendations are likely to be most effective if they consider species-level variation within targeted taxonomic units and across management areas. The methods implemented here can easily be applied to other contexts, and serve as a novel investigation into local-level population patterns using data from broad-scale monitoring programmes.

Key words: conservation, Integrated Waterbird Management and Monitoring, modelling, populations, waterfowl.

Migratory waterfowl have received intensive management focus (in terms of their habitat) because of the sheer volume of their recreational harvest, with approximately 15,000,000 ducks and geese harvested annually in the United States alone (Raftovich & Wilkins 2013). There is a missing link, however, between the spatial scale of this management focus and that of the migratory process (Soulliere *et al.* 2013; Berger *et al.* 2014). There is a clear need to evaluate the effects of local-scale features and management actions on migration at the continent scale, because such assessments would provide the basis for the improvement of habitat management programmes for migrating waterfowl (Mattsson *et al.* 2012; Soulliere *et al.* 2013; Davis *et al.* 2014; Humburg & Anderson 2014; Kaminski & Elmberg 2014; Stafford *et al.* 2014). The international movements of migratory waterfowl in North America, between Mexico, the United States and Canada (nations jointly charged with managing these populations under the North American Waterfowl Management Plan; NAWMP 2012), places a premium on this large-scale/local-scale integration. The data required for such evaluations are chronically lacking both in number and in collection rigour (*e.g.* lack of standardised collection methods, spatial and temporal biases, uncorrected sources of error, *etc.*; Lindenmayer & Likens 2010). The motivation here is to begin to bridge this gap in integration by elucidating the connection between local habitat conditions and migrating waterfowl populations in North America using data collected from a multi-flyway-scale monitoring programme.

Stopover locations for migrating waterfowl in the United States are often remnant or created wetlands managed by State agencies and the United States Fish and Wildlife Service (USFWS) (Andersson *et al.* 2015). Stopover locations are important to management efforts because they are the primary sources of mortality (via harvest and predation) for migrants (Lank & Ydenberg 2003; Newton 2006; Hope *et al.* 2011). Stopover locations are also pivotal nodes of overlap and interaction for populations that might otherwise be separated during the rest of the year, which has important implications for population structuring and hence conservation (Esler 2000; Sullivan *et al.* 2009). For instance, metapopulation theory could be applied to migratory species if we could identify discrete subpopulations (Mattsson *et al.* 2012), but to identify subpopulations we need to know more about local dynamics and conditions at stopover locations (Esler 2000). While there are some sources of data on populations during migration (*e.g.* eBird, a citizen science programme using opportunistic observations and voluntary reporting; Sullivan *et al.* 2009), the standardised nature of rigorous monitoring programmes provides clear advantages over data gathered opportunistically (Rondinini *et al.* 2006).

The models created here are meant to evaluate the ability of habitat structure and other local-level variables to explain local abundance of waterfowl populations during migration, and to assess the relative importance of selected factors in influencing waterfowl abundance during spring and autumn migration periods. Data from the recently implemented Integrated Waterbird Management and Monitoring programme (IWMM) targeting managed wetlands in the Atlantic and Mississippi flyways of the eastern United States were used to inform the models. This monitoring programme focuses on waterbirds broadly (*i.e.* waterfowl, shorebirds and wading birds), an economically and ecologically important biological group. Evaluation here is restricted to dabbling ducks because of the nature of data recorded in the programme's vegetation surveys (*e.g.* emergent vegetative material is most compatible with dabbling duck foraging behaviour and less informative about goose or diving duck patterns). The approach employed here involves constructing mixed-effects, log-linear models describing time- and place-specific abundances for waterfowl species as a function of potential forage availability and habitat structure covariates. These models are separated into domains by flyway (Atlantic and Mississippi) and season (spring and autumn), and individual variables were compared with groups of covariates to identify the importance of these predictors in estimating local waterfowl abundance.

There are broad generalisations about the differences among the modelling domains (flyways and seasons) that help elucidate the benefit of grouping them thusly. For example, a recently developed energetics-based simulation model for predicting bird movements through the Mississippi and Atlantic flyways as a function of caloric gains and losses *en route* suggested that greater availability of calories in autumn (largely from waste grain following the harvest) allowed dabbling ducks to spend more time at a given stopover during migration, whereas during spring these birds moved more frequently between stopover sites (Lonsdorf *et al.* in press). Perhaps the lower availability of forage on agricultural land during spring migration would lead to heightened importance of forage-related covariates through competition for a scarce resource at staging areas, whereas an over-abundance of forage during autumn migration allowed birds to focus on risk-minimising behaviour associated with optimal migration strategies (Alerstam & Lindström 1990), leading to an increased importance of habitat structure. Additionally, and from a modelling perspective, it is conceivable that physiographic differences between the flyways may drive the variation between the relative importance of habitat structure-related and forage-related covariates. The Mississippi flyway, for example, is more highly influenced by large swathes of agricultural land and has much less topographical variability than the Atlantic flyway. Additionally, the Atlantic flyway has coastal habitat that is completely absent in the Mississippi flyway (until birds reach overwintering areas along the Gulf of Mexico). It could be that the relative homogeneity of the Mississippi flyway makes simpler models sufficient, while the complexity of the landscape in the Atlantic flyway demands correspondingly more complex models to approximate migratory reality. Our modelling domains are consistent with the suggestion that every migratory flyway presents a unique spatial and temporal arrangement of resources, and a unique set of challenges to successful migration (Lyons *et al.* 2008).

Methods

Study area

The IWMM established 192 survey units in the Mississippi and Atlantic flyways, each under a unique management authority participating in frequent and recurring waterbird management actions. Units varied in size (Fig. 1, see also Supporting Information Fig. S1 on http://wildfowl.wwt.org.uk/), and contained different numbers of wetlands. In total, these units comprised 1,069 wetlands, from Wisconsin to Louisiana, and Vermont to Florida (Fig. 1). The wetlands included in the study had a mean (± s.d.) area of 65 ha (± 274 ha), with a range of 0.3–5,016 ha.

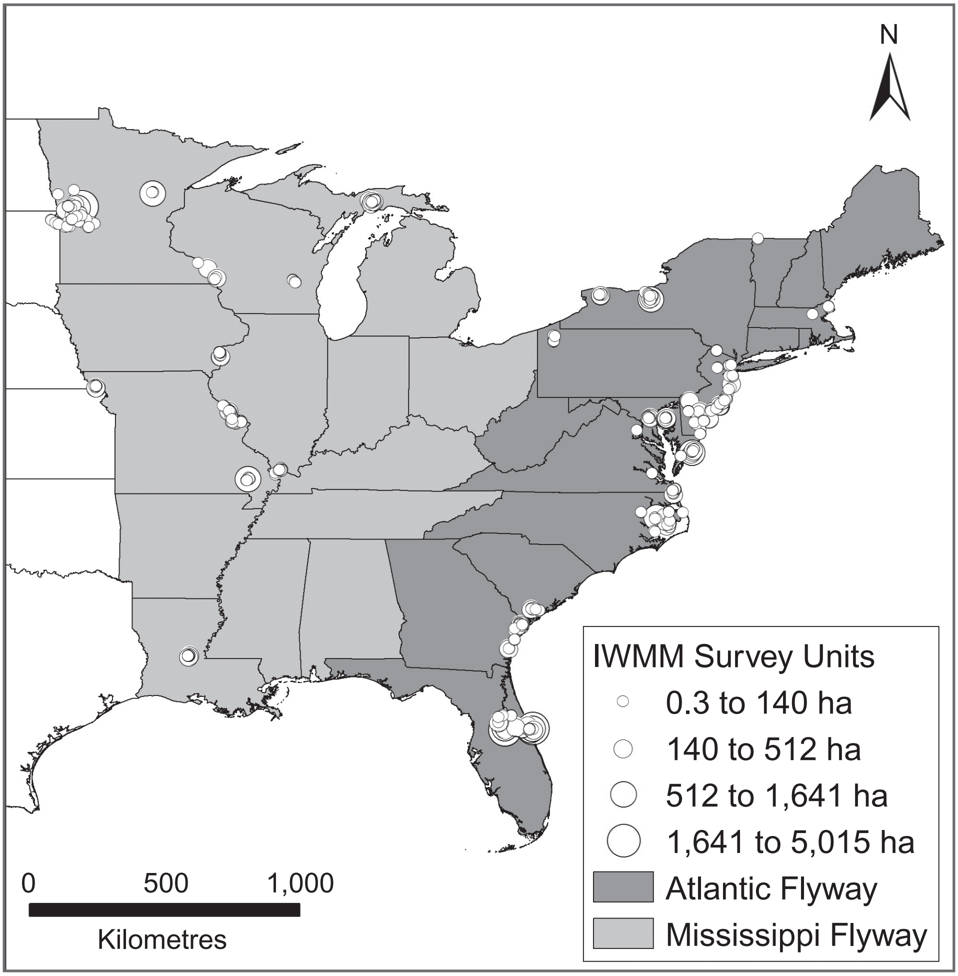

Figure 1. Distribution of survey units (circles) for the Integrated Waterbird Monitoring and Management (IWMM) programme in the eastern United States.

Table 1. List of dabbling duck species used in local abundance models. N_{obs} is the total number of individuals recorded in IWMM surveys, from autumn 2010 to spring 2013 inclusive, used in model development.

Scientific name	Common name	Species Codes	N_{obs}
Anas platyrhynchos	Mallard	MALL	7,235,753
Anas carolinensis	Green-winged Teal	AGWT	1,978,973
Anas acuta	Northern Pintail	NOPI	1,662,212
Anas strepera	Gadwall	GADW	991,693
Anas clypeata	Northern Shoveler	NOSH	632,362
Anas americana	American Wigeon	AMWI	266,634
Anas discors	Blue-winged Teal	BWTE	253,879
Anas rubripes	American Black Duck	ABDU	187,279

Data source

Survey data from the IWMM between autumn 2010 and spring 2013 were used in the analyses (see Table 1 for species included here). Briefly, the IWMM is a collaborative, multi-agency monitoring programme designed to provide wildlife managers with decision support tools for managing wetland birds and their habitats at multiple scales. The primary efforts of IWMM are focused on gathering local-scale information on waterbird use and habitat conditions of wetlands across large geographic ranges. Bird counts and habitat data are collected voluntarily by agency staff and volunteers following standardised data collection protocols, designed by IWMM scientists. A detailed description of the current data collection methods is available on the IWMM website (http://iwmmprogram.org/). The protocols used to collect the data have recently been revised, but the salient details of the protocols implemented for the data used here are described below.

Land-based bird surveys were conducted weekly (or bi-weekly, though weekly surveys predominated) during peak migration, and bi-weekly (or monthly, with bi-weekly predominating) during subsequent migratory pulses, depending on logistical constraints and resources available at each unit. Primary migration is considered to be from mid-October to late-December during autumn, and early-January to mid-April during spring migration, depending on latitude. Bird surveys consisted of an intensive area-search method in which observers traversed the unit and recorded all birds detected. Observers did not collect data to estimate detection probability directly, but bird counts were conducted from fixed locations on the perimeter of the wetland, chosen to maximum visibility. The total number of individuals seen of each species was recorded during the survey, along with factors relating to the observability of birds and the level of recent disturbance that could influence the number of birds present on the survey unit. This information allowed for observer error and biases to be accounted for in the modelling framework, detailed below. Additionally, the disturbance severity parameter included hunting pressure (which is likely to be low on refuges); by including this random effect, the variation in abundance attributable specifically to environmental factors can be diagnosed more accurately. Essentially, regardless of why waterfowl are using refuges, they are not likely to be distributed at random within them, and the models presented here seek to identify factors that might illuminate their distributional patterns (in terms of local abundance, not truly spatial).

Vegetation surveys were conducted early during the migration period; however, additional vegetation surveys can be conducted throughout the migration period if logistical resources are available. When multiple vegetation surveys were conducted, we applied an inverse distance weighting approach to quantify habitat conditions during bird surveys (*e.g.* vegetation surveys conducted four days prior to and eight days after a bird survey would be weighted 0.67 and 0.33 times, respectively). Vegetation surveys consisted of estimates of vegetative cover, vegetation height, vegetation density, and levels of water depth and interspersion.

Model design

Models of daily abundance for eight dabbling duck species were fit using Markov chain Monte Carlo (MCMC) methods. The eight species were represented by ≥ 5,000 observations within the IWMM data (Table 1). Models were built separately for the Atlantic and Mississippi flyways and for the autumn (8 October to 31 December) and spring (1 January to 21 April) migration periods, resulting in four unique modelling domains for each species (Autumn/Mississippi, Autumn/Atlantic, Spring/Mississippi, Spring/Atlantic).

IWMM sampling protocols call for the collection of a large amount of environmental data. As these metrics were chosen carefully by IWMM scientists, there was no strong basis for excluding some but not others from the models. Using data from a standardised monitoring programme like the IWMM to generate a close representation of reality often requires a complex model with parameters associated with each variable influencing a species. However, efforts to increase model realism through additional model complexity risk decreasing the precision necessary for sound inference (Burnham & Anderson 2002; Morris *et al.* 2006). Results of complex models may be difficult to interpret (Merow *et al.* 2014), especially when higher-order interactions of predictor variables are included. Comparing candidate models containing different numbers and combinations of parameters can help to elucidate which predictor variables, or sets of predictor variables, are associated with observed patterns in species response and which may be of little use (Burnham & Anderson 2002). This procedure (*i.e.* comparing models with different numbers and combinations of parameters) was employed to evaluate the utility of the individual variables monitored by the programme, and to compare models with collections of these variables acting in concert as interacting covariates.

To accomplish this, the data were grouped into two categories representing different influences on waterfowl abundance (Table 2). First, variables relating to vegetation and food were grouped into a forage availability covariate group. This group included plant density features relating to known vegetative food sources. Second, variables relating strictly to structural components of the local system were grouped into a habitat structure covariate group. This category included abiotic factors, such as water depth, as well as physical traits of biotic factors, such as plant height. These two covariate group models were compared with a survey-only model consisting of timing of the survey (number of days since 1 January), the interaction of timing and latitude, and the area of the IWMM unit. This was the survey covariate group. Finally, all variables were combined into a global model for each modelling domain.

Models of local waterfowl abundance were constructed in a hierarchical Bayesian mixed-effects framework (Bolker *et al.* 2009; Forcey *et al.* 2011). The count of waterfowl at each wetland was the response variable, and was modelled as a zero-inflated Poisson process. The logarithm of the mean count was modelled as a linear function of observed covariates. All random effects were included in all models to account for issues associated with the sampling process (Table 2). For instance, "observer" was treated as a random effect to account for potential differences among observers in their ability to count birds (Pagano & Arnold 2009); similarly, sites may differ in their attractiveness as stopovers because of their proximity to the core flight path, which may vary by year.

Model selection and covariate importance

For each species in each modelling domain, the relative support of the four competing models was quantified using Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002). The fit of the models to the data was assessed by comparing the deviance of each model to the null model (which contained only wetland area as a fixed-effect, and observer as a random-effect). A relative deviance was calculated by taking the difference in the deviance of a given model and the null model, and then dividing by null model deviance. Models were fitted using MCMC sampling techniques with the package "MCMCglmm" in R (R Core Team 2014). Models were initialised with a chain length of 60,000 iterations and a burn-in length of 10,000 iterations. We used non-informative normal prior distributions for all model parameters, with mean = 0 and variance = 1.0e + 10.

To assess the relative importance for each covariate group, model weights (w_i) were calculated for each competing model i and the weights for all models that included a particular covariate group were summed (Spiegelhalter *et al.* 2002; Ward 2008). Parameters were included in an equal number of models in the candidate model set.

Table 2. List of fixed- and random-effects used in dabbling duck abundance models.

Fixed effects

Covariate group/variable	Description
Survey	
Day of Year	Day of the year (not Julian Date)
Day of Year × Latitude	Interaction between days since Jan-1 and site latitude
Wetland area	Total area (in hectares) of surveyed wetland
Forage	
Preferred plant density	Ordinal, representing density of plants identified as preferred waterfowl food
Annual plant cover	Percentage of total survey area that is covered by annual plants
Perennial plant cover	Percentage of total survey area that is covered by perennial plants
Total stem density	Ordinal, stem density of dominant plants
Seed head density	Ordinal, density of seed heads per unit area
Habitat structure	
Water depth	Percentage of wetland in each of six water depth categories
Open water	Percentage of total survey area that is open water
Plant height	Percentage of total vegetative cover in each of seven height categories
Interspersion	Ordinal, level of interspersion between vegetated and non-vegetated areas
Percent near edge	Percentage of total survey area within 50 m of tall (10 m) trees

Random effects

Variable	Description
Observer	Individual observer conducting waterfowl survey
IWMM Survey Unit	Unique IWMM survey unit within which wetlands were monitored
Year	Year of observation
Disturbance severity	Ordinal (1–4) measure of recent disturbance events

It is useful to understand the direction of the relative importance of the covariate groups. That is, a particular metric may be of equal relative importance for two species, but for one species it is the presence of the metric that is important (a positive association), while for the other species it is the absence of the metric that is important (a negative association). To gauge the direction and significance of the relative importance of the parameters, the posterior mean value of each parameter was calculated and compared across species for each model, in each modelling domain. If the 95% posterior credible interval (C.I.) of the posterior mean value for a parameter overlapped 0, the parameter was non-significant. If the 95% C.I. was entirely negative or entirely positive, the parameter was negatively or positively significant, respectively.

Principal components analysis

Finally, principal component analyses (PCAs) were applied to the model weight results and the posterior mean value comparisons to elucidate associations of species in the context of certain modelling domains and covariate groups.

Results

Data source

In total, we used data from 33,631 bird surveys and 3,747 vegetation surveys from 1,069 wetlands. Over 13 million dabbling ducks were counted (13,229,133) by the IWMM programme between 2010 and 2013. The Mallard *Anas platyrhynchos* was the most commonly recorded species (54.7% of total birds counted, *n* = 7,235,753), whereas the American Black Duck *Anas rubripes* was the least common (1.4% of total, *n* = 187,279). Approximately 55% fewer birds were counted in spring (31.1% of total, *n* = 4,108,170) than autumn (68.9% of total, *n* = 9,103,596), and approximately 67% fewer in the Atlantic flyway (28.2% of total, *n* = 3,725,764) than the Mississippi Flyway (71.8% of total, *n* = 9,503,369).

Model selection

Few patterns for dabbling ducks emerged from the model selection analysis. The most prominent of these patterns was the lack of support for models containing only survey-related covariates (Table 3). In only five cases was there any appreciable support for the survey model; the Mallard and American Wigeon *Anas americana* during autumn in the Mississippi flyway, the Gadwall *Anas strepera* during spring in the Mississippi flyway, and the Northern Pintail *Anas acuta* and Northern Shoveler *Anas clypeata* during spring in the Atlantic flyway (Table 3).

During autumn migration in the Mississippi flyway, the survey + forage model was among the poorest performing for every species (Table 3). The global and survey + habitat structure models showed evidence of being optimal for three species each (Table 3). During spring migration in the Mississippi flyway, the survey + habitat structure model outperformed all others for three species, and the survey + forage model outperformed all others for three species (Table 3). The difference was stark in each case as well, with the next-most supported model almost always having an order of magnitude larger DIC score.

Table 3. ΔDIC values for dabbling duck model selection. The best models for each species are in bold and highlighted in grey. S = survey, H = habitat structure, F = forage, G = global. See Table 1 for species name abbreviations.

ΔDIC Scores								
Species	**Autumn**							
	Mississippi				**Atlantic**			
	S	**S + H**	**S + F**	**G**	**S**	**S + H**	**S + F**	**G**
MALL	**0.00**	22.95	14.80	26.99	56.00	24.20	**0.00**	24.20
AGWT	165.26	16.16	127.31	**0.00**	30.55	25.97	45.64	**0.00**
NOPI	19.42	**0.00**	88.98	3.78	56.26	7.72	**0.00**	31.16
GADW	218.13	18.45	188.19	**0.00**	347.79	219.97	**0.00**	295.76
NOSH	158.19	**0.00**	184.41	2.39	31.47	130.15	13.34	**0.00**
AMWI	**0.00**	4.44	170.83	46.75	1.79	66.49	**0.00**	104.78
BWTE	116.91	**0.00**	87.27	54.26	4.75	50.75	**0.00**	107.79
ABDU	259.61	57.51	240.72	**0.00**	36.93	**0.00**	51.14	1.10
Species	**Spring**							
	Mississippi				**Atlantic**			
	S	**S + H**	**S + F**	**G**	**S**	**S + H**	**S + F**	**G**
MALL	3.74	**0.00**	3.60	11.76	62.51	**0.00**	80.13	60.42
AGWT	50.38	**0.00**	55.37	27.58	4.52	85.35	23.91	**0.00**
NOPI	6.75	18.88	**0.00**	108.27	**0.00**	15.73	29.02	3.31
GADW	**0.00**	139.70	39.44	125.12	116.27	85.01	94.18	**0.00**
NOSH	51.96	34.59	**0.00**	110.79	**0.00**	32.53	59.10	49.60
AMWI	46.73	**0.00**	228.92	25.29	57.48	2.40	46.42	**0.00**
BWTE	116.62	18.59	27.86	**0.00**	23.91	80.52	**0.00**	4.69
ABDU	25.65	17.24	**0.00**	63.57	30.14	**0.00**	147.24	5.58

During autumn migration in the Atlantic flyway, the survey + forage model had the most support for five of eight species (Table 3). Green-winged Teal *Anas carolinensis* and Northern Shoveler were best approximated with the global model, American Black Duck by the survey + habitat structure model. During spring migration in the Atlantic flyway, the global model had more support for more species than any other model (three out of eight species), and was the second best model in four additional instances (Table 3). The global model was not the first- or second-most supported model only for the Green-winged Teal.

The models exhibited poor fit in most cases. The best fitting model (the global model for the Green-winged Teal in the Atlantic flyway during autumn migration) had a relative deviance of 0.225 (Table 4).

Covariate importance

The relative importance of forage-related covariates was greater than for habitat structure-related covariates during autumn migration in the Atlantic flyway (Fig. 2, Table 5). Only the American Wigeon, Green-winged Teal and Northern Shoveler showed strong associations with habitat structure-related covariates, while every species except the Northern Shoveler associated mainly with forage-related covariates (relative importance < 0.3 for Northern Shoveler, > 0.6 for all other species considered; Fig. 2). This difference among species disappeared during spring migration in the Atlantic flyway, when the Blue-winged Teal *Anas discors*, Green-winged Teal and Northern Pintail were not associated with habitat structure-related covariates and there was an equal split among species for forage-related covariates (*i.e.* four species associated mainly with the forage covariates and four did not; Fig. 2, Table 4).

During autumn migration in the Mississippi flyway the pattern of covariate importance reversed, with habitat structure-related covariates displaying greater importance than forage (Fig. 2, Table 4). During spring migration in the Mississippi flyway, however, there was an even split of species between the two covariate groups (Fig. 2, Table 4).

In general there were very few covariate groups of moderate importance to most species, as species grouped together either near 1 (maximum importance) or 0 (minimum importance). However, these species grouping assemblages were not consistent with respect to their members; *i.e.* the same subset of species did not group together across seasons and flyways.

The majority of parameters were non-significant when analysed independently (*i.e.* without grouping them into covariate categories; see Supporting Information Figs. S2–S17; individual species graphs are available upon request of the authors—an example is provided in Fig. S34). Among those parameters that were significant, the response by each species varied greatly, with some species positively associated with a given parameter and others negatively associated with the same parameter (see Fig. 2). Water depth in particular seemed to engender a fair degree of divergence among species; Mallards tended to show positive associations with water depth, while Northern Pintails were more consistently negatively associated with this metric (Fig. 2).

Table 4. Explained relative deviance for each dabbling duck model. This value is calculated using the model deviance for each model, subtracted from the deviance of the null model. The more positive the relative deviance, the better the fit of the model compared to the null; the more negative the relative deviance, the worse the fit of the model. Fits were generally poor, suggesting that unmodelled factors, in addition to those used in our analyses (Table 2), may be influencing waterfowl abundance patterns. See Table 1 for species name abbreviations.

Species	**Autumn**							
	Mississippi				**Atlantic**			
	S	**S + H**	**S + F**	**G**	**S**	**S + H**	**S + F**	**G**
MALL	0.167	0.067	0.121	0.080	0.066	0.074	0.076	0.068
AGWT	0.185	0.190	0.179	0.217	0.198	0.202	0.175	0.225
NOPI	–0.040	–0.021	–0.032	–0.030	0.056	0.088	0.051	0.067
GADW	–0.063	–0.061	–0.012	–0.039	0.138	0.140	0.136	0.150
NOSH	–0.077	–0.097	–0.095	–0.072	0.037	0.038	0.040	0.037
AMWI	–0.020	–0.024	–0.017	–0.016	0.022	0.018	0.011	0.019
BWTE	–0.015	–0.003	–0.034	–0.020	0.039	0.119	0.117	0.121
ABDU	0.003	–0.049	–0.076	–0.053	0.136	0.140	0.140	0.136
Species	**Spring**							
	Mississippi				**Atlantic**			
	S	**S + H**	**S + F**	**G**	**S**	**S + H**	**S + F**	**G**
MALL	0.013	0.088	0.101	0.146	0.002	0.009	0.003	0.003
AGWT	0.136	0.150	0.134	0.138	0.014	0.016	0.012	0.007
NOPI	–0.047	–0.014	0.008	–0.010	0.082	0.133	0.055	0.091
GADW	0.025	0.014	0.022	0.020	0.060	0.055	0.059	0.061
NOSH	0.018	0.022	0.021	0.017	0.002	0.004	0.001	0.003
AMWI	0.046	0.052	0.047	0.049	–0.003	–0.003	–0.007	–0.002
BWTE	0.128	0.152	0.157	0.126	0.012	0.011	0.012	0.011
ABDU	0.002	0.004	0.013	0.013	0.035	0.036	0.034	0.028

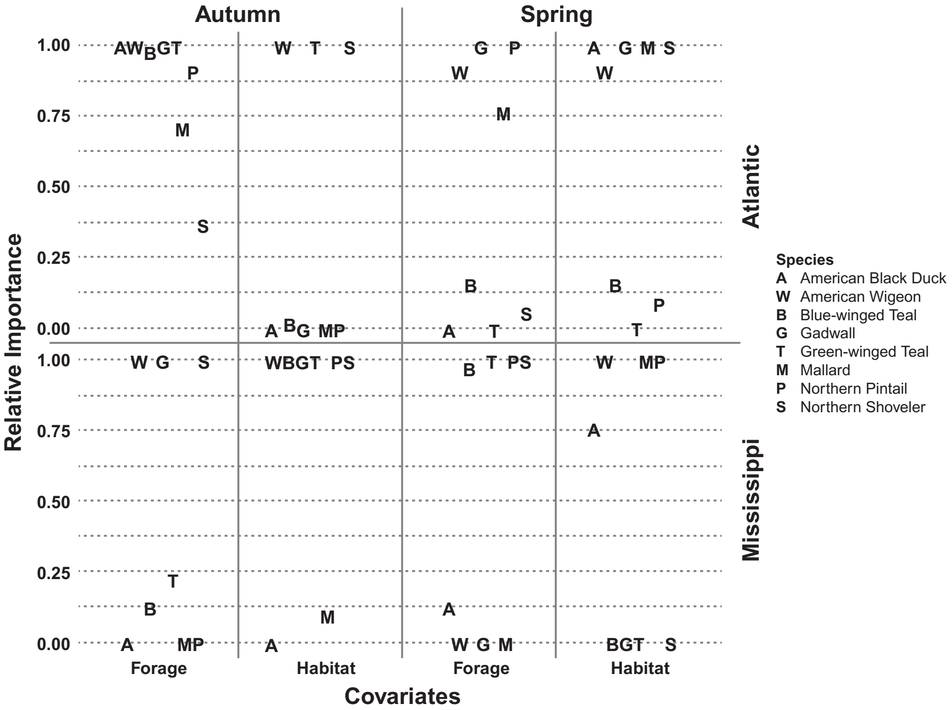

Figure 2. Here we show the relative importance of covariate groups used in predictive models. The Atlantic and Mississippi flyways are shown above and below, but the relevant comparisons are between the covariate groups from autumn to spring. Individual species scores for each covariate group are shown as jittered symbols to avoid obfuscating-overlap. While few patterns clearly emerged in terms of which covariate group was most influential in a given season/flyway combination, it is clear that species rarely react moderately to the metrics examined; relative importance scores were usually < 0.25 or > 0.75. Symbols are dodged for visualisation.

Principal component analysis

Corroborating the model selection results showing little evidence of guild-level patterns in effects of environmental features, the PCAs revealed few associations among the eight dabbling duck species evaluated (Fig. 3). The majority of the variation was explained by flyway-level differences rather than seasonal differences. There was also some grouping along the axis of PC1, though in general the species-covariate combinations were distributed widely across the plot.

The lack of consistency across species was also seen throughout the individual covariate group PCAs (Supporting Information Figs. S18–S33). In some cases, when evaluating survey- and habitat structure-related covariates during autumn migration in the Mississippi flyway, for example, there were clear associations among the eight dabbling duck species (Fig.

Table 5. Relative importance of each covariate group (Forage, Habitat structure [here, Structure]) for each of the competing models of dabbling duck abundance, listed for each modelling domain. Each covariate group appeared in the same number of models in the candidate model set. The relative importance for each covariate group is calculated by summing the model weights (exp[-ΔDIC/2]/Σ(exp[-ΔDIC/2])) for each competing model that included a particular covariate group.

	Relative importance			
Species	**Atlantic (autumn)**		**Mississippi (autumn)**	
	Forage	**Structure**	**Forage**	**Structure**
American Black Duck	1.00	0.00	0.00	0.00
American Wigeon	1.00	1.00	1.00	1.00
Blue-winged Teal	0.98	0.02	0.13	1.00
Gadwall	1.00	0.00	1.00	1.00
Green-winged Teal	1.00	1.00	0.23	1.00
Mallard	0.71	0.00	0.00	0.10
Northern Pintail	0.91	0.00	0.00	1.00
Northern Shoveler	0.37	1.00	1.00	1.00
Species	**Atlantic (spring)**		**Mississippi (spring)**	
	Forage	**Structure**	**Forage**	**Structure**
American Black Duck	0.00	1.00	0.13	0.76
American Wigeon	0.91	0.91	0.00	1.00
Blue-winged Teal	0.16	0.16	0.97	0.00
Gadwall	1.00	1.00	0.00	0.00
Green-winged Teal	0.00	0.00	1.00	0.00
Mallard	0.77	1.00	0.00	1.00
Northern Pintail	1.00	0.09	1.00	1.00
Northern Shoveler	0.06	1.00	1.00	0.00

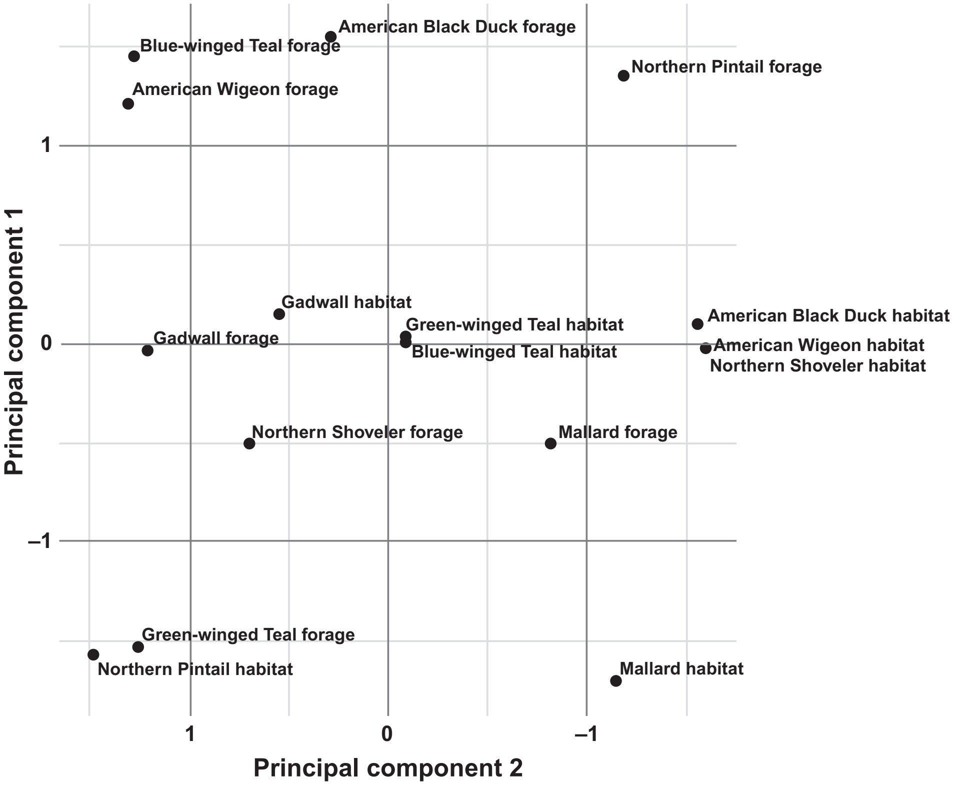

Figure 3. The results of a principal components analysis (PCA) of the relative importance of covariate groups to each species in each modelling domain are plotted. The principal components (PC) were more strongly associated with flyways than seasons; PC1 is Mississippi, while PC2 is Atlantic, indicating more variation is described by geographical differences than seasonal.

S19). In most cases, however, there were several species that did not group with the rest, and the species involved were not consistent across modelling domains.

Discussion

We examined the most comprehensive dataset available for migrating waterfowl to identify a set of environmental and biotic factors capable of predicting waterfowl abundance in autumn and spring migration. We found a high degree of inter-specific variation in terms of the effects of each potential predictor on dabbling duck abundance. This inter-specific variation indicates that efforts to manage the entire group of dabbling ducks must include the broad spectrum of environmental features in their considerations. Additionally, all of the models we used had marginal (at best) explained deviance, suggesting that a large amount of variation present in the system is not well explained by our models. It is likely, therefore, that other factors are contributing to local waterfowl abundance patterns that are not currently captured by IWMM sampling protocols. For instance, the data used here could be tested in conjunction with larger-scale information (*e.g.* climate, land-cover/land-use) to generate better fitting expectations. Additionally, there is some evidence to support the notion that waste grain during autumn migration (especially in the Mississippi flyway) might have decreased the importance of forage-related covariates during this migration period (see Table 3; S + F is never the most supported model during autumn migration in the Mississippi flyway, but it is the most supported for three species during spring migration in this flyway).

The influence of environmental features and the prioritisation of resources implicit in any management action yield a complicated portfolio of conservation recommendations. Below, we expand on this issue in the context of community ecology and stable coexistence of heterospecific populations. These relations simultaneously elucidate the nuanced complexity of dabbling duck management requirements, and the lack of guild-wide patterns evinced by our analysis.

Inter-specific variation explained

We review three theories that illuminate the inter-specific variation of predictor effects in dabbling duck abundance here. First, biological differences in species may enable stable coexistence of mixed-assemblages at stopovers. Second, there may be temporal partitioning of niche dynamics throughout the life cycles of waterfowl to avoid exclusionary overlap during periods of otherwise-shared resource use. Finally, it is possible that different species are relying on each other as stimuli to evaluate habitat conditions. A discussion of these three concepts follows below.

Guillemain *et al.* (2002) explain how subtle differences in the morphology of Anatidae lead to differences in foraging behaviour. With slightly different densities of lamellae, waterfowl species (specifically *Anas* species) might be able to selectively filter forage material such that certain species only eat certain sizes of food (especially in shallower water features where all species can reach the sediment; Guillemain *et al.* 2002). This is in keeping with the observation of divergent foraging behaviours among the *Anas* species (Eadie *et al.* 1979; Kaminski *et al.* 1981). Similarly, it has been proposed that differing body lengths of dabbling ducks may lead to differing foraging depths, and thus a stratified feeding range among species throughout the water column (particularly in deeper water features; Guillemain *et al.* 2002). These slight physical differences may be responsible for the diverse species assemblages observed at stopovers during migration in North America.

In addition to morphological stratification, differentiation of niche space through time may contribute to the variety of waterfowl species coexisting on refuges during migration. Nudds (1983), for example, discovered niche partitioning driven by competition among species is a result of variation in ecosystem features (*e.g.* habitat structure and forage availability). Indeed, in all cases niche separation was found to be at least marginally positively associated with species diversity, indicating increasing partitioning of resources with increasing numbers of species (Nudds 1983). An emergent conclusion from this investigation is that waterfowl may be experiencing stability (in terms of community structure in breeding areas) on an evolutionary time scale, consistent with the long-term stability of waterfowl species at refuges during migration stopovers.

Lastly, and contrary to the competition-at-stopovers perspective, there is recent evidence to suggest that waterfowl species may be taking cues from other species to determine if a particular location has suitable habitat structure and forage resources. While it is expected that heterospecific populations are not as useful as conspecifics for information gathering, it is possible that the transient nature of stopovers during migration can make heterospecifics more complementary (Németh & Moore 2014). This strategy (using other species to determine the value of a location) can help reduce energetically costly explorations and save fuel for longer flights during migration.

Management schemes

The results of this exercise serve to emphasise the well-known need for careful consideration of the impacts that altering a given environmental feature will have on the suite of dabbling duck species. Local and targeted execution of management strategies can be beneficial by offering a diversity of management prescriptions among multiple units, thus providing a suite of available conditions for waterfowl to choose from to best meet their needs. Similarly, on a regional scale, particular environmental features could be targeted at specific wetland sites to benefit a set of migrating dabbling duck species, while other features could be targeted at other wetlands to benefit a different set of species. In this way local management actions can focus on specific species-environment responses that, when aggregated across a region, will serve the needs of a broader guild of species than is possible at a given wetland or wetland complex. This would produce a dynamic, adaptable, and geographically-heterogeneous implementation of management practices across the landscape that might be effective for the greatest number of dabbling duck species (Runge *et al.* 2014). Such an approach is not without challenges. It is difficult to identify a specific set of rules for multi-species management across multiple units because management prescriptions will vary by location, current management activities, and past disturbances. In addition, effective regional management for a broad suite of species would require careful collaborative efforts among disparate management authorities, an issue that is not easily resolved. Nevertheless, in a time of limited budgets for managing biodiversity and inevitable changes to wetland systems as a result of climate change, a thoughtful regional approach to wetland management may be the most effective way to maintain migratory populations of waterfowl and other waterbirds.

Data bias

The results of this study may be influenced to some extent by a geographic bias in the sampling locations. The IWMM programme has a relatively small number of participants in the southern half of the Mississippi flyway (where many waterfowl end their migration; Fig. 1). This lack of representation from an area known to be important to migrating waterfowl may have inadvertently introduced bias into the results for this flyway, as the observed patterns may be representative only of the central and northern portions of the flyway. Additional monitoring and participation in the IWMM programme within this region would provide greater spatial coverage and remove this source of potential bias.

Additionally, the forage-related covariate group we included in this study focused exclusively on vegetative matter. While plant material is an important food source for dabbling ducks, it is conceivable that insects and molluscs are a stronger attractor (and, thus, predictor of abundance) than vegetation despite their low proportions in the overall diets of some dabbling ducks (again, like American Wigeon).

Conclusions

This study highlights some of the issues associated with analyses of data from widespread monitoring programmes. Several of the parameters included in the models presented above were required simply to account for stochasticity in the system and nuisance effects associated with monitoring procedures. Four random effects were included in our models to account for heterogeneity in bird counts introduced by the sampling process. There are, however, additional factors that may have influenced bird counts that we did not consider. For example, spatial correlation among site-level counts was not explicitly accounted for (Thogmartin *et al.* 2004; Latimer *et al.* 2006), which would have greatly increased model complexity and difficulties associated with model convergence. This is not to say that latent spatial autocorrelation was not present in the data, but rather that accounting for such heterogeneity would introduce a substantial challenge beyond the scope of this work.

The modelling framework described in this paper, which is easy to implement and to generalise to other situations, makes use of a system of large-scale monitoring data for waterfowl. It has been applied here to dabbling ducks, but similar lines of inquiry could be made for diving ducks or geese. The salient questions would more likely be restricted to habitat structure variables, as diving ducks and geese have foraging behaviours that are not currently captured by IWMM data collection protocols (Loges *et al.* 2014). For instance, diving ducks are not likely to respond to emergent or surface-level vegetation as they forage deeper under water (Tome & Wrubleski 1988), and geese rely more on areas surrounding wetlands than on the vegetation within the pools themselves (Black *et al.* 1992). Indirect measures of foraging availability could still be addressed, however. Water depth, for example, might be positively associated with diving ducks that need a certain threshold depth for their foraging tendencies. Geese, on the other hand, may be more likely associated with shallower wetlands providing suitable roosting habitat and dryer foraging areas. Additionally, if there were some cause for a specific metric to be modified in a wetland, managers could use these models to identify the association between that metric and a suite of waterfowl species, enabling the creation of a prioritisation list for resource allocation to the species present.

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Photograph: Two Northern Pintails and one Northern Pintail × Mallard hybrid on ice, by Kathy L. Carlyle.

Supplementary material at http://wildfowl.wwt.org.uk/index.php/wildfowl/rt/suppFiles/2628/0