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Research Paper

Models to predict the distribution and abundance of breeding ducks in Canada

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ABSTRACT. Detailed knowledge of waterfowl abundance and distribution across Canada is lacking, which limits our ability to effectively conserve and manage their populations. We used 15 years of data from an aerial transect survey to model the abundance of 17 species or species groups of ducks within southern and boreal Canada. We included 78 climatic, hydrological, and landscape variables in Boosted Regression Tree models, allowing flexible response curves and multiway interactions among variables. We assessed predictive performance of the models using four metrics and calculated uncertainty as the coefficient of variation of predictions across 20 replicate models. Maps of predicted relative abundance were generated from resulting models, and they largely match spatial patterns evident in the transect data. We observed two main distribution patterns: a concentrated prairie-parkland distribution and a more dispersed pan-Canadian distribution. These patterns were congruent with the relative importance of predictor variables and model evaluation statistics among the two groups of distributions. Most species had a hydrological variable as the most important predictor, although the specific hydrological variable differed somewhat among species. In some cases, important variables had clear ecological interpretations, but in some instances, e.g., topographic roughness, they may simply reflect chance correlations between species distributions and environmental variables identified by the model-building process. Given the performance of our models, we suggest that the resulting prediction maps can be used in future research and to guide conservation activities, particularly within the bounds of the survey area.

Des modèles pour prédire la répartition et l'abondance des canards nichant au Canada

RÉSUMÉ. Le manque de connaissances détaillées sur l'abondance et la répartition des espèces de sauvagine dans l'ensemble du Canada limite notre capacité à conserver et à gérer leurs populations de façon efficace. Au moyen de 15 années de données provenant d'inventaires aériens réalisés par transects, nous avons modélisé l'abondance de 17 espèces ou groupes d'espèces de canards dans les parties méridionale et boréale du Canada. Nous avons inclus 78 variables relatives au climat, à l'hydrologie et au paysage dans des modèles amplifiés d'arbres de régression, pour lesquels des courbes de réponse flexibles et les interactions multidimensionnelles entre les variables ont pu être examinées. Nous avons évalué la capacité de prédiction des modèles à l'aide de quatre paramètres et avons estimé l'incertitude en calculant le coefficient de variation des prédictions d'un jeu de 20 répétitions de modèles. Des cartes de l'abondance relative prédite ont été produites à partir des modèles et elles correspondent bien au profil spatial des données récoltées dans les transects. Nous avons observé deux tendances principales dans la répartition : l'une centrée sur les Prairies et les forêts-parcs, l'autre plus dispersée à la grandeur du Canada. Ces tendances coïncidaient avec l'importance relative des variables explicatives et les statistiques d'évaluation des modèles pour les deux groupes de répartition. Les variables qui expliquaient le mieux la répartition de la majorité des espèces avaient trait à l'hydrologie, bien que plus spécifiquement, elles différaient quelque peu d'une espèce à l'autre. Pour certaines variables importantes d'après les modèles, nous avons pu établir des liens clairs entre celles-ci et la répartition des espèces, tandis que pour d'autres, par exemple l'irrégularité du relief, nous pensons qu'elles pourraient simplement être le fruit de corrélations, attribuables au hasard, entre la répartition des espèces et les variables environnementales retenues lors du processus de consolidation des modèles. Considérant les performances de nos modèles, nous proposons que les cartes de répartition prédite soient utilisées dans le cadre de recherches futures et à des fins d'orientation des activités de conservation, surtout à l'intérieur des limites de notre aire d'étude.

Key Words: *abundance; Boosted Regression Tree; Canada; distribution; ducks; habitat; North America; species distribution model; waterfowl*

INTRODUCTION

Species distribution models (SDMs) provide quantitative descriptions of species' distributions based on associations between observational data and environmental predictors (Guisan and Zimmermann 2000, Elith and Leathwick 2009a). SDMs built with count data, called species abundance models (SAMs), quantify indices of abundance or density rather than

occurrence (Elith and Leathwick 2009a). Given suitable predictors, SDMs and SAMs can identify key habitat factors for species of interest (Millsom et al. 2000, Morrison et al. 2006), providing insight on autecology and informing conservation decisions. Predictive maps generated from these models provide basic information on species distribution and abundance (Guisan and Zimmermann 2000, Austin 2002). These maps can be used

to improve species range delineation (Loiselle et al. 2003), to test biogeographical hypotheses (Leathwick 1998, Anderson et al. 2002), to inform conservation strategies (Ferrier 2002, Ortega-Huerta and Peterson 2004, Moilanen et al. 2005, Elith and Leathwick 2009b), and to predict population responses to climate and land use change (Araújo et al. 2004, Thuiller 2004, Jetz et al. 2007). The focus of this paper is on SAMs for breeding waterfowl in boreal and southern Canada.

The urgency of conservation challenges in the Canadian boreal forest is increasingly recognized (Schindler and Lee 2010, Badiou et al. 2013, Berteaux 2013). To meet these challenges, we must quantify species abundances, distributions, and habitat relationships to target locations for conservation and identify the conflicts between wildlife habitat and intensive human activities (Slattery et al. 2011). The predictive maps generated through SDMs and SAMs may be particularly useful for these purposes in remote or unsurveyed areas, such as much of the boreal regions of northern Canada. A number of such studies are now under way, directed at boreal forest songbirds (Cumming et al. 2014), and waterfowl in eastern Canada (Lemelin et al. 2010, Börger and Nudds 2014) and western Canada (L. Armstrong, J. Devries, D. Howerter, B. Kazmerik, A. Richard, S. Slattery, and B. Tedford, *unpublished report*; Ducks Unlimited Canada, *unpublished report*). However, there has been no attempt to model the abundance of individual waterfowl species at national levels.

The lack of national waterfowl distribution models is surprising given the existence of an extensive and long-term aerial survey, the Waterfowl Breeding Population and Habitat Survey (WBPBS; Smith 1995). Each May since 1955, the U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) survey much of the breeding distributions of many waterfowl species (Fig. 1). The survey has created a large data set on individual species' abundances; this information was collected using relatively consistent sampling methods and survey design. The survey was originally designed to provide annual estimates of total duck population to inform hunting regulation (Nichols et al. 1995), although a substantial body of secondary research exists.

Some secondary applications exploit the survey's time series to model population dynamics, exploring relationships between population size and wetland availability, adult survival, annual productivity, and climate change (Pospahala et al. 1974, Anderson 1975, Johnson and Shaffer 1987, Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Podrutzny et al. 2002, Drever et al. 2012). More recently, the data set has been used to test new methodological approaches (Jamieson and Brooks 2004, Gimenez et al. 2009, Ross et al. 2012, Lawrence et al. 2013). However, there have been only limited attempts to use these data in predicting species distribution and abundance over large areas. Species abundance patterns have been mapped for several species at low spatial resolution (Johnson and Grier 1988). Annual abundances were correlated with the number of available wetlands (Johnson and Grier 1988), but only for regions with annual pond counts. Spatial interpolation of survey data has been used to predict abundances of Scaup (*Aythya affinis*, *Aythya marila*) pairs across their range (Hobson et al. 2009). However, no SAMs and their derived predictive abundance maps have been published for any waterfowl species at national extent.

Fig. 1. Top: Survey strata and transects of the Waterfowl Breeding Population and Habitat Survey (WBPBS) in Canada. Bottom: Some major lakes, rivers, and ecoregions referred to herein. The orange colors depict the four ecoregions of the prairie-parkland. References to “prairies” denote the northwestern glaciated plains if confined to Canada, or the union of the two plains ecoregions when including the USA. We split the boreal region (Brandt 2009) along the Ontario-Manitoba border to facilitate discussion of regional variation in waterfowl abundances.

We used the WBPBS database to develop high spatial resolution, predictive SAMs for 17 waterfowl species or species groups. Our modeling methodology was Boosted Regression Trees (BRTs) with a library of 78 environmental predictor variables selected a priori for their biological or physical effects on waterfowl species. We used the models to develop predictive relative abundance maps for most of Canada, excluding tundra areas where certain hydrological covariates were not available. In this paper, we present an evaluation of the models in terms of their predictive power and bias. We summarize the importance of different classes of environmental covariates: climatic, bioclimatic, hydrological, and landscape, and informally examine whether their relative importances differ by feeding or nesting habit.

Table 1. Species and species groups included in this study, along with the feeding and nesting guild assigned to each. Guild classifications are based on Bellrose (1980) and Johnsgard (2010).

Abbreviation	Common Name	Scientific Name	Feeding Guild	Nesting Guild
ABDU	American Black Duck	<i>Anas rubripes</i>	Dabbling	Ground
AGWT	Green-winged Teal	<i>Anas crecca</i>	Dabbling	Ground
AMWI	American Wigeon	<i>Anas americana</i>	Dabbling	Ground
BWTE	Blue-winged Teal	<i>Anas discors</i>	Dabbling	Ground
GADW	Gadwall	<i>Anas strepera</i>	Dabbling	Ground
MALL	Mallard	<i>Anas platyrhynchos</i>	Dabbling	Ground
NOPI	Northern Pintail	<i>Anas acuta</i>	Dabbling	Ground
NSHO	Northern Shoveler	<i>Anas clypeata</i>	Dabbling	Ground
BUFF	Bufflehead	<i>Bucephala albeola</i>	Diving	Cavity
GGOL	Goldeneye species	<i>Bucephala clangula</i> <i>Bucephala islandica</i>	Diving	Cavity
GMER	Merganser species	<i>Mergus merganser</i> <i>Mergus serrator</i> <i>Lophodytes cucullatus</i>	Diving	Cavity
GSCO	Scoter species	<i>Melanitta americana</i> <i>Melanitta fusca</i> <i>Melanitta perspicillata</i>	Diving	Ground
CANV	Canvasback	<i>Aythya valisineria</i>	Diving	Over-water
REDH	Redhead	<i>Aythya americana</i>	Diving	Over-water
RNDU	Ring-necked Duck	<i>Aythya collaris</i>	Diving	Over-water
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>	Diving	Over-water
GSCA	Scaup species	<i>Aythya affinis</i> <i>Aythya marila</i>	Diving	Over-water

METHODS

Waterfowl population data

We obtained waterfowl count data from the WBPHS (Smith 1995). Observers count adults of common waterfowl species seen within 200 m of fixed-wing aircraft flight transects. Within transects, counts are spatially assigned to segments of about 28.8 km (by 0.4-km width for a segment area of 11.2 km²). For details on survey methodology see Smith 1995, U.S. Fish and Wildlife Service 2012, and Zimmerman et al. 2012.

We modeled segment-level counts of total indicated pairs from the Canadian portion of the WBPHS survey area (2273 segments; Fig. 1). Total indicated pairs are an estimate of the number of pairs present based on the raw counts of actual pairs and lone males detected, taking into account species-specific life history (Dzubin 1969, Smith 1995, U.S. Fish and Wildlife Service 2012). We used 15 years of data from 1995 to 2010; data from 2007 were excluded because of a deviation in that year from the usual survey design (Silverman 2011). We used this temporal subset to capture a relatively static, recent, and representative sample of waterfowl counts.

We created 17 species abundance models, 13 for individual species and 4 for species that are grouped within the survey protocol (Table 1): Goldeneye (*Bucephala clangula*, *Bucephala islandica*), Merganser (*Mergus merganser*, *Mergus serrator*, *Lophodytes cucullatus*), Scoter (*Melanitta americana*, *Melanitta fusca*, *Melanitta perspicillata*), and Scaup. These four groups are referred to as species hereafter. To explore how characteristics of fitted models might vary with life history, species were assigned feeding and nesting guilds (Table 1) following Bellrose 1980 and

Johnsgard 2010. We classified the Merganser group as cavity nesting, despite the Red-breasted Merganser being a ground nester (Titman 1999), to reflect the more specialized nesting habit of the other two species in the group.

Environmental data

We selected environmental predictor variables based on previous studies of waterfowl habitat selection (Horn et al. 2005, Paszkowski and Tonn 2006, Suhonen et al. 2011) and songbird distribution (Cumming et al. 2014, Stralberg et al. 2014). Selection criteria included a priori hypotheses on likely ecological relationships (Mac Nally 2000, Barry and Elith 2006, Wenger and Olden 2012), constrained by availability and coverage. Where possible, we prioritized variables with more direct and likely causal relationships with waterfowl abundance, although proxy or indirect variables (Austin 2002) were used in many cases. We used a total of 78 climatic, bioclimatic, landscape, and hydrological predictor variables (Appendix 1).

Annual climatic variables and most bioclimatic indices were extracted from interpolated weather station data provided by Natural Resources Canada (McKenney et al. 2011). We calculated 30-year means of maximum and minimum monthly temperature, summarized to season, to capture potential temperature limits imposed on waterfowl abundance through vegetation, invertebrate phenology, and other seasonal influences (Appendix 1). We calculated 30-year means of total monthly precipitation, summarized to season, to capture the influence of precipitation through wetland conditions. We calculated 30-year standard deviations of monthly maximum temperature, minimum temperature, and precipitation as proxies for the probabilities of extreme events (Cumming et al. 2014, Lynch et al. 2014) Thirty-

year means of bioclimatic variables capture effects of seasonality in temperature and precipitation, the duration of the breeding season, and other factors (Appendix 1). Gross primary productivity was included as a proxy for food availability, both directly as plant food and indirectly through the provision of food for invertebrate prey.

We included variables for land cover to capture the influence of upland vegetation on waterfowl abundance and distribution, using the 250-m resolution Land Cover Map of Canada (Canada Centre for Remote Sensing 2008). The original 39 land cover classes were reclassified to 16 (Appendix 2). Proportional class areas were calculated per segment. Shannon's diversity index was calculated from these land cover proportions as an index of habitat heterogeneity. Topographic ruggedness (Integrated Remote Sensing Studio 2010) was included to represent the influence of landform or terrain.

To measure the type and abundance of surface waters, we used Ducks Unlimited Canada's Hybrid Wetland Layer (N. Jones, unpublished report) to calculate the proportional area of wetlands, including swamps, marshes, bogs, and fens, and open water, including shallow open water and deeper water systems, in each segment. Shoreline length and complexity, stream length, and the density and mean size of water bodies were measured from the National Hydrology Network product (Appendix 1; Natural Resources Canada 2007). These variables were included to represent influences of size, depth, and shape of wetlands as surrogates for availability of different foods for waterfowl.

All environmental variables were measured over a 1-km buffer around each segment, to account for imprecision in survey flight lines among years and to capture the influence of local environmental conditions. Spatial analysis relied on the integration of raster and vector data in PostGIS 2.0 (Obe and Hsu 2011).

Statistical methods

We built SAMs using BRTs, a machine learning technique that combines the advantages of decision-tree analyses with boosting and bagging algorithms to improve predictive performance (Friedman et al. 2000, Friedman 2002). BRTs have several advantages: they detect important relationships from large sets of predictor variables; they accommodate the complex, nonlinear relationships that often exist between species and habitat (Gaston 2003); they accommodate multiway interactions among predictor variables; they are insensitive to outliers and transformations of the predictor variables (Elith et al. 2008); and they show good predictive performance (Elith et al. 2006, 2008, Oppel et al. 2012).

We assumed that the annual counts of waterfowl pairs per segment were independent Poisson random variables conditional on the environmental predictors. We used BRT models with Poisson error and logarithmic link. The response variable was segment-level total indicated pairs. Because segments were surveyed for variable numbers of years, we summed total indicated pairs over all years sampled and included $\log(\text{years sampled})$ as an offset. Under the Poisson assumptions, this correctly accounts for variation in sampling effort among segments (Sólymos et al. 2013, Cumming et al. 2014). The model-fitted values and predictions were interpreted as the expected annual abundance in a segment.

To fit models, perform cross-validation analyses, and derive predictions, we used the *dismo* (Hijmans et al. 2012) and *gbm* (Ridgeway 2013) packages, running under R 2.15.2 (R Core Team 2012).

Within BRTs, user-selected parameters and constraints customize the complexity of the trees to prevent the overfitting that is common in simpler tree methods such as classification and regression trees (Guisan and Zimmermann 2000, Elith et al. 2008). The tree complexity parameter controls the number of permitted interactions among predictor variables (Elith et al. 2008). Based on preliminary analysis of model performance, we set the tree complexity parameter to four as representing a reasonable trade-off between flexibility and overfitting. Learning rates necessary to obtain approximately 1000 trees using a 10-fold cross-validation procedure detailed by Elith et al. 2008 varied among species, ranging from 0.015 for the Ruddy Duck (*Oxyura jamaicensis*) to 0.65 for the Mallard (*Anas platyrhynchos*).

We assessed the predictive performance of our models using repeated random subsampling cross-validation (Lu et al. 2011, section 10.6.1). We built 20 replicate BRT models for each species, using independent random samples of 70% of the segments ($n = 1591$). Model predictive performance was assessed by comparing predictions with observations for the remaining segments ($n = 682$). For each replicate model, we calculated four evaluation statistics. The first two statistics were the estimated intercepts and slopes of linear regression models of predictions against observations. The intercept measures the magnitude and direction of bias, with values close to 0 indicating low or no bias. The slope yields information about the consistency in the bias as a function of the mean, with a value of 1 indicating a consistent bias if the intercept is a nonzero value. The third statistic is Spearman's rank correlation, which measures overall consistency of predictions and observations. Finally, the squared deviance explained, D^2 , is the Poisson equivalent to the Normal R^2 and quantifies the goodness of fit. Spatial autocorrelation was assessed by comparing Moran's I calculated using residuals from BRT models with that calculated using residuals of a null model including only the mean. We calculated residual autocorrelation at two scales: the segment and the transect (see Appendix 3 for details). At each scale, we report statistics for both null model and BRT model residuals and their ratio. The ratio measures the degree to which the BRTs reduce spatial autocorrelation by conditioning on the covariates.

We mapped predicted pair abundance by applying BRT models to environmental variables, resampled to a consistent projection, i.e., geographic North American Datum 1983, on a 300-arcsecond grid. Cell areas over the prediction zone ranged from 27.9 to 68.1 km^2 . Predicted values were the expected pair abundance within a representative 11.2- km^2 section of each grid cell, conditional on the values of environmental predictors within the cell. For mapping and statistical comparison, these values were scaled to densities of pairs per square kilometer. Maps of species' abundances show means over 20 model replicates. We mapped prediction uncertainty as the coefficient of variation in density over the 20 replicates. This measure is independent of the mean and provides information on variability in the predictions resulting from particular data subsets and subsequent contributions of different environmental predictor variables.

We evaluated patterns of relative importance of different classes of predictor variables across feeding and nesting guilds. The relative importance of a predictor represents its influence within the model based on how often it is selected for splitting a tree, combined with how much it improves the model as a result of the split, averaged over all trees (Friedman 2001, Friedman and Meulman 2003, Elith et al. 2008). Relative importance was calculated for all predictor variables in a BRT model using formulas within the gbm package (Elith et al. 2008, Ridgeway 2013). For each predictor and each species, we calculated the mean $\pm$ 1 SD relative importance over the 20 BRT replicates. One caution in examining these models in terms of variable importance is that complex, nonlinear responses are permitted within BRTs. Therefore, simply examining variable importance only captures one element of the results.

To understand patterns in variable importance across species, we identified the class (Appendix 1) of the most influential variable across all species, and for each feeding and nesting guild. We also calculated the cumulative relative importance for each variable class across all species and for each feeding and nesting guild.

RESULTS

Model evaluation

Overall, models performed well. Across all species, mean $\pm$ SD was 0.78 ± 0.09 for Spearman's rank coefficient and 0.75 ± 0.13 for D^2 , indicating good correspondence between predictions and observations. Model calibration metrics indicated little bias in the predictions. A mean $\pm$ SD slope of 0.94 ± 0.03 and an intercept of 0.17 ± 0.08 across all species suggest slightly positively biased predictions, with slightly greater overprediction at low abundances. There was some variability in evaluation metrics among species and guilds (Fig. 2), indicating that models were better for some species than others. The residuals of 13 out of 17 species exhibited significant ($p < 0.05$) spatial autocorrelation at either the segment or transect scale (Appendix 3). Null ratios were much larger than 1 in all cases, indicating that the BRT models removed most of the spatial autocorrelation. The magnitude of Moran's I was generally higher at the segment scale than at the transect scale.

Most species had the lowest prediction uncertainty in the prairie-parkland region (Appendix 4), where the density of WBPHS transects is highest. Notable exceptions were the Canvasback (*Aythya valisineria*) and Redhead (*Aythya americana*), which showed localized areas of high uncertainty in western Ontario and eastern Manitoba (Appendix 4). The Ruddy Duck showed high uncertainty at the northern limits of the survey area and along the St. Lawrence water way (Appendix 4).

The mean coefficient of variation across all 17 species indicated that the highest uncertainty occurred in the Yukon, and along parts of the Pacific, northern, and Atlantic coasts (Fig. 3). Localized areas of high uncertainty also were scattered throughout the prediction area. These were mostly outside the area covered by the WBPHS (Fig. 1), especially in the tundra or western cordillera. Within the survey area, areas of localized high uncertainty were associated with large lakes or, as in northern Québec, with hydroelectric reservoirs.

Fig. 2. Evaluation metrics calculated from repeated subsample cross-validation, showing all 20 replicate Boosted Regression Tree (BRT) models for each species. Intensity of color represents overlapping of points from model replicates. Spearman and D^2 measure concordance between predictions and observations, and the amount of variance explained by the model, respectively. The slope and intercept are model calibration metrics related to the presence and consistency of bias. Refer to Table 1 for species abbreviations.

Fig. 3. Mean prediction uncertainty across 17 species models. Species-level uncertainty calculated as coefficient of variation of predicted abundance across 20 replicate Boosted Regression Tree (BRT) models. The blue outline shows the limits of the survey area (see Fig. 1).

Species abundance patterns

The highest total waterfowl density was predicted to occur in the prairie-parkland region (Fig. 4), and in scattered areas throughout the western boreal, including the MacKenzie River Delta, the unsurveyed southwestern Yukon, the Peace-Athabasca Parklands, the Athabasca River Delta, and the Saskatchewan River Delta. Within the survey area, total predicted densities were

lower in the eastern than in the western regions. The lowest total predicted densities occurred in the unsurveyed western cordillera, between the Pacific Ocean and the Rocky Mountains, and the Atlantic coastal areas.

Fig. 4. Summed relative abundances (per km²) of all 17 species or species groups. The prediction zone is limited by the area for which we had environmental data. The blue outline shows the limits of the survey area (see Fig. 1).

Within the WBPBS survey area, predictions of species' density from BRT analyses closely resembled spatial patterns in the raw observations (Appendix 4). Maximum raw densities exceeded maximum predicted densities for nine species (Green-winged Teal [*Anas crecca*], Blue-winged Teal [*Anas discors*], Goldeneye spp., Merganser spp., American Black Duck [*Anas rubripes*], American Wigeon [*Anas americana*], Canvasback, Redhead, and Scaup spp.), whereas the opposite was true for two species (Gadwall [*Anas strepera*] and Scoter spp.). Maximum densities were similar between observations and predictions for the remaining six species. The preponderance of underpredictions at high densities is consistent with mean model calibration slopes being less than 1.0 for all but one species (Fig. 2).

Ground-nesting dabbling species tended to have highest predicted densities in the prairie-parkland (Appendix 4). Exceptions include the American Black Duck, the Mallard, and the Green-winged Teal. The American Black Duck was predicted to occur across the entire eastern portion of our study area, including the boreal, Laurentians, and lowlands. It was predicted to occur at comparable densities on the west coast and in the southern interior of British Columbia. In addition to the prairie-parkland region, the Mallard was predicted to occur in most of the western boreal and the Laurentians and lowlands of Ontario. The Green-winged Teal was predicted to occur at low densities throughout nearly the entire study area. Predicted densities of American Wigeon, Northern Pintail (*Anas acuta*), and Northern Shoveler (*Anas clypeata*) were highest in the prairie-parkland region, but substantial abundances were also predicted in parts of the western boreal, including the northern limits of the region.

Cavity-nesting diving ducks were predicted to occur at low densities over most of our study area, excluding the prairies (Appendix 4). The Bufflehead (*Bucephala albeola*) had the most restricted distribution, covering most of the western boreal and

the aspen parkland, but was rare or absent in the eastern half of the study area. The Merganser group had the broadest predicted spatial distribution, occurring almost everywhere except the prairie region, with highest overall predicted abundances occurring in forested areas of Saskatchewan and the eastern boreal. The Goldeneye group showed a pattern similar to that of Mergansers, except for occurring at apparently lower abundances within the lowlands along the St. Lawrence River. The single ground-nesting diving species, the Scoter group, was predicted in highest densities along the northern limit of our study area, covering much of the northern boreal, including the unsurveyed Yukon (Appendix 4).

Overwater-nesting diving ducks tended to have high predicted densities in the prairie-parkland region, particularly in the aspen parkland (Appendix 4). Exceptions included the Ring-necked Duck (*Aythya collaris*), which according to the model, is very broadly distributed at low densities, and the Scaup group, which was predicted to occur over much of the western boreal and the northern portion of the eastern boreal in addition to the prairie-parkland region.

Habitat associations

The most important single variable within models was most frequently hydrological. Hydrological variables were selected more frequently than expected given their representation within the predictor set (Fig. 5). The next most important class was landscape variables, followed by climatic variables. Bioclimatic variables were never the most influential variable. Overwater-nesting ducks never had climatic variables as the top variable. None of the cavity nesters had landscape variables as the top variable.

Fig. 5. The number of species with each variable class as the most influential variable, expressed as a proportion of the number of species in the full species set or each feeding/nesting guild. Background shading represents the proportion of each variable class in the predictor dataset of 78 variables. Hydrological and landscape variables were most commonly the top variable, despite comprising a small proportion of the predictor dataset.

Within variable classes, some specific variables were frequently important across species. The proportion of open water was most commonly the top hydrological variable, being most important for five out of eight species (Appendix 4), followed by climate moisture index, which was most important for three out of eight species. Proportion of cropland was the top variable for four out of six species. The other top variables were each represented by only a single species (Appendix 4).

Across all species, the class total of variable relative influence was highest for climatic variables, followed by hydrological, landscape, and lastly bioclimatic variables (Fig. 6). This was also the case for all nesting and feeding guilds. For all species and among all guilds, hydrological variables had a disproportionately large share of influence given the number of variables in each class (Fig. 6). Species-specific tables of variable relative importances are presented in Appendix 4.

Fig. 6. The cumulative relative influence of each class, for the full species set, and for each feeding/nesting guild. Background shading represents the proportion of each variable class in the predictor dataset of 78 variables. Climatic variables had the highest total relative influence, while hydrological variables contributed a disproportionately high cumulative influence relative to their contribution to the predictor dataset (8 out of 78).

DISCUSSION

BRT models of waterfowl relative abundance performed well, according to a suite of standard evaluation metrics. Uncertainty maps show that predictions were most precise within the prairie-parkland region, where WBPHS transect density is highest. On visual inspection, large-scale patterns in predicted species' abundances were congruent with spatial patterns in the raw data (Appendix 4). A map of total predicted waterfowl abundance identified many areas traditionally recognized for their importance to waterfowl, including the prairie-parkland region, the MacKenzie River Delta, the Peace-Athabasca Parklands, and the Saskatchewan River Delta. The differing magnitudes of residual spatial autocorrelation across scales are consistent with the main sources of unexplained spatial structure being processes

acting at scales on the order of 10 km, i.e., among adjacent segments. Possible examples would be population processes such as short-distance natal dispersal or unmeasured environmental factors varying at that scale. In either case, we do not expect parameter estimates or variable selection to be markedly biased.

Species' abundances followed two main patterns. In the first pattern, high abundances were predicted within a relatively small area, most often the prairie-parkland region. This pattern was most common for ground-nesting dabbling ducks. In the second pattern, comparatively low abundances were predicted evenly across much of Canada, with no well-defined core area. This pattern was most common among the cavity-nesting ducks but also applied to the Green-winged Teal and Ring-necked Duck. Model statistical performance varied consistently among these two patterns, with models for ground-nesting and dabbling species having higher predictive performance than those for other nesting and feeding guilds.

For many species, the most influential predictor variable appeared to correspond to spatial pattern rather than to a clear biological process. Species with most of their population contained within the prairie-parkland region tended to be associated with the amount of cropland, climate moisture index, and water body density. These three variables likely delineate the prairie-parkland region through its hydrological regime or soil composition (Environment Canada 2010), either directly or as reflected in the abundance of farmland in the region. Species with higher densities in the aspen parkland, such as the overwater-nesting diving ducks, showed more relationships with the amounts of open water and shoreline and with the abundance of cropland and cropland-woodland landcover classes. Wetlands in the aspen parkland tend to have less emergent vegetation than those in the prairies (Johnson et al. 2005), so the open-water variable may represent these parkland wetlands. Similarly, the aspen parkland has more wooded areas than the nearby prairie region, while also maintaining large amounts of farmland (Johnson et al. 2005, Wiken et al. 2011), so amounts of cropland and cropland-woodland would help to distinguish this region from the prairies to the south and closed forests to the north. For species not concentrated within the prairie-parkland region, climate means and bioclimatic indices were more important than landcover variables. Species with larger, more homogenous distributions, including the cavity nesters and Ring-necked Ducks, had relatively high associations with variability in seasonal temperatures. Species with geographic distributions not corresponding to the two main patterns, such as Scoters in the North and the American Black Duck in the East, showed unique combinations of variable importance: an overwhelming importance of climate for Scoters and an extremely strong influence of topography for the Black Duck. Our results for waterfowl contrast somewhat with those showing that climate and climate variability are most important in describing or determining songbird distributions (Cumming et al. 2014).

When the importance of environmental correlates is determined primarily by the continental-scale geographic distribution of species abundances, the variables selected as most important may not be causally related to the pattern of interest. For instance, the importance of cropland variables does not suggest that prairie-parkland species prefer to nest within cropland. We are more likely

to see noncausal relationships when using indirect environmental predictors. One could improve the biological correspondence of important variables by repeating the analyses at regional scales (e.g., N. Barker, *unpublished report*). For example, restricting the analysis of prairie-parkland species to segments within the prairie-parkland would likely reduce the apparent importance of amount of cropland and instead yield insight into drivers of finer-scale patterns in abundance. In a regional analysis, it might be possible to use more direct environmental predictors rather than the proxies used here, because of increased data availability. These analyses might therefore yield more insight into biological relationships and habitat selection.

Waterfowl habitat selection has been summarized as “ducks like water” (Pimm 1994). Indeed, the most influential variable in 8 of our 17 species’ models was a hydrological one, and at least 1 hydrological variable was among top 5 most important variables for 16 species. The single exception was the Scoters, for which the top water-related variable was ranked 23rd. Our findings confirm that ducks do, in fact, like water. However, we have also shown that this glib summary is not the whole story. The type or distribution of water, or the way in which water is quantified, differs among species’ models, depending on either life history traits or spatial distributions. For ground-nesting dabbling ducks, the top hydrological variables were usually water body density, climate moisture index, amount of shoreline, and amount of open water. For overwater-nesting ducks, both the amount of open water and the amount of shoreline were important. These variables likely help identify the prairie-parkland region and separate the prairies from the aspen parkland. For the broadly distributed cavity-nesting species and the Ring-necked Duck, the amount of open water was highly important, potentially because it best identified available wetlands outside of the prairie-parkland region. The “amount of wetland” variable was in the top 20 variables for 9 species, but in the top 10 variables for only 2 species. Given the known dependence of many duck species on wetlands and marshes, particularly those with a hemimarsh condition of 50% plants and 50% open water (Murkin et al. 1982), it is surprising that this variable was relatively unimportant. We posit that this result stems from the difficulty of classifying wetlands from satellite imagery. A finer wetland classification system that separates wetlands into classes such as marsh, swamp, bogs, fens, river, and lake might shed more light on actual habitat selection and preference, although such a product has yet to be developed at the national extent. An even finer classification that incorporates detailed wetland attributes such as size, shoreline characteristics, bathymetry, phosphorus, food supply, and presence of fish would likely prove more effective, but no such data are available at national extents.

Model limitations

Visibility correction

The primary use of WBPBS data is to estimate annual continental waterfowl populations. Detection of waterfowl from aerial surveys is not perfect. The resulting counts are nearly always underestimates, although overestimates do occur, e.g., for Scaup (Austin et al. 2002). To account for incomplete detection in estimating continental population sizes, raw counts are adjusted by visibility correction factors (VCFs). VCFs are estimated from ground surveys on a subsample of survey segments (Smith 1995).

We did not incorporate these VCFs in our models for three reasons: (1) they were generated at the coarser crew area scale (Smith 1995), and this imprecision may lead to inaccurate visibility correction at the segment scale; (2) they were generated by different methods and frequencies for different regions (e.g., boreal vs. prairie-parkland; Smith 1995), casting doubt on the validity of comparing corrected abundances among regions; and (3) none are available for the eastern half of the survey area (Zimmerman et al. 2012), precluding the creation of Canada-wide models. We modeled the uncorrected observed counts. Under the assumption that detectability is constant across habitats, all observed counts are underestimated in the same proportion. Thus, our model predictions could be interpreted as relative abundances.

In fact, detectability does vary among habitats and species, as shown by the variation in VCFs among species and regions: 0.42-12.6 in the boreal, 0.60-29.10 in the prairie-parkland, and 0.92-10.30 in the tundra. Therefore, we expect results of our models to be biased in some degree, both in terms of predicted abundances and in the habitat associations identified. We have conducted some preliminary analyses comparing models with and without VCFs, and found that they yielded visually similar spatial patterns in predicted abundances and fairly similar identification of at least the top three influential habitat associations. Despite these apparent similarities, we encourage caution when comparing relative abundances between regions or among species, because VCFs are variable and our predicted maps are a combination of true abundances and unknown detection probabilities. We expect that our maps are most reliably used for single species within regions with relatively homogenous detectability. If desired, one could adjust our predictions post hoc using known VCFs. Our preliminary analyses suggested that the spatial variation in predictions echoed the variation in VCFs across crew areas. Therefore, one could simply multiply our predicted densities by VCFs where available, yielding a very rough approximation of VCF-corrected models. Our models and resulting predictions could certainly be improved were regionally specific VCFs, obtained at fine spatial scales using consistent methods, to become available.

Late nesters

For some species, surveys are conducted before pairs are settled on the breeding grounds (Austin et al. 2002). As a consequence, late-nesting species such as Scaup and Scoters may be observed outside their breeding ranges (Schummer et al. 2013). However, if migrating in groups, staging and migrating birds would be excluded from the total indicated pair count. We expect the numbers of out-of-range birds to be low relative to the numbers observed on the breeding grounds, even in late-nesting species. Therefore, we expect the influence of these observations on our models to be low. This is one advantage of having used segment-level counts, rather than presence, as the response variable.

Variable interpretation

There are limits to interpreting a BRT simply in terms of the most important variables. BRTs permit complex, nonlinear responses. Here, we specified a tree complexity of four, allowing several levels of interactions. With enough predictor variables, BRT models can likely match most observed spatial patterns. Therefore, even when the top variables are the same or similar across species, individual

response curves and interactions can lead to substantial variation among fitted models and subsequent predictions of species' abundance. BRTs are therefore better suited for prediction than for biological understanding (Elith et al. 2008).

Extrapolation

Extrapolation, or out-of-sample prediction, occurs when we predict for times or locations not represented in the data (Wenger and Olden 2012). Coefficient-of-variation maps (Fig. 3 and Appendix 4) indicated more uncertainty outside the survey area than within, as expected. Within the survey area, we noticed localized areas of particularly high uncertainty near the coasts of very large water bodies, e.g., big lakes or oceans. This uncertainty may further be associated with extrapolation error. Models were built using data sampled near smaller water bodies, but were extrapolated to raster cells adjacent to extremely large water bodies.

We observed a few instances of clear overprediction outside the survey area, notably for the Scoters and the American Black Duck. The northern range of the Scaup group was best explained by climatic variables. These variables typically exhibit gradients, but only part of the range of these covariates was contained within the sampling space. As one consequence, predicted Scaup abundance was high in the far North of our study area, probably further north than they actually occur (Savard et al. 1998). Similarly, climatic and topographic variables explained spatial variation in American Black Duck numbers across the area sampled by the WBPBS. Conditions in Eastern Canada, where the Black Duck occurs, are also found in western coastal and southern interior British Columbia, where the species does not occur except as a few local introductions. Because these western areas are unsurveyed, our data set contained no information to constrain model creation. Therefore, the models predicted high abundances of the species because the habitat is theoretically suitable. One approach when faced with extrapolation errors would be clipping maps to regions of high confidence. We chose not to do this because these errors represent information, either pointing to potentially suitable habitat or to a need for methodological refinement.

Four factors may limit the extrapolation reliability of our models. First, while machine-learning techniques typically have high in-sample prediction reliability, they tend to have somewhat limited extrapolative ability because the models include complex nonlinear relationships (Wenger and Olden 2012). We attempted to restrict overfitting by using relatively simple trees, but this is not always sufficient. One solution is to use simpler models (Wenger and Olden 2012), such as generalized linear models, but these do not readily accommodate the number of predictor variables used here. An a priori reduced covariate set would be necessary, a step we specifically intended to avoid. As suggested by Cumming et al. (2014), it should be possible to use the most influential variables identified in this study as predictor variables in future generalized linear model analyses. Regional analyses may further facilitate the selection of a smaller set of predictors.

Second, model extrapolation is more accurate when predictions are restricted to the range of environmental conditions sampled and when the full relationship of species' abundance to predictors is captured (Thuiller et al. 2004, Randin et al. 2006, Elith and Leathwick 2009a). The figures within Appendix 1 suggest that

unsurveyed portions within our study area present novel environmental conditions. This would account for the extrapolations of Scoters beyond the northern limit of published range maps. There is no easy solution to this problem. Ideally, new data or data from other sources would be collected or otherwise obtained for these regions (Audubon and Cornell Lab of Ornithology, eBird, <http://ebird.org/content/ebird/>).

Third, the set of environmental variables used in this analysis was limited by availability and extent, and included many indirect or proxy variables. This can degrade model prediction reliability (Mac Nally 2000, Randin et al. 2006). Prediction errors may occur if proxies are not causal or consistent across the study area (McIntire and Fajardo 2009).

Fourth, these models were based on environmental variables only, and did not account for historical or biological factors such as dispersal, evolution, or competition. If current patterns in waterfowl presence or abundance were influenced by such factors, then the resulting habitat model may predict theoretically suitable habitat rather than actual patterns in abundance or distribution. For example, the western limit of the American Black Ducks in central Canada may be because of biogeohistorical factors having nothing to do with current climate or topography. Further methodological research is necessary to explore the incorporation of such historical factors.

Applications

These models and the resulting maps suggest where, and for which species, existing range maps are in need of revision. For example, we predicted relatively high extralimital abundances of Ring-necked Duck. Having confirmed with raw survey data that our predictions accurately reflect observations of this species (Appendix 4), the range map of Ring-necked Duck could be updated. For other species, such as American Wigeon and Scoters, we predicted high extralimital abundances beyond the survey area. However, we would not recommend updating existing range maps for these species. Rather, in such cases, our predictions represent hypotheses derived from the existing data that should be tested against independent data.

Our models may also serve as guides for future modeling exercises or field studies. For instance, some future analyses may involve regional subsets of the data, to compare the variables identified as important in continental versus regional models. The prediction and associated uncertainty maps may guide where more research effort is needed, for instance in the southern Yukon where high abundances were predicted in association with high uncertainty. Future modeling focused on this area, particularly if accompanied by ground-truthing surveys, may identify important waterfowl areas for some species, or may simply show the current predictions to be an extrapolation error. In that case, definitive information would lead to reformulation of the models, possibly identifying more mechanistically informative variables. Extralimital predictions provide information for models of nonwaterfowl species as well. These unexpected occurrences can point to directions for future research in poorly surveyed areas of the breeding or wintering ranges.

Our goal was to produce predictive maps of waterfowl relative abundance, in large part to support the waterfowl conservation initiatives of Ducks Unlimited Canada. Although transect-level

observations can yield an overall picture of waterfowl distributions and coarsely suggest some areas of high abundance, model prediction maps provide finer-scaled information over larger regions. The maps can also be used in future research to improve or compare modeling methods, to quantify aspects of waterfowl distribution ecology, and to evaluate and execute conservation planning strategies.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/699>

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Appendix 1. Environmental variables used in Boosted Regression Trees of waterfowl abundance. The table describes each variable while the figures depict the range of each variable within the WBPHS segments (model input) and within the entire study area (study area).

Variable	Time Period	Resolution	Source	Calculation
<i>Climatic</i>				
mumaxtx : 30-year mean maximum temperature in season x^a (n=4 seasons)	1981-2010	10 km	NRCAN ^b	Mean calculated for each cell across 30 years of monthly grids. Weighted mean calculated for each unit ^c . Seasonal mean calculated.
mumintx : 30-year mean minimum temperature in season x^a (n=4 seasons)	"	"	"	"
mupcpix : 30-year mean precipitation in season x^a (n=4 seasons)	"	"	"	"
sdmaxtx : 30-year standard deviation of maximum temperature in month x (n=12 months)	"	"	"	Standard deviation calculated for each cell across 30 years of monthly grids. Weighted mean calculated for each unit.
sdmintx : 30-year standard deviation of minimum temperature in month x (n=12 months)	"	"	"	"
sdpcpix : 30-year standard deviation of precipitation in month x (n=12 months)	"	"	"	"
<i>Bioclimatic</i>				
timpseas : 30-year mean temperature seasonality; monthly mean variance around the annual mean (n=1)	"	"	"	Mean calculated for each cell across 30 annual grids. Weighted mean calculated for each unit.
pcpseas : 30-year mean precipitation seasonality; monthly mean variance around the annual mean (n=1)	"	"	"	"
temprange : 30-year mean temperature annual range; difference between the maximum of the warmest month and the minimum of the coldest month (n=1)	"	"	"	"
wetmonth : 30-year mean of precipitation in wettest month (n=1)	"	"	"	"
drymonth : 30-year mean of precipitation in driest month (n=1)	"	"	"	"
mugrow : 30-year mean of growing season length; number of days above 5°C (n=1)	"	"	"	"
sdgrew : 30-year standard deviation of growing season length (n=1)	"	"	"	"
gpp : 7-year average gross primary productivity, in gC/m ² /yr ^e (n=1)	2000-2006	1 km	Numerical Terradynamic Simulation Group ^f	Weighted mean calculated for each unit.

Variable	Time Period	Resolution	Source	Calculation
<i>Landscape</i>				
lcc.C.i : Proportion of area covered by land cover class <i>i</i> , described in Table A2 (n=12 cover classes).	Static (2005)	250 m	Centre for Remote Sensing ^g	C_i / C_t C _i = Count of cells of land c class <i>i</i> within unit C _t = Total cell count in unit
sdi : Shannon Diversity Index for land cover classes (n=1)	"	"	"	$\sum_{i=1}^m (P_i * \ln(P_i))$ m = number of land cover types P _i = proportion of area covered by land cover type
topo : Index of topographic ruggedness; calculated as coefficient of variation from a DEM (n=1)	Static (2000 and 1993-1996)	1 km	Integrated Remote Sensing Studio ⁱ	Weighted mean calculated for each unit.
<i>Hydrological</i>				
cmi : 30-year average climate moisture index; cm precipitation – cm potential evaporation per year ^d (n=1)	1961-1990	10 km	NRCAN	Weighted mean calculated for each unit.
hwlwetland/hwlwater : Proportion of area covered by open water or wetlands ⁱ (n=2 classes)	Static (2000 and 2009)	25 m	Ducks Unlimited Canada	Count of water or wetland cells within each unit, expressed as a proportion of total number of cells within unit.
streamlength : Total length of streams in m stream/km ² area (n=1)	Static (created from data from 1994-2010)	1:10,000-1:50,000	National Hydrology Network ⁱ	Length of all streams, divided by unit area (to standardize).
wbdens : Density of water bodies in unit neighbourhood (n=1)	"	"	"	Number of water bodies intersected by unit, divided by unit area (to standardize).
muareawbods : Mean size of water bodies in unit neighbourhood (n=1)	"	"	"	Mean area of water bodies intersected by unit, divided by unit area (to standardize).
shorelength : Length of shoreline in km shoreline/km ² area (n=1)	"	"	"	Total shoreline (perimeter of water bodies) contained within unit, divided by unit area (to standardize).
shorecx : Shoreline complexity (area-weighted shape index for water bodies in unit neighbourhood) (n=1)	"	"	"	Ratio of water body perimeter to area measured against a circle standard. Mean across water bodies weighted by area of water body within unit.

^a Seasons as follows: *Winter*: Dec, Jan, Feb; *Spring*: Mar, Apr, May; *Summer*: Jun, Jul, Aug; *Autumn*: Sept, Oct, Nov.

^b McKenney, D. W., M. F. Hutchinson, P. Papadopol, K. Lawrence, J. Pedlar, K. Campbell, E. Milewska, R. F. Hopkinson, D. Price, and T. Owen. 2011. Customized spatial climate models for North America. *Bulletin of the American Meteorological Society* 92:1611–1622.

^c unit = segment buffer or grid cell (see *Methods: Environmental data*).

^d Calculated from modified Penman-Monteith potential evapotranspiration. Hogg, E. H. 1994. Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research* 24:1835–1845.

^e from the MOD17A3 product. Zhao, M., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment* 95:164–176.

(<http://www.ntsg.umn.edu/project/mod17>)

^f NTSG at the University of Montana. (<http://www.ntsg.umn.edu/>)

^g Latifovic 2008. Landcover Map of Canada 2005. (<http://www.nrcan.gc.ca/earth-sciences/geography-boundary/remote-sensing/optical/2208>)

^h Integrated Remote Sensing Studio (<http://databasin.org/datasets/14d70746535e4be99aaf66595cc0b677>)

ⁱ Jones, N. 2010. Hybrid Wetland Layer (Version 2.1) User Guide. Ducks Unlimited Canada.

^j National Hydrology Network. 2007. Government of Canada. Available on Geobase. (<http://www.geobase.ca/geobase/en/data/nhn/description.html>)

Appendix 2. Reclassification of Land Cover of Canada (2005)’s original 39 land cover classes to 16. Note that the following classes were excluded from the analyses to exclude duplication with other covariates or because of low values within the study area, although they were included in the calculation of SDI: burn (7), water (14), wetland/bog (15), and snow/ice (16).

Reclass Name	Reclass Number	Original Class Name
High density evergreen	1	Temperate or subpolar needle-leaved evergreen closed tree canopy
Medium density evergreen	2	Temperate or subpolar needle-leaved evergreen medium density, moss-shrub understory Temperate or subpolar needle-leaved evergreen medium density, lichen-shrub understory
Low density evergreen	3	Temperate or subpolar needle-leaved evergreen low density, shrub-moss understory Temperate or subpolar needle-leaved evergreen low density, lichen (rock) understory Temperate or subpolar needle-leaved evergreen low density, poorly drained Sparse needle-leaved evergreen, herb-shrub cover
Deciduous	4	Cold deciduous closed tree canopy Cold deciduous broad-leaved, low to medium density Cold deciduous broad-leaved, medium density, young regenerating
Mixed, deciduous-dominated	5	Mixed cold deciduous - needle-leaved evergreen closed tree canopy Low regenerating young mixed cover
Mixed, evergreen-dominated	6	Mixed needle-leaved evergreen - cold deciduous closed tree canopy Mixed needle-leaved evergreen - cold deciduous closed young tree canopy Mixed needle-leaved evergreen - cold deciduous, low to medium density needle-leaved evergreen, low to medium density
Burn	7	Recent burns Old burns
Shrubland	8	High-low shrub dominated Herb-shrub-bare cover

Reclass Name	Reclass Number	Original Class Name
Barren	10	Polar grassland, herb-shrub
		Shrub-herb-lichen-bare
		Lichen-shrub-herb-bare soil
		Low vegetation cover
		Lichen barren
		Lichen-sedge-moss-low
		Rock outcrops
Cropland	11	High biomass cropland
		Medium biomass cropland
		Low biomass cropland
Cropland-woodland	12	Cropland-woodland
Urban	13	Urban and Built-up
Water	14	Water bodies
		Mixes of water and land
Wetland/bog	15	Herb-shrub poorly drained
		Wetlands
		Lichen-spruce bog
Snow/Ice	16	Snow or ice

Appendix 3. Assessment of spatial autocorrelation in BRT model residuals.

For each species, we tested for spatial autocorrelation by calculating Moran's I statistics on Pearson residuals. For BRT models, we calculated the residuals using the mean of 20 segment-level predictions, and corrected for the bootstrap variance. We also calculated Pearson residuals for a null model including only the mean effect. The "Null Ratio", which measures the reduction in spatial autocorrelation resulting from conditioning on model covariates, is calculated as the Moran's I statistic for the null model divided by that for the BRT models. In both cases, Moran's I was calculated over two distance bands, corresponding to the range of distances between adjacent segments (20-50 km) and between adjacent transects (30-120 km).

Species	Scale	Moran I Statistic	p-Value	Null Ratio
ABDU	segment	0.043	0.005	12.233
ABDU	transect	0.022	0.001	22.634
AGWT	segment	0.022	0.091	23.072
AGWT	transect	-0.009	0.887	43.500
AMWI	segment	0.046	0.003	16.038
AMWI	transect	0.018	0.003	35.358
BUFF	segment	0.029	0.040	19.101
BUFF	transect	0.006	0.154	65.070
BWTE	segment	0.055	0.001	13.793
BWTE	transect	0.037	< 0.001	18.998
CANV	segment	0.046	0.003	11.356
CANV	transect	0.015	0.010	26.021
GADW	segment	0.096	< 0.001	7.299
GADW	transect	0.042	< 0.001	15.183
GGOL	segment	-0.018	0.853	20.608
GGOL	transect	< 0.001	0.468	2816.706
GMER	segment	-0.018	0.845	28.130
GMER	transect	-0.002	0.610	177.650
GSCA	segment	0.039	0.011	13.840
GSCA	transect	0.019	0.002	23.881
GSCO	segment	0.016	0.171	54.310
GSCO	transect	0.034	< 0.001	25.290
MALL	segment	0.066	< 0.001	11.906
MALL	transect	0.026	< 0.001	27.338
NOPI	segment	0.104	< 0.001	7.041
NOPI	transect	0.028	< 0.001	21.967
NSHO	segment	0.061	< 0.001	11.688
NSHO	transect	0.018	0.003	35.621
REDH	segment	0.072	< 0.001	6.867
REDH	transect	0.035	< 0.001	11.513
RNDU	segment	0.024	0.074	15.842
RNDU	transect	0.003	0.284	72.741
RUDU	segment	0.039	0.010	5.979
RUDU	transect	0.016	0.008	10.793

Appendix 4. Individual species results.

For each species, we present three maps: 1) observed segment-level density from the WBPHS dataset; 2) mean predicted relative density per km² with NatureServe range map (BirdLife International and NatureServe 2012; blue outline); and 3) coefficient of variation (CV) of predicted abundance with an outline of the survey area as reference. We also present a table of the relative importance of environmental predictors. This relative importance table includes the mean and SD across 20 replicates for each variable, in descending order of importance (a percentage of 100), up to a cumulative sum of 80%. For each species, we discuss our predicted distribution and influential predictor variables in relation to published range maps and habitat associations.

American Black Duck – ground nesting dabbling

Our models predicted a relatively homogenous distribution of Black Ducks across eastern Canada, including the Boreal, Laurentians, and Great Lakes Lowlands, which is consistent with Longcore et al. (2000) and Johnsgard (2010). Our models also predicted relatively high densities on the west coast of Canada. We interpret these predictions as artefacts of extrapolation error from a model that does not incorporate biogeohistory of the Black Duck. This region of predicted high abundances outside of the Black Duck's range represents theoretically suitable habitat in an uninhabited area. The existence of a small, introduced population of American Black Ducks in southwest British Columbia on the mainland and Vancouver Island (Campbell et al. 1990, Longcore et al. 2000) suggests that this area represents suitable Black Duck habitat. See Model Limitations, in the Discussion for a thorough discussion of model limitations related to extrapolation.

Variable	Mean %	SD	Cumulative %
Topographic Ruggedness	13.77	3.88	13.77
Mean Climate Moisture Index	7.24	2.37	21.01
Standard Deviation of Maximum Temperature in November	5.85	1.67	26.86
Mean Autumn Precipitation	5.67	1.93	32.53
% Wetland (HWL)	3.14	0.95	35.68
Standard Deviation of Minimum Temperature in April	3.06	1.48	38.74
Standard Deviation of Maximum Temperature in February	2.77	1.16	41.51
Standard Deviation of Maximum Temperature in December	2.75	0.99	44.25
Standard Deviation of Minimum Temperature in February	2.38	0.99	46.63
Mean Waterbody Area (neighbourhood metric)	2.29	1.20	48.93
Standard Deviation of Precipitation in October	2.09	0.63	51.02
Mean Summer Precipitation	1.94	0.28	52.97
Standard Deviation of Maximum Temperature in August	1.93	1.14	54.90
Standard Deviation of Maximum Temperature in September	1.89	0.56	56.80
Standard Deviation of Maximum Temperature in March	1.70	0.44	58.49
Standard Deviation of Maximum Temperature in October	1.59	0.63	60.09
Mean Summer Maximum Temperature	1.58	0.71	61.67
Amount of Shoreline (km/km ²)	1.56	0.49	63.22
Standard Deviation of Maximum Temperature in January	1.25	0.39	64.47
Standard Deviation of Precipitation in May	1.22	0.64	65.69
Standard Deviation of Maximum Temperature in June	1.10	0.70	66.79
Standard Deviation of Precipitation in December	1.09	0.28	67.88

Mean Summer Minimum Temperature	1.06	0.66	68.94
Mean Gross Primary Productivity	1.03	0.35	69.97
Standard Deviation of Maximum Temperature in April	1.02	0.47	70.99
Standard Deviation of Precipitation in April	0.96	0.23	71.95
Precipitation Seasonality	0.91	0.41	72.86
Standard Deviation of Minimum Temperature in October	0.90	0.38	73.76
Shannon's Diversity Index of Land Cover Types	0.84	0.37	74.60
Amount of Streams (km/km ²)	0.78	0.27	75.38
Standard Deviation of Precipitation in August	0.78	0.53	76.16
Standard Deviation of Minimum Temperature in November	0.75	0.53	76.91
% Cropland-woodland	0.75	0.60	77.66
% Shrubland	0.74	0.24	78.40
Standard Deviation of Minimum Temperature in March	0.74	0.24	79.13
Mean Shoreline Complexity (neighbourhood metric)	0.73	0.19	79.86
Standard Deviation of Precipitation in March	0.72	0.24	80.58

Black Duck abundance was associated with topographic ruggedness, CMI, variability in maximum November temperature, mean autumn precipitation, and amount of wetland. The top four of these variables may capture the species' eastern-restricted distribution, while the amount of wetland represents the species' association with water. Black Ducks are reported to nest in most wetland types, including coastal marshes, beaver ponds, and boreal bogs (Longcore et al. 2000, Johnsgard 2010). Given this wide range in habitat suitability, along with the eastern-restricted range, most of the most important variables likely capture the spatial correlation rather than a mechanistic association with any given habitat type or limiting factor.

Green-winged Teal – ground nesting dabbling

Our models predicted the highest densities of Green-winged Teal in the aspen parkland, the Peace-Athabasca Delta, and the Slave River Lowlands, consistent with Johnsgard (2010). Lower densities were observed in the prairies, which is consistent with a reported avoidance of eutrophic, agricultural lakes in favour of wooded ponds of the aspen parkland (Moisan et al. 1967). Our observed distribution extended well north of published ranges

(Johnsgard 2010, BirdLife International and NatureServe 2012), but these areas were partly extrapolations beyond the survey area (see Model Limitations, in Discussion).

Variable	Mean %	SD	Cumulative %
Mean Climate Moisture Index	7.82	1.26	7.82
Density of Waterbodies (neighbourhood metric)	6.67	1.16	14.49
Precipitation Seasonality	3.31	0.63	17.79
Mean Gross Primary Productivity	3.17	0.65	20.96
Standard Deviation of Maximum Temperature in March	2.75	0.87	23.71
Amount of Streams (km/km ²)	2.68	0.77	26.39
Standard Deviation of Maximum Temperature in October	2.66	0.61	29.05
Amount of Shoreline (km/km ²)	2.57	0.78	31.61
% Cropland-woodland	2.53	0.67	34.14
Topographic Ruggedness	2.50	0.57	36.64
% Deciduous Forest	2.44	0.70	39.09
Standard Deviation of Minimum Temperature in November	2.41	0.61	41.49
Standard Deviation of Maximum Temperature in December	2.36	0.72	43.86
Standard Deviation of Maximum Temperature in September	2.13	0.64	45.99
Standard Deviation of Precipitation in August	1.78	0.53	47.77
Mean Spring Maximum Temperature	1.78	0.59	49.55
Standard Deviation of Growing Season Length	1.78	0.38	51.32
Standard Deviation of Minimum Temperature in June	1.73	0.48	53.05
% Wetland (HWL)	1.69	0.33	54.74
Standard Deviation of Precipitation in October	1.55	0.53	56.29
Mean Shoreline Complexity (neighbourhood metric)	1.36	0.24	57.65
Standard Deviation of Minimum Temperature in January	1.34	0.48	58.99
Mean Autumn Maximum Temperature	1.33	0.49	60.32
Standard Deviation of Precipitation in December	1.33	0.46	61.65
Mean Spring Precipitation	1.31	0.47	62.97
% Open Water (HWL)	1.29	0.30	64.26
Mean Summer Precipitation	1.25	0.40	65.51
Mean Autumn Minimum Temperature	1.25	0.41	66.76
Standard Deviation of Maximum Temperature in February	1.23	0.54	67.99
Standard Deviation of Minimum Temperature in March	1.17	0.40	69.16
Mean Summer Maximum Temperature	1.13	0.35	70.29
Standard Deviation of Maximum Temperature in January	1.12	0.30	71.41
Standard Deviation of Maximum Temperature in August	1.08	0.38	72.49
Standard Deviation of Minimum Temperature in December	1.07	0.30	73.56
% Shrubland	1.05	0.37	74.61
Annual Range in Temperature	0.99	0.25	75.60
Standard Deviation of Precipitation in September	0.98	0.23	76.58
% Cropland	0.90	0.28	77.48
Mean Waterbody Area (neighbourhood metric)	0.89	0.30	78.38
Standard Deviation of Maximum Temperature in April	0.87	0.28	79.25
% Mixed Forest - Deciduous-dominated	0.87	0.26	80.11

Green-winged Teal abundance was most closely associated with climate moisture index (CMI) and segment-level water body density. The next two most important covariates were precipitation seasonality and gross

primary productivity (GPP). CMI may play a role in isolating the aspen parkland, where highest densities occurred, from the drier prairies to the south and the more western boreal to the North. The relationship with water body density is consistent with (Johnson and Grier 1988), and may also represent selection for smaller water bodies, as reported by Toft et al. (1982), Décarie et al. (1995), Rempel et al. (1997), and Kindopp (2002). This association with water body density may also represent a spatial rather than biological relationship, since this variable appeared higher in the aspen parkland than the surrounding areas, when assessed visually. The sixth most important variable was stream length, which is consistent with Lemelin et al. (2010)'s finding that the species prefers moving water to lakes or ponds. Even the top variables showed low relative importance, which agrees with previous findings that this species shows few and weak habitat associations (Kindopp 2002). At the individual wetland scale used by Kindopp (2002), this result may indicate flexibility in habitat selection (Johnson 1995, Nummi and Pöysä 1997). At large scales such as in our study, it also likely represents the extremely broad distribution with homogenous abundance across much of the species' range (Johnsgard 2010). Most of the broadly-distributed species we studied exhibited the same pattern, where top predictor variables had lower relative importance, or explanatory power, than the top variables for narrowly-distributed species.

American Wigeon – ground nesting dabbling

Our models predicted high abundances of American Wigeon in the prairie-parkland and throughout the western boreal forest, with the highest densities in the prairie-parkland region and the MacKenzie Delta. While this is generally consistent with published range maps (Johnsgard 2010, BirdLife International and NatureServe 2012), our predictions extended beyond the recognized northern limits, though these areas were partly extrapolations.

Our maps also predict limited abundances in Eastern Canada, while the NatureServe range excludes most of this region. These eastern predictions are consistent with observations from the WBPHS and from the Breeding Bird Atlases of Ontario and Québec (Bird Studies Canada et al. 2009, Regroupement QuébecOiseaux et al. 2014).

Variable	Mean %	SD	Cumulative %
Standard Deviation of Minimum Temperature in October	12.36	4.02	12.36
Standard Deviation of Maximum Temperature in September	10.76	1.99	23.12
Amount of Shoreline (km/km ²)	6.92	1.52	30.04
Mean Climate Moisture Index	4.40	0.73	34.44
Mean Autumn Precipitation	4.22	1.82	38.66
Standard Deviation of Growing Season Length	3.77	0.93	42.42
% Open Water (HWL)	3.44	1.07	45.86
Density of Waterbodies (neighbourhood metric)	3.10	0.80	48.96
Precipitation Seasonality	3.04	0.96	52.00
% Cropland	2.92	0.76	54.91
Topographic Ruggedness	2.38	0.67	57.30
Standard Deviation of Maximum Temperature in January	2.10	0.63	59.40
Standard Deviation of Precipitation in April	1.96	1.00	61.36
Standard Deviation of Minimum Temperature in April	1.93	1.06	63.29
Standard Deviation of Maximum Temperature in October	1.40	0.93	64.68
Standard Deviation of Maximum Temperature in February	1.37	1.01	66.05
Mean Winter Precipitation	1.28	0.47	67.33
Standard Deviation of Minimum Temperature in February	1.19	0.69	68.52
% Shrubland	1.19	0.64	69.71
Standard Deviation of Minimum Temperature in September	1.11	0.58	70.82
Standard Deviation of Maximum Temperature in November	1.09	0.42	71.91
Standard Deviation of Maximum Temperature in May	1.09	0.62	73.00
Mean Gross Primary Productivity	1.05	0.29	74.05
Standard Deviation of Precipitation in October	0.99	0.41	75.05
Mean Summer Maximum Temperature	0.95	0.35	75.99
Standard Deviation of Maximum Temperature in December	0.91	0.31	76.91
Shannon's Diversity Index of Land Cover Types	0.88	0.22	77.79
% Cropland-woodland	0.86	0.21	78.64
Standard Deviation of Maximum Temperature in August	0.84	0.16	79.49
Standard Deviation of Maximum Temperature in March	0.76	0.39	80.25

American Wigeon abundance was most closely associated with variability in minimum October temperature and maximum September temperature, as well as amount of shoreline and CMI. The bioclimatic variables likely capture the large-scale spatial pattern of abundance. The seventh and eighth most important variables were amount of open water and water body density. In association with the amount of shoreline, these variables capture the relationship of American Wigeon to water. In particular, the amount of open water may relate to the American Wigeon's use of more open water for feeding, compared to other *Anas* species (Johnsgard 2010).

Blue-winged Teal – ground nesting dabbling

Our models predicted high densities of Blue-winged Teal concentrated in the prairie-parkland region and lower densities elsewhere. This pattern is generally consistent with Johnson and Grier (1988). NatureServe (BirdLife International and NatureServe 2012) and Johnsgard (2010) suggest a larger range than depicted in our map, but Johnsgard highlights that the species is not a common breeder outside of the prairies. Our map therefore

highlights the difference in abundances within and outside of the core breeding area. The map of raw observations suggest that Blue-winged Teals inhabit southern Ontario, which is consistent with the Breeding Bird Atlas of Ontario (Bird Studies Canada et al. 2009) and the NatureServe range map. Our model, however, predicted very low abundances (effectively absence) of Blue-winged Teals within southern Ontario. There may be insufficient data within the survey to allow the model to accurately predict Blue-Winged Teals in this location.

Variable	Mean %	SD	Cumulative %
% Cropland	24.92	2.53	24.92
Density of Waterbodies (neighbourhood metric)	10.34	2.94	35.26
Amount of Shoreline (km/km ²)	8.08	2.21	43.34
Standard Deviation of Minimum Temperature in June	6.22	1.92	49.57
Mean Climate Moisture Index	6.06	1.75	55.63
Standard Deviation of Precipitation in August	3.12	1.29	58.75
Standard Deviation of Maximum Temperature in August	3.12	1.48	61.87
Precipitation Seasonality	2.94	0.56	64.81
Standard Deviation of Maximum Temperature in April	2.12	1.29	66.93
% Open Water (HWL)	1.97	0.60	68.90
Topographic Ruggedness	1.82	0.38	70.72
Amount of Streams (km/km ²)	1.39	0.36	72.11
Standard Deviation of Precipitation in December	1.36	0.74	73.47
Standard Deviation of Maximum Temperature in June	1.25	0.88	74.72
% Deciduous Forest	1.23	0.27	75.95
Standard Deviation of Precipitation in November	1.22	1.13	77.18
% Cropland-woodland	1.18	0.31	78.36
Standard Deviation of Minimum Temperature in May	1.14	0.74	79.49
Standard Deviation of Precipitation in October	1.13	0.72	80.63

Abundance of Blue-winged Teal was most closely associated with amount of cropland, followed by water body density, amount of shoreline, and the standard deviation of minimum June temperature. The most important variable contrasts with Rohwer et al. (2002)'s suggestion that Blue-winged Teals prefer grassland over cropland. However, we suspect that at the scale of our study, cropland was associated with grassland habitat and pothole type wetlands. Therefore, the amount of cropland likely acted as a proxy, capturing the high abundance of Blue-winged Teal within the prairie-parkland and low abundance elsewhere. The association with water body density and amount of shoreline may relate to the species' dependence on small, shallow, and productive wetlands Rohwer et al. (2002), though it could also represent a spatial association of the species with the aspen parklands of Saskatchewan and Manitoba where the species was most abundant.

Gadwall – ground nesting dabbling

Our models predicted apparently high densities of Gadwall concentrated in the prairie-parkland region, and lower densities elsewhere, which is consistent with published range maps (Johnson and Grier 1988, Johnsard 2010, BirdLife International and NatureServe 2012).

Variable	Mean %	SD	Cumulative %
% Cropland	29.77	2.64	29.77
% Open Water (HWL)	11.22	1.42	40.99
Mean Climate Moisture Index	9.04	2.90	50.03
Amount of Shoreline (km/km ²)	6.09	1.83	56.12
Precipitation Seasonality	5.06	1.42	61.18
Density of Waterbodies (neighbourhood metric)	3.21	1.20	64.39
Standard Deviation of Maximum Temperature in August	2.86	1.25	67.25
Amount of Streams (km/km ²)	2.46	0.91	69.71
Standard Deviation of Maximum Temperature in September	2.10	0.64	71.81
% Cropland-woodland	1.58	0.25	73.38
% Wetland (HWL)	1.13	0.17	74.52
Topographic Ruggedness	1.06	0.17	75.58
Mean Gross Primary Productivity	1.04	0.34	76.61
Standard Deviation of Precipitation in October	0.93	0.53	77.55
Mean Shoreline Complexity (neighbourhood metric)	0.93	0.25	78.48
Standard Deviation of Precipitation in July	0.90	0.41	79.37
Shannon's Diversity Index of Land Cover Types	0.85	0.22	80.22

Gadwall abundance was most closely associated with amount of cropland, followed by amount of open water and CMI. As with Blue-winged Teals, Gadwalls avoid cropland in favour of untilled upland (Higgins 1977), but at our study's scale and resolution, this positive association with cropland likely represents a continental spatial association with the prairie-parklands rather than actual selection for cropland habitat. CMI may separate the prairies from the parkland via a negative water balance. A positive association with open water may reflect the preference of Gadwall for wetlands comprised of 50:50 water to emergent vegetation compared to those with more vegetation (Kaminski and Prince 1981).

Mallard – ground nesting dabbling

Our models predicted high densities of Mallards in the prairie-parkland region, and throughout the Peace-Athabasca Delta, the Slave River Lowlands, and the Great Lakes Lowlands. Pockets of relatively high density were also predicted in the MacKenzie Delta and in southern Yukon. The overall range appears similar to

published accounts (Johnsgard 2010, BirdLife International and NatureServe 2012), including the fact that highest densities are reported in the prairie-parkland region (Drilling et al. 2002).

Variable	Mean %	SD	Cumulative %
% Cropland	41.50	1.88	41.50
Amount of Shoreline (km/km ²)	6.29	1.50	47.79
Density of Waterbodies (neighbourhood metric)	5.38	1.37	53.17
Mean Climate Moisture Index	3.65	1.46	56.82
Precipitation Seasonality	3.56	1.16	60.38
% Open Water (HWL)	3.17	0.73	63.55
Standard Deviation of Minimum Temperature in June	2.73	1.23	66.28
Standard Deviation of Maximum Temperature in August	1.89	1.01	68.17
% Cropland-woodland	1.76	0.29	69.93
Topographic Ruggedness	1.74	0.55	71.67
Standard Deviation of Maximum Temperature in April	1.27	0.49	72.93
Amount of Streams (km/km ²)	1.22	0.46	74.15
Standard Deviation of Maximum Temperature in June	1.13	0.54	75.29
Standard Deviation of Precipitation in August	1.00	0.62	76.28
% Wetland (HWL)	0.96	0.15	77.24
% Deciduous Forest	0.96	0.20	78.20
Mean Spring Maximum Temperature	0.75	0.29	78.95
Mean Summer Minimum Temperature	0.72	0.15	79.67
Shannon's Diversity Index of Land Cover Types	0.70	0.18	80.37

As with other dabbling species, Mallard abundance was associated with amount of cropland, amount of shoreline, water body density, and CMI. These variables seem to best explain high abundances in the prairie-parkland region and lower abundances in the surrounding area. The amount of shoreline and water body density may also relate to Mallards' preference for shallow wetlands (Stewart and Kantrud 1973). The association with cropland may or may not represent a biological correspondence in this case since Mallards prefer to nest in tall vegetation, including hayfields (Johnsgard 2010), but also reportedly avoid nesting in cropland (Greenwood et al. 1995). The sixth most important variable was the amount of open water, which may reflect the preference of Mallards for more open water areas in the boreal forest (Drilling et al. 2002).

Northern Pintail – ground nesting dabbling

Our models predicted high densities of Pintails in the prairies but also in the Yukon, along the northern limits of our study area, and among some of the parkland areas. Johnsgard (2010) classified Pintails as a low Arctic species, likely reflecting its high abundance in Alaska, which is consistent with our predictions of the species

living in the North. That the species is abundant in the prairies is also consistent with Johnson and Grier (1988) and Johnsgard (2010).

Variable	Mean %	SD	Cumulative %
Mean Climate Moisture Index	36.31	2.52	36.31
Amount of Shoreline (km/km ²)	7.72	1.86	44.03
% Cropland	5.43	1.48	49.46
Standard Deviation of Minimum Temperature in November	4.99	1.60	54.45
Topographic Ruggedness	3.97	0.62	58.41
Standard Deviation of Maximum Temperature in September	3.40	1.28	61.81
% Open Water (HWL)	2.94	0.83	64.75
Standard Deviation of Maximum Temperature in August	2.06	0.57	66.82
Density of Waterbodies (neighbourhood metric)	1.95	0.72	68.76
Standard Deviation of Maximum Temperature in February	1.87	0.52	70.64
Mean Winter Precipitation	1.64	0.46	72.28
Standard Deviation of Precipitation in October	1.58	0.70	73.85
Amount of Streams (km/km ²)	1.27	0.34	75.12
Standard Deviation of Minimum Temperature in February	1.24	0.66	76.36
Standard Deviation of Maximum Temperature in October	1.08	0.33	77.44
Standard Deviation of Maximum Temperature in July	1.03	0.33	78.46
% Cropland-woodland	0.95	0.15	79.41
Standard Deviation of Maximum Temperature in November	0.92	0.42	80.33

Pintail abundance was most closely associated with CMI, followed by amount of shoreline, amount of cropland, two temperature variability measures (November and September), and topographic ruggedness. As with other dabblers, the high abundance of the species in the western prairies likely explains the association with the former three variables. The Pintail reportedly has a stronger dependence on open habitats than other dabblers (Johnsgard 2010), which is reflected in higher abundances in the prairies. This pattern is reflected in the relationships with CMI and topographic ruggedness. When examining maps of predictor variables, variability in maximum temperature in September identifies the prairie region, while variability in minimum November temperature likely identifies portions of the boreal region where Pintails occurred in higher abundances. While the importance of amount of shoreline may reflect a biological relationship describing Pintails dependence on water, it appears that most of the variables simply reflect a spatial rather than mechanistic relationship. This finding is not surprising because observed Pintails likely represent at least two populations: those inhabiting the prairies and those that fly directly to the arctic (Miller et al. 2005, Mattsson et al. 2012). Modelling the two groups together may yield predictive environmental variables that are not mechanistically meaningful.

Northern Shoveler – ground nesting dabbling

Our models predicted high densities of Shovelers in the prairies, along with the Yukon and among some of the parkland areas around the Slave Lakes, which is generally consistent with published ranges (Dubowy 1996, BirdLife International and NatureServe 2012). Johnsgard (2010), however, states that it is an uncommon breeder in Alaska, suggesting that our predicted northern abundances are higher than traditionally recognized. Our model

predicted only very low abundances of Shovelers within Ontario and Québec, despite observations within Ontario in the raw data, and records of breeding Shoveler in the Breeding Bird Atlases of Ontario and Québec (Bird Studies Canada et al. 2009, Regroupement Québec Oiseaux et al. 2014).

Variable	Mean %	SD	Cumulative %
Mean Climate Moisture Index	22.91	3.46	22.91
% Cropland	19.06	3.43	41.97
Amount of Shoreline (km/km ²)	8.14	1.91	50.11
% Open Water (HWL)	5.65	1.10	55.76
Density of Waterbodies (neighbourhood metric)	3.83	1.86	59.60
Topographic Ruggedness	3.74	0.48	63.33
Standard Deviation of Maximum Temperature in August	3.09	1.10	66.42
Precipitation Seasonality	2.15	1.00	68.57
Standard Deviation of Maximum Temperature in September	2.00	0.69	70.58
Amount of Streams (km/km ²)	1.85	0.49	72.43
% Wetland (HWL)	1.32	0.26	73.75
% Cropland-woodland	1.24	0.26	74.99
Mean Shoreline Complexity (neighbourhood metric)	0.88	0.30	75.88
Standard Deviation of Maximum Temperature in January	0.85	0.29	76.72
Standard Deviation of Precipitation in October	0.79	0.32	77.51
Standard Deviation of Minimum Temperature in November	0.78	0.26	78.29
Standard Deviation of Precipitation in August	0.77	0.30	79.06
% Deciduous Forest	0.74	0.22	79.80
Mean Gross Primary Productivity	0.70	0.29	80.51

Shoveler abundance was most closely associated with CMI and amount of cropland, followed by three hydrological variables: amount of shoreline; amount of open water; and water body density. As with other western dabblers, the former two variables may capture the high densities of the species in the prairie-parkland region. Shovelers prefer hayland and avoid nesting in cropland (Greenwood et al. 1995), a subtle distinction our coarse-scale models likely did not identify. Since they especially favour shallow, eutrophic wetlands with abundant floating animal and plant life (Johnsgard 2010), we might have expected a strong relationship with GPP. Instead, we found a strong relationship with hydrological variables, suggesting that GPP may not indicate wetland productivity as intended, and/or that this coarse-scale analysis identifies variables associated with large-scale patterns in abundance but not reflecting fine-scale habitat selection.

Bufflehead – cavity nesting diving

Compared to dabblers, the predicted distribution of Buffleheads was more homogenous across the study area, with a less well-defined core area. The highest densities were located in the Peace-Athabasca Parklands, with a few areas of high abundance in the southern aspen parkland. The species was nearly absent from the prairies,

which is consistent with published ranges (Johnsgard 2010, BirdLife International and NatureServe 2012) and their dependence on trees for nesting.

Variable	Mean %	SD	Cumulative %
Standard Deviation of Minimum Temperature in July	18.81	3.02	18.81
% Deciduous Forest	9.04	1.28	27.85
Standard Deviation of Growing Season Length	5.40	0.91	33.26
Density of Waterbodies (neighbourhood metric)	4.62	1.14	37.88
Standard Deviation of Minimum Temperature in November	4.21	0.71	42.08
% Open Water (HWL)	4.10	1.11	46.19
Amount of Shoreline (km/km ²)	2.80	0.71	48.99
Standard Deviation of Minimum Temperature in December	2.36	0.53	51.34
% Cropland-woodland	2.15	0.80	53.50
Standard Deviation of Maximum Temperature in November	1.77	0.80	55.27
Standard Deviation of Maximum Temperature in December	1.72	0.41	56.99
Standard Deviation of Minimum Temperature in June	1.56	0.74	58.55
Standard Deviation of Minimum Temperature in January	1.30	0.38	59.85
Standard Deviation of Minimum Temperature in October	1.26	0.57	61.11
Mean Climate Moisture Index	1.24	0.41	62.35
Mean Summer Maximum Temperature	1.19	0.32	63.54
Mean Shoreline Complexity (neighbourhood metric)	1.15	0.36	64.69
Standard Deviation of Maximum Temperature in October	1.14	0.63	65.83
Mean Gross Primary Productivity	1.13	0.23	66.96
Precipitation Seasonality	1.12	0.52	68.08
Standard Deviation of Maximum Temperature in September	1.11	0.46	69.19
Standard Deviation of Maximum Temperature in March	1.06	0.37	70.24
Mean Summer Precipitation	1.06	0.58	71.30
Mean Autumn Minimum Temperature	1.00	0.41	72.30
Standard Deviation of Maximum Temperature in January	1.00	0.32	73.30
Topographic Ruggedness	0.94	0.30	74.24
Standard Deviation of Maximum Temperature in February	0.93	0.30	75.17
Mean Growing Season Length	0.91	0.47	76.08
Annual Range in Temperature	0.83	0.26	76.91
Standard Deviation of Maximum Temperature in April	0.83	0.40	77.74
Standard Deviation of Minimum Temperature in March	0.80	0.24	78.54
Standard Deviation of Precipitation in June	0.79	0.48	79.33
% Mixed Forest - Deciduous-dominated	0.78	0.28	80.11

Bufflehead abundance was closely associated with variability in minimum July temperature, followed by amount of deciduous forest and variability in growing season length. Three of the seven most important variables were hydrological: water body density; amount of open water; and shore length. We suspect that the bioclimatic variables are associated with the large-scale spatial pattern of abundance, though the variability in growing season may reflect the species' more boreal distribution. The relationship with amount of deciduous forest is as expected for a cavity-nesting species "associated with temperate forests" (Johnsgard 2010). The top three hydrological variables identified were wetland density, stream length, and the amount of open water as measured by the high resolution HWL product. These relationships are consistent with the species' association with small ponds (Gauthier 1993) on riparian networks such as produced by beavers (Naiman et al. 1988).

Goldeneye species – cavity nesting diving

Our models predicted that goldeneyes live across much of our study area, with higher densities in the East and around the aspen parkland. Although our models grouped the Barrow's and Common Goldeneye species together, we might conclude that the majority of the observations were for Common Goldeneye, given the larger distribution of this species. Our predictions largely match range maps (BirdLife International and NatureServe

2012), including absence from the southern lowlands, and are consistent with higher abundances in eastern provinces (Johnsgard 2010). As with the Bufflehead, goldeneye species are much less abundant in the prairies (Eadie et al. 1995), which is reflected in our predictions.

Variable	Mean %	SD	Cumulative %
% Open Water (HWL)	20.76	3.40	20.76
Precipitation Seasonality	7.75	2.26	28.51
Mean Summer Maximum Temperature	6.29	1.58	34.80
Standard Deviation of Minimum Temperature in July	3.09	0.74	37.89
Standard Deviation of Minimum Temperature in December	2.30	0.89	40.19
% High Density Evergreen Forest	2.21	0.52	42.40
Topographic Ruggedness	2.01	1.02	44.41
Mean Waterbody Area (neighbourhood metric)	1.99	0.57	46.40
Standard Deviation of Minimum Temperature in June	1.99	0.39	48.39
Shannon's Diversity Index of Land Cover Types	1.95	0.57	50.33
Mean Gross Primary Productivity	1.91	0.68	52.24
% Deciduous Forest	1.79	0.43	54.03
% Mixed Forest - Evergreen-dominated	1.73	0.45	55.76
Amount of Shoreline (km/km ²)	1.66	0.39	57.43
Standard Deviation of Minimum Temperature in August	1.66	0.55	59.08
Mean Winter Precipitation	1.65	0.68	60.73
Mean Autumn Minimum Temperature	1.58	0.82	62.31
Standard Deviation of Maximum Temperature in August	1.53	0.46	63.84
Mean Spring Minimum Temperature	1.50	0.47	65.35
% Low Density Evergreen	1.34	0.53	66.69
Mean Growing Season Length	1.29	0.44	67.98
Mean Summer Minimum Temperature	1.21	0.38	69.20
Standard Deviation of Minimum Temperature in January	1.10	0.86	70.30
Standard Deviation of Growing Season Length	1.08	0.43	71.38
Density of Waterbodies (neighbourhood metric)	1.05	0.60	72.43
Mean Spring Maximum Temperature	1.03	0.49	73.46
Standard Deviation of Minimum Temperature in March	1.02	0.53	74.49
% Mixed Forest - Deciduous-dominated	0.97	0.28	75.46
Standard Deviation of Minimum Temperature in November	0.94	0.44	76.40
Mean Shoreline Complexity (neighbourhood metric)	0.90	0.30	77.30
Standard Deviation of Precipitation in January	0.84	0.39	78.14
Mean Summer Precipitation	0.84	0.22	78.99
Standard Deviation of Precipitation in November	0.84	0.43	79.83
Standard Deviation of Minimum Temperature in October	0.83	0.36	80.66

Goldeneye abundance was most closely associated with amount of open water, followed by precipitation seasonality and the mean maximum July temperature. The amount of high density evergreen forest was ranked sixth most important, and the amount of coniferous forest was ranked twelfth. The very strong association with amount of open water may represent both a biological and spatial association. It is the only hydrological variable in the top seven, and likely captures the dependence of the species on water bodies for feeding. Goldeneyes also prefer water bodies with less shoreline vegetation (Eadie et al. 1995), which may be reflected in this open water variable. Area of water bodies was the eighth most important variable, and the goldeneye group represents one of the only species with this variable ranked within the top 10 variables. Goldeneyes tend to prefer smaller lakes

over larger ones, but they also prefer lakes with a depth of at least 1 m (Eadie et al. 1995, 2000). Our water body area variable may be providing information about water depth, as we had intended. The roughly quadratic association with mean July temperature appears to be a spatial correspondence explaining the species' trans-continental distribution. The association with coniferous and deciduous forest further captures this trans-continental distribution, as well as the dependence of the species on trees for cavities, which is stronger for Common Goldeneyes than for Barrow's (Johnsgard 2010).

Merganser species – cavity nesting diving

Our models predicted a very similar distribution for merganser species as it did for goldeneye species. Like the goldeneyes, this model grouped more than one species, but our predictions are largely consistent with the combined distribution of the three species included in the group (BirdLife International and NatureServe 2012).

Variable	Mean %	SD	Cumulative %
% Open Water (HWL)	21.44	2.24	21.44
% High Density Evergreen Forest	10.60	1.22	32.04
Standard Deviation of Minimum Temperature in June	5.60	0.98	37.65
Mean Waterbody Area (neighbourhood metric)	4.48	1.46	42.13
Amount of Shoreline (km/km ²)	3.10	0.50	45.23
Density of Waterbodies (neighbourhood metric)	3.01	0.85	48.24
Standard Deviation of Maximum Temperature in November	2.85	0.46	51.09
Mean Gross Primary Productivity	2.12	0.66	53.21
Mean Shoreline Complexity (neighbourhood metric)	2.08	0.46	55.29
% Wetland (HWL)	1.98	0.72	57.27
Mean Summer Maximum Temperature	1.90	0.54	59.16
% Low Density Evergreen	1.80	0.53	60.96
% Mixed Forest - Evergreen-dominated	1.65	0.27	62.61
Standard Deviation of Maximum Temperature in July	1.48	0.22	64.09
Standard Deviation of Minimum Temperature in August	1.42	0.44	65.51
Shannon's Diversity Index of Land Cover Types	1.36	0.29	66.87
Topographic Ruggedness	1.25	0.21	68.13
Standard Deviation of Maximum Temperature in February	1.15	0.26	69.28
Mean Summer Minimum Temperature	1.09	0.46	70.37
Standard Deviation of Precipitation in June	1.05	0.23	71.43
Amount of Streams (km/km ²)	1.04	0.38	72.47
% Mixed Forest - Deciduous-dominated	1.01	0.22	73.47
Standard Deviation of Precipitation in July	0.98	0.37	74.46
Standard Deviation of Maximum Temperature in June	0.94	0.32	75.40
% Medium-density Evergreen Forest	0.93	0.31	76.33
Standard Deviation of Minimum Temperature in January	0.93	0.41	77.26
Mean Growing Season Length	0.90	0.54	78.16
Standard Deviation of Precipitation in April	0.90	0.33	79.06
Standard Deviation of Minimum Temperature in July	0.86	0.31	79.92
Standard Deviation of Maximum Temperature in April	0.80	0.22	80.72

Merganser abundance was strongly associated with amount of open water, followed by amount of high density evergreen forest, variability in minimum June temperature, area of water bodies in the surrounding area, amount of shoreline, and water body density. Relationships with forest and the climatic variable likely originate from the transcontinental distribution of this species group. The relationship with evergreen forest may capture the association of the Common Merganser with forested landscapes, but the more flexible, facultative ground-nesting Red-breasted Merganser is somewhat less associated with forests (Johnsgard 2010). This species group was closely associated with more water variables than most other species. In addition to the above four hydrological variables, shoreline complexity and amount of wetland were the ninth and tenth most important variables. This pattern may reflect the species' strong dependence on relatively deeper, more oligotrophic, open and clear water for foraging for fish (Mallory and Metz 1999, Johnsgard 2010).

Scoter species – ground nesting diving

Our models predicted the highest abundances of scoters along the northern limits of our study area and in much of the Yukon. Although the survey, and therefore our model, does not distinguish among the scoter species, published range maps suggest that our predictions likely represent Surf and White-winged Scoter, since these species live primarily in the surveyed western boreal forest (Johnsgard 2010, BirdLife International and

NatureServe 2012), with highest population densities in the northwestern boreal (Bellrose 1980). This is somewhat consistent with our prediction maps, but our models predictions extended well north of published ranges, likely due to extrapolation error (see Discussion).

Variable	Mean %	SD	Cumulative %
Mean Autumn Maximum Temperature	36.89	7.82	36.89
Mean Winter Minimum Temperature	16.02	5.22	52.91
Standard Deviation of Minimum Temperature in October	7.17	3.67	60.08
Mean Growing Season Length	6.56	4.77	66.64
Standard Deviation of Minimum Temperature in April	4.54	2.57	71.19
Mean Spring Precipitation	3.34	1.84	74.53
Standard Deviation of Minimum Temperature in September	2.69	1.20	77.22
Mean Gross Primary Productivity	2.52	2.74	79.74
Temperature Seasonality	2.37	1.00	82.11

Scoter abundance was strongly related to mean maximum autumn temperature, followed by mean minimum winter temperature, variability in minimum October temperature, and the mean growing season length. Moreso than any other species, the top variables for scoters were climatic in nature, many of which have a strong North-South gradient. This gradient explains the overprediction north of the treeline. Scoters are generally associated with freshwater lakes and ponds in boreal forests (Savard et al. 1998) and avoid tundra (Haszard and Clark 2007, Johnsgard 2010). However, since the raw survey data did not include areas of tundra to calibrate the models, scoter density appears to be increasing with latitude, which is captured by environmental variables with North-South gradients, leading to overprediction in northern areas beyond the survey limits and treeline.

Canvasback – over-water nesting diving

Our models predicted high densities of Canvasback in the aspen parkland, as well as some areas of higher abundance in the Yukon, which is largely consistent with published accounts of their distribution (Mowbray 2002) and range limits (Johnsgard 2010, BirdLife International and NatureServe 2012), however the

NatureServe range excludes the MacKenzie Delta, in contrast with relatively high observed and predicted abundances in the region.

Variable	Mean %	SD	Cumulative %
% Open Water (HWL)	10.87	1.50	10.87
Amount of Shoreline (km/km ²)	10.12	1.87	20.99
% Cropland	9.76	2.18	30.75
% Deciduous Forest	5.20	1.17	35.95
Precipitation Seasonality	4.11	0.89	40.06
% Cropland-woodland	3.97	0.78	44.03
Standard Deviation of Maximum Temperature in August	3.23	1.21	47.26
Topographic Ruggedness	3.17	0.66	50.43
Amount of Streams (km/km ²)	3.15	0.89	53.57
Density of Waterbodies (neighbourhood metric)	2.83	0.90	56.41
Mean Climate Moisture Index	2.75	1.52	59.16
Mean Spring Maximum Temperature	1.54	0.94	60.70
Mean Summer Precipitation	1.51	0.90	62.21
Mean Winter Maximum Temperature	1.46	0.64	63.68
Standard Deviation of Precipitation in August	1.46	0.60	65.13
Standard Deviation of Maximum Temperature in September	1.42	0.49	66.55
Standard Deviation of Minimum Temperature in November	1.35	0.78	67.90
Standard Deviation of Precipitation in November	1.31	0.52	69.21
Mean Winter Precipitation	1.09	0.18	70.31
Standard Deviation of Minimum Temperature in October	1.07	0.53	71.38
% Wetland (HWL)	1.01	0.38	72.39
Standard Deviation of Minimum Temperature in June	0.94	0.48	73.33
% Mixed Forest - Deciduous-dominated	0.93	0.59	74.26
Standard Deviation of Maximum Temperature in March	0.90	0.35	75.16
Standard Deviation of Precipitation in July	0.85	0.41	76.01
Standard Deviation of Precipitation in October	0.85	0.58	76.86
Standard Deviation of Maximum Temperature in February	0.81	0.32	77.67
Mean Autumn Precipitation	0.80	0.37	78.47
Shannon's Diversity Index of Land Cover Types	0.79	0.30	79.26
Mean Winter Minimum Temperature	0.75	0.52	80.01

The most important variables in predicting Canvasback abundance were the amount of open water, the amount of shoreline, and the amount of cropland, followed by the amount of deciduous forest. The first two variables capture the dependence of the species on water, and may reflect the Canvasback's need for relatively large, open bodies of water for nesting, landing, and takeoff (Johnsgard 2010). While Johnsgard (2010) states that Canvasbacks prefer shallow prairie marshes, Mowbray (2002) and our work suggest a closer dependence on lakes and deeper ponds and marshes. The association with cropland and deciduous forest likely reflects the high abundance in the aspen parkland (Mowbray 2002).

Redhead – over-water nesting diving

Our models predicted high densities of Redheads in the aspen parkland forest, which is largely consistent with published range maps (Johnsgard 2010, BirdLife International and NatureServe 2012).

Variable	Mean %	SD	Cumulative %
% Cropland	12.23	1.61	12.23
Amount of Shoreline (km/km ²)	11.47	2.42	23.70
% Open Water (HWL)	8.67	1.40	32.37
Density of Waterbodies (neighbourhood metric)	6.41	2.05	38.78
% Cropland-woodland	5.13	0.92	43.91
Precipitation Seasonality	3.52	0.80	47.43
Topographic Ruggedness	3.10	0.95	50.53
% Deciduous Forest	2.89	1.06	53.42
Amount of Streams (km/km ²)	2.53	0.66	55.95
Mean Summer Precipitation	2.44	1.02	58.39
Standard Deviation of Precipitation in August	1.86	0.68	60.25
Standard Deviation of Maximum Temperature in May	1.69	0.62	61.94
Standard Deviation of Precipitation in September	1.61	1.43	63.55
% Low Density Evergreen	1.49	1.30	65.05
Mean Gross Primary Productivity	1.41	0.77	66.46
Mean Precipitation in the Wettest Month	1.41	0.67	67.86
Shannon's Diversity Index of Land Cover Types	1.34	0.73	69.20
Standard Deviation of Maximum Temperature in August	1.31	0.49	70.51
Standard Deviation of Precipitation in December	1.20	0.85	71.71
% Wetland (HWL)	1.14	0.50	72.85
Standard Deviation of Precipitation in November	1.12	0.46	73.97
Mean Climate Moisture Index	1.10	0.56	75.07
Mean Spring Maximum Temperature	1.04	0.49	76.10
Standard Deviation of Maximum Temperature in November	1.00	0.59	77.10
Standard Deviation of Minimum Temperature in June	0.87	0.46	77.97
Standard Deviation of Maximum Temperature in September	0.81	0.25	78.79
Standard Deviation of Maximum Temperature in January	0.75	0.46	79.53
Standard Deviation of Precipitation in June	0.73	0.28	80.26

The variables most closely associated with Redhead abundance were similar to those for the Canvasback. Amount of cropland was most important, followed by amount of shore line, amount of open water, water body density, and amount of cropland-woodland. The first four describe the large-scale pattern of association with the prairie-parkland region as well as the association of the species with water. The association with cropland-woodland likely captures the high abundances in the aspen parkland. Like Canvasback, Redheads prefer deeper, more open water bodies (Woodin and Michot 2002), and they are more abundant in the parklands, despite a reported association with nonforested wetlands (Johnsgard 2010).

Ring-necked Duck – over-water nesting diving

Our models predicted an extensive range of relatively homogenous abundance for Ring-necked Ducks. Slightly higher abundances were predicted within the published breeding range (BirdLife International and NatureServe 2012), but our models also predicted relatively high abundances well outside the documented range limits. Since

raw observations of the species also indicate relatively high abundances outside the documented range, our modeled predictions may be more correct than current range maps in this case.

Variable	Mean %	SD	Cumulative %
% Deciduous Forest	7.37	1.33	7.37
% Open Water (HWL)	6.39	0.59	13.76
Amount of Shoreline (km/km ²)	4.51	0.94	18.28
Mean Gross Primary Productivity	4.22	0.54	22.50
Standard Deviation of Minimum Temperature in June	3.71	0.71	26.21
Density of Waterbodies (neighbourhood metric)	3.18	0.45	29.39
Mean Summer Maximum Temperature	2.88	0.78	32.27
Standard Deviation of Maximum Temperature in April	2.76	0.66	35.03
Standard Deviation of Growing Season Length	2.72	0.68	37.75
Standard Deviation of Precipitation in June	2.28	0.47	40.03
Mean Winter Precipitation	2.23	0.95	42.26
% Mixed Forest - Evergreen-dominated	2.00	0.43	44.26
Standard Deviation of Precipitation in November	1.83	0.27	46.09
Topographic Ruggedness	1.78	0.39	47.87
Standard Deviation of Minimum Temperature in December	1.76	0.52	49.63
% Mixed Forest - Deciduous-dominated	1.73	0.28	51.35
Amount of Streams (km/km ²)	1.62	0.23	52.98
% Wetland (HWL)	1.62	0.38	54.59
Standard Deviation of Precipitation in August	1.56	0.35	56.15
Mean Summer Minimum Temperature	1.55	0.36	57.70
Standard Deviation of Precipitation in January	1.54	0.39	59.23
Standard Deviation of Minimum Temperature in September	1.48	0.34	60.72
Standard Deviation of Precipitation in December	1.46	0.41	62.18
Standard Deviation of Precipitation in July	1.33	0.29	63.51
Standard Deviation of Maximum Temperature in November	1.26	0.31	64.77
% Medium-density Evergreen Forest	1.25	0.29	66.01
Standard Deviation of Maximum Temperature in June	1.22	0.22	67.23
Standard Deviation of Maximum Temperature in August	1.18	0.44	68.41
Standard Deviation of Minimum Temperature in July	1.17	0.26	69.58
% Low Density Evergreen	1.09	0.41	70.66
Standard Deviation of Maximum Temperature in September	1.01	0.38	71.67
Shannon's Diversity Index of Land Cover Types	1.00	0.23	72.67
Precipitation Seasonality	0.98	0.30	73.65
Standard Deviation of Minimum Temperature in October	0.96	0.19	74.61
% High Density Evergreen Forest	0.92	0.25	75.53
Standard Deviation of Maximum Temperature in July	0.91	0.25	76.43
Mean Climate Moisture Index	0.90	0.27	77.33
Standard Deviation of Minimum Temperature in August	0.90	0.12	78.23
Standard Deviation of Precipitation in September	0.84	0.21	79.07
Standard Deviation of Minimum Temperature in May	0.81	0.18	79.89
Mean Summer Precipitation	0.81	0.23	80.70

Ring-necked Duck abundance was associated with the amounts of deciduous forest, open water, and shoreline, as well as GPP, variability in minimum June temperature, and water body density. Given the relatively

homogenous distribution, it is difficult to identify clear spatial associations with environmental variables by examining predictor variable maps, except perhaps the variability in minimum June temperature, which may be associated with relatively higher abundances in the middle of the species' range. Ring-necked Ducks nest in shallow marshes, swamps, and bogs, but especially favour bogs (Hohman and Eberhardt 1998, Johnsard 2010). Our wetland classification did not differentiate between bogs and other wetlands, so it is possible that variables such as deciduous forest, a hydrological variable, GPP, or interactions among these variables acted as surrogates for bog wetlands.

Ruddy Duck – over-water nesting diving

The Ruddy Duck had the lowest predicted abundance of all species we studied. Its highest predicted densities occurred in the prairie-parkland region, which is mostly consistent with Johnsgard (2010) and Brua (2002). However, published ranges extend to unsurveyed areas of British Columbia where our models predict the species to be effectively absent. Our model predicted only very low abundances of Ruddy Ducks within Ontario and

Québec, despite observations from the WBPHS, and the Breeding Bird Atlases of Ontario and Québec (Bird Studies Canada et al. 2009, Regroupement QuébecOiseaux et al. 2014).

Variable	Mean %	SD	Cumulative %
% Open Water (HWL)	10.19	2.96	10.19
% Cropland-woodland	7.12	1.51	17.32
Density of Waterbodies (neighbourhood metric)	4.69	1.82	22.00
% Cropland	4.67	1.17	26.67
Standard Deviation of Maximum Temperature in December	4.65	3.12	31.32
Amount of Shoreline (km/km ²)	3.93	1.72	35.25
Precipitation Seasonality	3.45	1.15	38.70
Standard Deviation of Precipitation in May	3.31	2.59	42.01
Standard Deviation of Maximum Temperature in November	3.26	2.01	45.27
Standard Deviation of Growing Season Length	3.23	1.53	48.50
% Deciduous Forest	2.27	0.85	50.77
% Wetland (HWL)	2.11	0.97	52.88
Standard Deviation of Maximum Temperature in January	1.92	1.19	54.80
Standard Deviation of Maximum Temperature in February	1.90	1.29	56.70
Mean Climate Moisture Index	1.88	0.74	58.58
Amount of Streams (km/km ²)	1.85	0.79	60.43
Shannon's Diversity Index of Land Cover Types	1.62	1.19	62.06
Topographic Ruggedness	1.48	0.61	63.54
Standard Deviation of Maximum Temperature in May	1.48	0.57	65.02
Standard Deviation of Precipitation in June	1.41	0.90	66.43
% High Density Evergreen Forest	1.34	1.40	67.77
Standard Deviation of Maximum Temperature in September	1.30	0.59	69.07
Standard Deviation of Minimum Temperature in July	1.28	0.57	70.35
Standard Deviation of Minimum Temperature in June	1.28	0.41	71.63
Mean Precipitation in the Wettest Month	1.23	0.79	72.86
Standard Deviation of Minimum Temperature in October	1.23	0.99	74.09
Standard Deviation of Precipitation in April	1.13	0.46	75.22
Standard Deviation of Precipitation in September	1.11	0.66	76.34
Mean Gross Primary Productivity	1.03	0.50	77.37
Mean Summer Precipitation	1.00	0.52	78.37
% Mixed Forest - Deciduous-dominated	0.99	0.70	79.36
Standard Deviation of Minimum Temperature in December	0.94	0.58	80.30

Ruddy Duck abundance was related to amounts of open water, cropland-woodland, cropland, and to water body density. The landcover covariates appear to identify the prairie-parkland region where the species occurs in greatest abundance. A relationship with water body density may reflect an association of this species with potholes, while a relationship with amount of open water may relate to the species' preferences for permanent and semi-permanent wetlands rather than shallow, seasonal ones (Brua 2002, Johnsgard 2010).

Scaup species – over-water nesting diving

Our models predicted high scaup abundances in the northwestern prairie-parkland region, and in northwestern Canada. Since Lesser and Greater Scaup are not differentiated within the survey, these predicted densities represent a combination of both species. The relative contribution of each species at a given location is not known with any precision, but the Greater Scaup's range is reportedly more northerly than that of the Lesser

Scaup (Johnsgard 2010). Both species reportedly use the western boreal forest, but the Lesser Scaup's range extends further south into the prairie-parkland while the Greater Scaup extends north to the treeline and also into eastern Canada (Johnsgard 2010). Our predicted densities are consistent with these published maps, with slight overpredictions in the northeastern boreal.

Variable	Mean %	SD	Cumulative %
% Open Water (HWL)	10.59	1.42	10.59
Standard Deviation of Growing Season Length	5.43	1.35	16.02
Standard Deviation of Minimum Temperature in October	5.24	2.30	21.26
Density of Waterbodies (neighbourhood metric)	3.72	1.00	24.98
Mean Winter Precipitation	3.17	0.96	28.15
Mean Autumn Precipitation	3.07	0.78	31.22
Mean Climate Moisture Index	2.80	0.64	34.02
Topographic Ruggedness	2.78	0.72	36.80
Precipitation Seasonality	2.78	0.85	39.57
Mean Autumn Maximum Temperature	2.50	1.47	42.07
Amount of Shoreline (km/km ²)	2.30	0.78	44.37
Standard Deviation of Minimum Temperature in September	2.30	0.91	46.67
Standard Deviation of Maximum Temperature in April	2.09	0.65	48.76
Standard Deviation of Maximum Temperature in January	2.06	0.69	50.82
% Deciduous Forest	1.85	0.56	52.68
Mean Winter Minimum Temperature	1.73	1.03	54.40
% Cropland-woodland	1.56	0.47	55.96
Mean Gross Primary Productivity	1.45	0.53	57.41
Standard Deviation of Maximum Temperature in November	1.36	0.66	58.78
Standard Deviation of Minimum Temperature in April	1.36	0.67	60.14
Amount of Streams (km/km ²)	1.35	0.48	61.48
Standard Deviation of Precipitation in January	1.34	0.32	62.82
Standard Deviation of Precipitation in April	1.34	0.82	64.16
Mean Summer Precipitation	1.28	0.53	65.44
Standard Deviation of Maximum Temperature in March	1.20	0.27	66.65
Mean Spring Precipitation	1.17	0.84	67.82
Standard Deviation of Precipitation in October	1.15	0.60	68.98
Standard Deviation of Precipitation in September	1.13	0.40	70.11
Standard Deviation of Minimum Temperature in May	1.11	0.51	71.22
Standard Deviation of Minimum Temperature in August	1.11	0.50	72.33
Standard Deviation of Maximum Temperature in September	1.09	0.42	73.42
Mean Shoreline Complexity (neighbourhood metric)	1.06	0.27	74.48
Standard Deviation of Maximum Temperature in December	1.03	0.25	75.51
Annual Range in Temperature	1.01	0.53	76.52
Mean Precipitation in the Wettest Month	0.96	0.58	77.47
Standard Deviation of Precipitation in March	0.92	0.41	78.40
Standard Deviation of Maximum Temperature in October	0.92	0.31	79.32
Standard Deviation of Precipitation in June	0.89	0.44	80.20

Scaup abundance was most closely associated with the amount of open water, followed by inter-annual variation in growing season length and minimum October temperature, and water body density. The relatively high importance of climate variables may be related to the high abundances in the far North; many of the species

living in boreal regions tended to be more strongly associated with climatic than land cover variables. A relationship with both open water and water body density relates to the species' associations with water, and may capture the regional variation in the nature of open water habitats as between the southern and northern limits of the combined species ranges. Greater Scaup tend to prefer open, shallow wetlands in the tundra (Johnsgard 2010) while Lesser Scaup prefer prairie marshes, semipermanent wetlands, and partially wooded wetlands (Austin et al. 1998, Johnsgard 2010).

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