

**WETLAND CHARACTERISTICS AND ABUNDANCE OF
BREEDING DUCKS IN PRAIRIE CANADA**

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ABSTRACT

Wetlands of the Prairie Pothole Region of North America provide habitat for over 50% of the continent's breeding waterfowl, but most of the region's wetlands have been lost or degraded through intensive agricultural development. Despite widespread wetland losses in much of the Canadian prairies, there is little information about trends in degradation of remaining wetlands. Using habitat data collected for ~10,500 wetlands across the Canadian prairies during annual waterfowl surveys, 1985-2005, I employed multistate models in Program MARK to estimate rates of impact and recovery of wetlands resulting from agricultural activities. Then, I characterized the incidence of agricultural degradation to these wetlands. Rates of impact to wetland margins (natural vegetation around flooded basins) declined over time, likely due to a decreasing percentage of unaffected wetlands; recovery rates for margins were always lower than impact rates, suggesting increased cumulative degradation of wetlands over time. Unlike margins, impact and recovery rates for basins fluctuated with spring pond densities. Shallow ephemeral wetlands located in agricultural fields had the highest impact and lowest recovery rates. Multistate modeling could also be used to estimate rates associated with other landscape processes.

My second objective was to determine whether physical characteristics of prairie Canada wetlands could be used to predict breeding duck abundance. First, I sought to determine how pre-existing models developed in the Dakotas (USA) performed when predicting breeding duck abundances on Canadian prairie wetlands. I related duck pair abundance to pond area, and then compared observed to predicted duck abundance. The Dakota models performed reasonably well in predicting numbers of blue-winged teal (*Anas discors*), gadwall (*A. strepera*), and northern pintail (*A. acuta*), but predicted fewer mallards (*A. platyrhynchos*) and northern shovelers (*A. clypeata*) than were observed on wetlands. Pond area was an important predictor of duck abundance in all models, but results were less biased and more consistent in models developed specifically for Canadian wetlands. Spatiotemporal variation in the relationship of breeding duck abundance and wetland characteristics was also affected by regional duck and pond densities. Overall, the new applications and models developed and validated in this study will be useful for wetland and waterfowl management in the Canadian prairies.

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CHAPTER 1 INTRODUCTION

1.1 GENERAL BACKGROUND

Wetlands contribute significantly to global biodiversity but have undergone substantial losses and modifications. Although wetlands cover less than 9% of global land area, they support disproportionately high numbers of species (Zedler and Kercher 2005, Dudgeon et al. 2006) by providing habitat for waterbirds, amphibians, fish and other vertebrates, invertebrates, and aquatic and terrestrial flora (Mitsch and Gosselink 2000). In addition, wetlands provide valuable ecosystem services such as water quality improvement, flood control, and carbon sequestration (Zedler and Kercher 2005). Around the world, humans utilize wetlands for resource extraction, recreation, and sources of food and water (Mitsch and Gosselink 2000). Despite their recognized importance, over half of the world's wetlands have been lost, primarily through agricultural development, while most remaining wetlands are partially degraded through hydrological alteration, salinization, eutrophication, sedimentation, filling, or exotic species invasions (Zedler and Kercher 2005).

The Prairie Pothole Region (PPR) of North America is characterized by millions of wetlands formed in post-glacial depressions (Johnson et al. 2005). The core of the region is 780,000 km² of the North American Great Plains extending from northern Iowa through the Dakotas to the edge of the boreal forests in the Canadian prairie provinces (Greenwood et al. 1995, Mitsch and Gosselink 2000). Before European settlement, the area was composed of vast tracts of grassland interspersed with aspen bluffs in the northern portion of the region (Greenwood et al. 1995). Spatial heterogeneity and temporal instability characterize the region, and there exists strong north-south temperature and east-west precipitation gradients (Johnson et al. 1994). Most areas are subjected to periodic, extreme drought and deluge conditions (Johnson et al. 2005). As a result, wildlife in the PPR has adapted to the characteristic wet-and-dry cycles of the climate. In fact, the persistence of PPR wetlands, and high levels of productivity and biodiversity depend on periods of drought for plant turnover and nutrient mobilization (Mitsch and Gosselink 2000, Johnson et al. 2004). The importance of the region to breeding waterfowl has been extensively documented, and although the PPR comprises

only 10% of the continental breeding area, it produces over 50% of North America's duck population (Crissey 1969, Greenwood et al. 1995, Higgins et al. 2002). Generally, there is a strong positive correlation between May pond and breeding duck densities in a given area (Johnson and Grier 1988, Bethke and Nudds 1995). As the annual number of ponds varies widely because of periodic drought conditions, duck numbers fluctuate accordingly (Johnson and Grier 1988).

Fertile soils and accessibility have made the PPR ideal for agriculture, and since European settlement, much of the area has been converted to cropland (Turner et al. 1987, Johnson et al. 1994, Stephens et al. 2008). Wetlands were traditionally considered marginal lands to be drained, filled, and leveled to further increase the agricultural land-base, and as a consequence, an estimated 40-70% of the PPR's original wetlands have been lost (Cox 1993, Dahl 2000). Currently, there are few large, contiguous tracts of natural grassland remaining in the PPR, and North American prairie is one of the most endangered and intensively managed ecosystems on the continent (Johnson et al. 1994, Stephens et al. 2008). Despite recent conservation efforts (see below), some evidence suggests that wetland losses continued in the Canadian PPR in the last quarter of the twentieth century (Watmough and Schmoll 2007). However, a knowledge gap exists because there is scant information on trends in degradation for the remaining wetlands over that same time period.

In the 1980s, breeding populations of many North American duck species were reaching record lows, and the relationship between May pond densities and duck abundance was weakening (Johnson and Shaffer 1987, Greenwood et al. 1995, Miller and Duncan 1999). Destruction and degradation of wetland and upland habitat through agricultural practices likely contributed to these declines in duck populations (Boyd 1985, Bethke and Nudds 1995, Podruzny et al. 2002). In response, the North American Waterfowl Management Plan (NAWMP) was established in 1986 to increase duck populations to average levels of the 1970s (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). To achieve this goal, NAWMP placed priority on restoring habitat and preventing further habitat loss and degradation. To implement NAWMP strategies in the Canadian PPR, the Prairie Habitat Joint Venture (PHJV) was created, and since its inception, PHJV has secured over 1.9 million ha of nesting and wetland

habitat (North American Waterfowl Management Plan - <http://www.nawmp.ca/pdf/HabMat2007e.pdf>, *public communication*). Activities on these lands include enhancement, restoration, preservation, and land stewardship. Since NAWMP was signed, many duck populations have recovered to levels higher than objectives, but some populations remain well below NAWMP goals (Afton and Anderson 2001, Podruzny et al. 2002).

The PHJV has adopted an adaptive management approach and routinely employs evaluation studies to assess the current impact of habitat programs and guide future program delivery. The PHJV recently began setting new habitat objectives for each province, and a Waterfowl Productivity Model (WPM) is being used to predict duck productivity responses to different suites of habitat programs in the context of varying agricultural landscape composition (North American Waterfowl Management Plan - <http://www.nawmp.ca/pdf/HabMat2006e.pdf>, *public communication*). A key component of the WPM involves the relationship between abundance of breeding ducks and wet area of wetlands (i.e., pond area; Cowardin 1982), a function that is based on regression models developed using data from U.S. PPR studies (hereafter Dakota models; Cowardin et al. 1995, Devries et al. 2004). Using the Dakota models, Devries et al. (2004) estimated a reduction in waterfowl carrying capacity in the Canadian PPR due to wetland losses. However, it was unclear whether relationships generated in North Dakota could accurately predict duck abundance in the Canadian PPR because of different duck communities and landscape compositions (Devries et al. 2004). The Canadian portion of the PPR is distinct from its United States counterpart because it contains aspen parkland and boreal transition ecoregions (Marshall et al. 1999). Habitat compositions, agricultural land uses, and wetland characteristics in these ecoregions are distinct from those in the south, which may cause birds to behave differently in these zones (Turner et al. 1987, Bethke and Nudds 1995, Watmough et al. 2002). Consequently, there was need to validate the Dakota models with independent data collected in Canada.

1.2 THESIS OBJECTIVES AND ORGANIZATION

My first thesis objective was to address a knowledge deficiency by evaluating trends in agricultural impacts to prairie Canada wetlands, 1985-2005 (Chapter 2). First, I use multistate models to estimate impact and recovery rates of wetland margins and

basins, and I examine how putative factors, such as location, land use, wetland type, and moisture, may affect those rates. Then, I summarize the incidence of degradation for Canadian prairie wetlands. My second thesis objective (Chapter 3) was to determine whether physical features of Canadian prairie wetlands could be used to predict breeding duck abundance. In particular, I evaluate the predictive performance of models that were developed in the Dakotas and are currently being applied to the Canadian prairies as part of habitat conservation planning efforts by the PHJV. In addition, I develop new models based on independent data collected in Canada. Finally, I assess how relationships in newly-developed models could vary with changes in regional duck and pond densities. I conclude the thesis (Chapter 4) with a synthesis of major findings and their implications for wetland and waterfowl conservation programs on the Canadian prairies.

CHAPTER 2 ESTIMATING HABITAT DEGRADATION AND RECOVERY RATES USING MULTISTATE MODELING: AGRICULTURAL IMPACTS ON WETLAND HABITAT IN THE CANADIAN PRAIRIES (1985-2005)

2.1 INTRODUCTION

Natural and anthropogenic processes are constantly modifying terrestrial and aquatic ecosystems. Rates of natural landscape change can range from gradual to abrupt through processes such as glaciation, climate change, erosion, desertification, succession, fires, floods, volcanism, and hurricanes. Currently, humans are principal drivers of global landscape changes, in terms of magnitude and pace, through urbanization, resource extraction and consumption, pollution, and agriculture (Sinclair et al. 1995, Wilson and King 1995). Habitat loss and degradation have been cited as major causes of worldwide declines in biodiversity (Polasky et al. 2005, Dudgeon et al. 2006), and an increase in rate of species extinctions has been attributed to anthropogenic activities (Vitousek et al. 1997, Chapin et al. 2000). Long-term cumulative effects of human activities on ecosystem functions and overall biodiversity are more difficult to quantify (Naeem et al. 1994, Loreau et al. 2001, Balmford et al. 2002). Given complex interactions, it is often difficult to isolate and quantify the relative impact of single stressors (Tongway et al. 2003, Daniels and Cumming 2008). Furthermore, landscape changes may not be unidirectional, and depending on the type, duration, and/or severity of change, landscapes may recover to previous conditions (e.g., Lindig-Cisneros et al. 2003, Suding et al. 2004, Thrush et al. 2008). However, to more effectively design and implement conservation programs, and potentially mitigate adverse effects of human activities, it is crucial to evaluate the impact and resilience of habitats to potential landscape stressors. Here, I address both of these general problems in a novel way, by applying multistate modeling (Brownie et al. 1993) to estimate impact and recovery rates of natural wetland habitats in agricultural landscapes.

Wetlands cover less than 9% of global land area, but support disproportionately high numbers of species (Zedler and Kercher 2005, Dudgeon et al. 2006), providing habitat for waterbirds, amphibians, fish and other vertebrates, invertebrates, and aquatic and terrestrial flora (Mitsch and Gosselink 2000). In addition, wetlands provide valuable

ecosystem services such as water quality improvement, flood control, nutrient cycling, and carbon sequestration (Zedler and Kercher 2005, Daniels and Cumming 2008). Over half of the world's wetlands have been lost, primarily to agriculture, while most remaining wetlands are partially degraded through hydrological alteration, salinization, eutrophication, sedimentation, filling, and/or exotic species invasions (Zedler and Kercher 2005). Although wetland losses are well documented, effects and persistence of degrading activities can be difficult to estimate, and depending on impact severity, wetlands may recover given time and/or restoration efforts (Brock et al. 2003, Lindig-Cisneros et al. 2003).

To effectively plan and deliver wetland restoration and protection programs, it is critical to understand whether and how quickly wetlands can recover from impacts (Lindig-Cisneros et al. 2003, Heffernan 2008). Significant variation in wetland impact and recovery rates may arise as a result of variability in (1) anthropogenic factors, such as land uses and economies, (2) climatic factors, such as temperature and precipitation, (3) conditions specific to individual wetlands, such as depth and wetland type, and/or (4) other environmental factors, such as local wetland density and vegetation. Multistate models, extensions of standard mark-recapture models (i.e., Cormack-Jolly-Seber models; Lebreton et al. 1992), provide a powerful solution because they can simultaneously estimate several probabilities for dynamic processes such as wetland impact and recovery (Brownie et al. 1993, White et al. 2006). In addition, spatiotemporal factors can be incorporated into these models to determine how rates covary with environmental and anthropogenic conditions. Although multistate models were originally developed to quantify movement and other "state" transitions among marked individuals, they may be ideally suited for estimating rates of change associated with landscape processes.

Wetlands of the North American Prairie Pothole Region (PPR) are landscape features that are continuously undergoing change through natural and anthropogenic stresses (Mitsch and Gosselink 2000). Spatial heterogeneity and temporal instability characterize the region; there are strong north-south temperature and east-west precipitation gradients, and most areas are subjected to periodic drought and deluge conditions (Johnson et al. 1994, Johnson et al. 2005). Before European settlement, large

expanses of native grasslands were common, but fertile soils and accessibility made the PPR ideal for agriculture. As a result, most land has been converted to cropland or is managed as hay or pasture land (Johnson et al. 1994, Horn et al. 2005). To expand the agricultural land-base, many wetlands were drained, filled and cultivated, resulting in estimated wetland losses between 40% and 70% (Whigham 1999, Dahl 2000).

Wetland loss in the PPR continued in the last quarter of the twentieth century, but there is scant information on rates and incidence of wetland degradation for that same time period (Dahl and Watmough 2007). In Canada, there is no comprehensive, periodic monitoring program for prairie wetlands, and thus, trends in wetland impacts are uncertain (Dahl and Watmough 2007). However, since 1980, some wetland habitat data have been collected during the annual Waterfowl Breeding Population and Habitat Surveys (WBPHS; U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987). Based on an analysis of these data, my objectives were to (1) assess spatiotemporal variation in wetland impact rates across the Canadian PPR, and (2) determine how factors such as precipitation, land use, and wetland permanence may influence those rates. In particular, use of a multistate modeling approach allowed me to conduct a broad scale, yet comprehensive, assessment of trends in wetland impacts, and enabled me to evaluate predictions of how wetland “states” (i.e., impacts to margins and basins) were related to characteristics of flooding regimes, geographic region and land use. To my knowledge, this is the first study to apply these modern estimation techniques to questions of broad scale changes in landscape features and to employ these methods in quantifying wetland impact and recovery rates.

2.1.1 Hypotheses and Predictions

During drought, wetland basins (i.e., the area extending from the centre of the wetland to the outer edge of the wet meadow zone; Stewart and Kantrud 1971) become exposed and vulnerable to agricultural impacts, but activities in affected basins cease when they re-flood (Whigham 1999). Therefore, I predicted that rates of impact to wetland basins should be lower in high water springs and greater when basins are drawn down or dry. Because wetland margins (i.e., the area of native vegetation extending 10 m from the edge of the basin) are less prone to flooding than basins, I predicted margins would have a higher incidence of impacts than basins, and rates would be affected less by

varying water conditions. From 1981-1985, Turner et al. (1987) reported that margin degradation had progressively increased, and I expected this trend had continued after 1985. Although native land conversion to agriculture has slowed, activities on existing farmlands have intensified through conversion of remnant marginal lands, “improvement” of pastureland to support larger cattle herds, and diminished use of summerfallow, a practice of leaving land uncropped for an entire growing season (Bethke and Nudds 1995, Carlyle 1997, Beaulieu and Bedard 2003). Due to this agricultural intensification, I expected increasing agricultural pressure on wetland margins and less opportunity for recovery.

The study area encompassed two major ecoregions: grassland and parkland (see Methods). Because water conditions tend to be more variable in grassland regions (Bethke and Nudds 1993), I expected that incidence of impacts would generally be highest in grassland, and thus transition rates and percentages of affected basins in that region would fluctuate more than in parkland. Also, surrounding wood-rings of parkland wetlands could provide a buffer against agricultural activities such as grazing and cultivation when parkland basins are drawn down. I also expected jurisdictional differences in rates and incidence of impact to wetlands because of provincial differences in agricultural and wetland protection policies, and other socioeconomic drivers (Douglas and Johnson 1994).

Finally, I anticipated that permanent wetlands, being less susceptible to agricultural practices, would have a lower impact rate when compared with ephemeral or seasonal wetlands (Whigham 1999). Likewise, wetlands in cultivated fields or pastures were expected to be more susceptible to impacts than wetlands located in idle grasslands or wooded areas.

2.2 METHODS

2.2.1 Study Area

The Canadian portion of the PPR encompasses approximately 480,000 km² extending north from the Canada / United States border to the southern edge of the boreal forest (Fig. 2.1). The Canadian PPR is comprised of several ecoregions (i.e., zones characterized by distinct biotic and abiotic factors including climate, physiography,

vegetation, soil, water, and fauna; Marshall et al. 1999), but was classified into two zones to simplify analysis and reporting: (1) grassland in Southern Alberta and Southwestern Saskatchewan, and (2) parkland/boreal transition (hereafter referred to as parkland) in Northern Alberta and Saskatchewan, Eastern Saskatchewan, and the entire prairie portion of Manitoba (Fig. 2.1). I used these broad ecoregions because (1) landscape processes and impacts to wetlands should be similar within these regions, (2) use of these ecoregions facilitated comparisons with previous studies, (3) sample coverage was adequate at these scales, and (4) there were constraints in computing capabilities when analyzing data collected at finer spatial resolutions.

2.2.2 Survey Methods

The WBPHS has been conducted annually by the U.S. Fish and Wildlife Service and Canadian Wildlife Service since 1955 (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987). To estimate sizes of duck populations, aerial surveys are conducted each spring over major breeding areas in Canada and the United States. These breeding areas are delineated into survey strata according to political boundaries, habitat conditions, and duck densities. In addition to duck counts, ground crews visually assess habitat conditions at each wetland visited during surveys. All wetlands within survey segment boundaries have been assigned unique numbers and labeled on aerial photos, so observers revisit every wetland annually; in rare cases, wetlands are missed because of logistical issues. Consequently, a complete history of spring habitat conditions exists for individual wetlands within ground segments. Six major variables are assessed on each visit: (1) wetland type, (2) water level stage, (3) upland margin width, (4) basin impacts and conditions, (5) margin impacts and conditions, and (6) adjacent land uses (Turner et al. 1987). Wetland type is related to water permanency and follows a classification scheme developed, in part, by Stewart and Kantrud (1971); artificial wetlands, such as dug-outs and irrigation canals, are also recorded. Water level stage, a numerical index describing water levels relative to “normal” conditions and ranging from dry to overflowing, is assigned to each wetland. Impacts and conditions of basins and margins are identified and expressed as percentages of the area affected by haying, draining, clearing, grazing, burning, cultivation, filling, road building, farmyard impacts and wooded area (Turner et al. 1987). In addition, margin widths are estimated visually

(nearest 1 m), and widths ≥ 10 m are fixed at 10 m. Upland conditions adjacent to the outer edge of the margin are expressed as percentages of the perimeter of a wetland margin influenced by crop, stubble, fallow, hay, native grass, wood, pasture, wooded pasture, and farmyard.

2.2.3 Reliability of Wetland Impact Assessments

Survey protocol requires that the previous year's habitat data are edited on-site during surveys to reduce observer bias and to ensure that only real habitat changes are recorded (Turner et al. 1987). Because wetland and upland assessments may be subjective, I quantified inter-observer variation in habitat assessments during the 2006 and 2007 Saskatchewan surveys. When duck surveys were completed each day, crews returned to the last 2-4 wet ponds on segments and a new observer re-assessed habitat conditions, as above, using only habitat information for the previous year's wetland conditions. The types and number of discrepancies between observers were recorded and then expressed as percentages of the total wetland revisits each year. I first determined if there was a discrepancy in detecting whether or not an impact had occurred; this is relevant to multistate modeling which requires correct designation of a wetland's "state" of impact (see below). If both observers detected impacts, I then calculated the percent of misclassification of types of impacts between observers. Finally, if both observers detected the same types of impacts, I calculated the percentage of those observations that had different estimates of percentage affected.

2.2.4 Analyses

Program MARK provides a suite of mark-recapture models that are used to estimate survival and recapture/recovery parameters from marked individuals (White and Burnham 1999). Multistate models are extensions of these standard models that also estimate transition probabilities (Ψ) between states (White et al. 2006). States can be physical locations where Ψ represents movement probabilities, or they can be conditions (e.g., breeding and non-breeding status) where Ψ represents rates of change between those conditions (Nichols et al. 1994). I considered wetlands as marked individuals and used multistate models to estimate rates of transition among impact states in relation to explanatory variables described below (Fig. 2.2). Because an objective of the ground

survey is to visit every wetland every year, I selected wetlands that had complete records for all 21 occasions (1985-2005), which resulted in encounter histories for 10,437 individual wetlands from 56 survey segments (Fig. 2.1). Exclusive use of wetlands that were visited each year of study allowed me to fix recapture probability = 1 (White and Burnham 1999). Because destruction events were infrequently observed (<1%), and because I restricted analysis to wetlands with complete records, I also set survival probability = 1. As a result, model development and parameter estimation was based solely on transition probabilities. Because impact rates may vary between wetland margins and basins, I considered three possible wetland states (Fig. 2.2): (1) *no visible impact* – no impacts recorded (hereafter referred to as pristine), (2) *margin impact* – an impact recorded only for a wetland’s margin (hereafter referred to as partially degraded), and (3) *margin and basin impact* – an impact recorded both for a wetland’s margin and basin (hereafter referred to as fully degraded). Between years, wetlands could remain in their current state or shift to another state. Probabilities of transition of wetlands to more-degraded states are synonymous with impact rates, and probabilities of transition to less-degraded states represent recovery rates. Note that the term “recovery” as used here refers to the probability of a wetland reverting to a less-degraded state, and should not be confused with “recovery” as it applies to conventional mark-encounter studies. In the latter case, “recovery probability” is the probability that a marked individual is killed, retrieved, and reported by a hunter (Brownie et al. 1985).

I considered spatiotemporal effects, as well as characteristics of individual wetlands as sources of variation in transition probabilities. I defined five attribute groups based on provincial and regional locations (Fig. 2.1): Alberta grassland and parkland; Saskatchewan grassland and parkland; and Manitoba parkland. Survey strata were classified according to these attribute groups based on their provincial location, and ecoregion that made up the majority of each stratum’s area (Fig. 2.1). I calculated two annually varying wetness indices at the level of attribute group, and analysed these as cohort-level covariates (White and Burnham 1999). The first index, pond density (PD), was calculated from historical May pond estimates per stratum and stratum areas provided by the WBPHS (Wilkins et al. 2006). After I calculated ponds per km² for each stratum, I calculated an average pond density weighted by stratum areas for each

attribute group. The second index, conserved soil moisture (CSM), was developed by Williams and Robertson (1965) to aid in forecasting prairie wheat production on the basis of precipitation data. CSM is a form of weighted precipitation mean calculated as follows:

$$\text{CSM} = 0.36A + [0.37B - 0.2(0.36A)] + 0.13C + \{0.30D - 0.2[0.36A + (0.37B - 0.2(0.36A))] + 0.13C\}$$

where A = total precipitation from August through October in year $t - 2$, B = total precipitation during November in year $t - 2$ through April in year $t - 1$, C = total precipitation during May through October in year $t - 1$, and D = total precipitation during November in year $t - 1$ to April in year t . CSM has been used as an index of wetness regimes and wetland conditions, and has had stronger correlations to duck abundance than pond numbers in some instances (Boyd 1981, Bethke and Nudds 1995). To calculate annual CSM for each attribute group, I used monthly precipitation values averaged over all Environment Canada (2007) weather stations operating from 1983-2005. Because I calculated two wetness indices, I substituted these for each other in models to determine which index performed best in explaining variation in wetland impact rates. In some models, I constrained transition rates to vary as linear-logistic function of time (calendar year; T). Such models are useful for identifying systematic changes (i.e., trends) in transition rates over time.

In addition to assessing spatial and temporal variation in impact and recovery rates, I also included dominant wetland type (POND) and land use (LAND) as covariates. Although these factors can vary over time and Program MARK allows for time-varying individual covariates, I assigned a single dominant classification due to computing-related constraints on model complexity. Each wetland was assigned a dominant wetland type based on its type designation at full water stage because I felt more confident that wetlands would be correctly classified at this stage. If a wetland was typed differently at full stages on different occasions, then its designation was the type assigned on a majority of visits. When different type-designations occurred with equal frequency, wetlands were assigned to the more permanent type. If wetlands were never observed at full water level stages, they were assigned a dominant wetland type based on the highest water level stage encountered. For purposes of analysis, Type 1 (temporary) and 3 (seasonal)

wetlands were combined as seasonal wetlands, and type 4 (semi-permanent) and 5 (permanent) were combined as permanent wetlands. Artificial ponds (e.g., dugouts, gravel pits, irrigation canals, etc.) and streams were given separate respective classes from other wetlands. Finally, wetlands that never held enough water to last more than a few days were classified separately as ephemeral wetlands (Brock et al. 2003). Each wetland was assigned a dominant land use based on most frequently observed upland condition. Categories included pasture, hayed/yard, cultivated, wood, native grass, and mixed in cases where different land uses occurred with equal frequency over time.

I used a two-stage approach for candidate model set development and model selection. First, I assessed which spatial factor (province, ecoregion, or province and ecoregion combined) was best supported by the data. Based on results of this initial analysis, I selected the most appropriate spatial factor for inclusion in all subsequent models testing temporal and individual covariates. Based on *a priori* predictions, I developed a candidate set of models (see Appendix A) which included all possible additive combinations of the most supported spatial factor and the aforementioned covariates, a null model, and additive and multiplicative models allowing for both group- and time-dependence (group + t, group * t, respectively). Model notation follows Lebreton et al. (1992); '+' indicates an additive relationship between explanatory variables, and '*' indicates an interactive relationship. I used a logit link function to model the relationships between transition parameters and covariates.

As a preliminary step, I assessed overall goodness-of-fit using the median- \hat{c} test in Program MARK (White and Burnham 1999). Because median- \hat{c} goodness-of-fit testing does not allow inclusion of individual covariates, I performed the test on a highly parameterized non-global model, group + t (Burnham and Anderson 2002). The median- \hat{c} test had a computer run-time of three weeks, which is why I did not run the median- \hat{c} test on the most parameterized model, group * t. I also adjusted the variance inflation factor (\hat{c}) from 1-4 in computing model diagnostics to observe effects on model rankings (QAICc values; see below).

Model selection was based on an information-theoretic approach by computing Akaike's Information Criterion adjusted for sample size and overdispersion (QAIC_c; Burnham and Anderson 2002). QAIC_c indicates a model's degree of parsimony, which

represents a balance between model fit and precision of parameter estimates. Consequently, models within each candidate set can be ranked based on their QAIC_c values, with the lowest QAIC_c indicating the most parsimonious model. To aid in model selection, I also computed Δ QAIC_c (QAIC_c values expressed relative to QAIC_c of the most parsimonious model) and AIC-based model weights (Burnham and Anderson 2002). After identifying the most parsimonious additive model, I ran a multiplicative equivalent that included an interaction between spatial factors and cohort-level covariates. I report transition parameter estimates and standard errors from the best approximating model, and also examine percentages of affected wetland margins and basins over the study period for validation and interpretation of the multistate model results.

2.3 RESULTS

2.3.1 Reliability of Wetland Impact Assessments

An estimated 47% (n =70) and 60% (n=63) of revisited wetlands had a least one discrepancy between observers in 2006 and 2007, respectively. When each habitat parameter was examined individually, the proportion of observations with discrepancies ranged from 0%-18% (Table 2.1). In 2006, 93% and 91% of margin and basin impacts, respectively, were consistently detected by two observers; in 2007, corresponding estimates were 100% and 97%. These last two sets of values are especially relevant to the multistate modeling exercise because detections of impacts determine a wetland's "state", so I consider detection failures further when interpreting results.

2.3.2 Transition probabilities of wetlands

Using the median- \hat{c} method, the variance inflation factor (\hat{c}) was estimated at 1.72 for the model that contained additive effects of group variation and time. Although group + t was not the most parameterized model, adjusting \hat{c} from 1-4 did not change the Δ QAIC_c ranking or QAIC_c weight of the most parsimonious model. Therefore, I felt confident in using a \hat{c} value of 1.72 in quasi-likelihood adjustments; the most parameterized model, group * t, would likely have had a lower \hat{c} value, which would have only further increased relative support for the top-ranked model.

Of the spatial factors considered, the model that allowed for both provincial and ecoregional variation (i.e., group) was most supported (QAIC_c weight = 1.00; Table 2.2). I subsequently included this grouping factor in all models testing for effects of individual and time-varying covariates (Table 2.3). Models that included pond density always received more support than the CSM equivalents, so I included pond density in the following combined-effects model. Because I predicted that different transition parameters would respond differently to specific covariates, I developed a model (group + T/PD + LAND + POND) that constrained three transition parameters (m_3 , b_3 , and n_2) to vary as a function of pond density, and three transition parameters (m_2 , b_2 , and n_3) to vary as a function of T (Fig. 2.2). Of the additive models, this combined-effects model received the most support, and its multiplicative equivalent (group * T/PD + LAND + POND) was most parsimonious (QAIC_c weight = 1.00; Table 2.3). Consequently, I report transition parameter estimates from this multiplicative model.

To illustrate spatial and temporal patterns of variation in transition rates (group*T/PD), I present estimates corresponding to seasonal ponds in cultivated landscapes because these were the most common wetland type and land use, respectively. Because land use and wetland type were additive effects in the best approximating model, the following temporal trends are the same for all land uses and wetland types, although the magnitudes of estimates may vary. At the beginning of the study period, there were group differences in rates of transition from pristine to partially degraded wetlands (Fig. 2.3). Alberta had the lowest impact rates (\pm SE) at 0.12 ± 0.04 for grassland and 0.11 ± 0.03 for parkland, Manitoba had the highest rate at 0.26 ± 0.02 , and Saskatchewan grassland and parkland regions were intermediate at 0.20 ± 0.02 and 0.23 ± 0.02 , respectively. Rates declined for all groups over time and converged on a similar value near 0.02 in 2005. The reverse transition probabilities, recovery rates, displayed similar declining trends over time. However, magnitudes of recovery rates were much lower, implying progressive degradation of wetlands over the study period (Fig. 2.3).

The most parsimonious model constrained transition probabilities between partially and fully degraded wetlands to vary as a function of pond densities (Fig. 2.4). In general, as pond densities increased, rates of impact on wetland basins declined. Conversely, recovery rates increased with increasing pond density, but at lower

magnitudes than impact rates. Alberta grassland was exceptional in displaying a slight decline in recovery rates with an increase in pond density. Where pond densities overlapped for all groups, Saskatchewan grassland and parkland had the highest impact rates, Manitoba was mid-range, and Alberta parkland and grassland rates were the lowest (Fig. 2.4).

Rates of transition from pristine to fully degraded wetlands were constrained to vary by pond density, and corresponding recovery rates were constrained to vary as a linear-logistic function of time (Fig. 2.5). Impact rates declined similarly (slopes close to parallel) in all groups with an increase in pond density, but occurred at different magnitudes (intercepts) along provincial divisions. Saskatchewan wetland basins had the highest impact rates, and Alberta basins had the lowest rates. Recovery rates were low (≤ 0.01) and declined through time for all groups, except Alberta parkland where recovery rates remained constant throughout the study period (Fig. 2.5).

To determine whether variation in wetland impacts between attribute groups was merely a function of landscape-specific differences in wetland densities, I considered an additional *a posteriori* model. As a proxy for total wetland basin density, I substituted each group in the best supported *a priori* model with its maximum pond density (MPD) recorded during the study period ($MPD * T/PD + LAND + POND$). If this *a posteriori* model had received more support than the *a priori* equivalent with group variation, then I may have concluded that the observed group variation was likely a function of differences in the densities of total wetland basins in each geographic region. However, the *a posteriori* model was ranked second in the candidate set and did not receive any support (QAIC_c Weight = 0.00; Table 2.3).

I chose seasonal wetlands in the Saskatchewan parkland from 1995 to illustrate land use effects because these wetlands comprised the majority of sampled wetlands at the midpoint of the study period. Generally, wetlands in cultivated or pasture lands had the highest impact and lowest recovery rates (Figs. 2.6a and 2.6c). In contrast, wetlands in native grassland and wooded areas, respectively, had lowest impact and highest recovery rates. Exceptions were transition probabilities between partially and fully degraded wetlands (Fig. 2.6b), where impact rates and corresponding recovery rates were

close to equal for all land uses. Impact rates were still highest in cultivated and pasture lands, but their recovery rates were almost as equally high.

As with land use effects above, I chose Saskatchewan parkland in 1995 to illustrate effects of wetland type, and I chose wetlands with adjacent cultivation because this was the most common land use. For the transitions between pristine and partially degraded wetlands (n_3 and m_2), and pristine and fully degraded wetlands (n_2 and b_2), impact rates were higher than recovery rates for all types of wetlands (Table 2.4). Artificial and permanent wetlands had highest impact rates for pristine to partially degraded, while ephemeral wetlands had highest impact rates for pristine to fully degraded wetlands (Table 2.4). Seasonal and permanent wetlands had similar impact and recovery rates for transitions between pristine and partially degraded states, but seasonal wetlands had a higher impact rate for pristine to fully degraded. For the transitions between partially and fully degraded wetlands (m_3 and b_3), ephemeral wetlands had highest impact rate, but lowest recovery rate, and artificial wetlands had lowest impact rate and highest recovery rate (Table 2.4). Seasonal wetlands had a higher impact rate than permanent wetlands, but recovery rates were relatively similar between the two types (Table 2.4).

2.3.3 Incidence of Wetland Impacts

I also used survey data to examine spatiotemporal variation in frequency of impacts to validate inferences made from multistate model results. In 1985, the percentage of wetlands with margin impacts ranged from 82% in Manitoba to 97% in Alberta grassland (Fig. 2.7). Until early 1990s, the percentage of affected margins increased in Saskatchewan and Manitoba, but declined in Alberta. From 1992 onward, margin impact percentages remained relatively stable in all areas, and in 2005, Alberta grassland and Manitoba had the lowest percentage at 92%; Saskatchewan grassland was highest with 95%.

Directional trends in percentage of wetlands with basin impacts were not as clear as the trends in margin impacts. Proportions fluctuated in both Saskatchewan and Manitoba, but Alberta displayed a slight downward trend for the first half of the study period before leveling off (Fig. 2.7). Generally, percentages of basin impacts were less

than margin impacts, ranging from as low as 55% in Manitoba to 86% in Alberta grassland.

2.4 DISCUSSION

Landscape change is a dynamic process, involving loss, degradation, restoration, natural recovery and succession of diverse landscape elements. Quantifying these changes over space and time is difficult and made more challenging when seeking to understand interactions among diverse human and natural factors which potentially mediate these processes. I believe that the modeling framework I describe provides a powerful way of resolving hypotheses about landscape processes, and holds much potential for further development. Although my work focused on Canadian prairie wetlands, I believe that similar approaches could be applied to a wide range of issues and putative causes of habitat change in terrestrial and aquatic systems.

Until now, quantitative information on trends and status of Canadian prairie wetlands has been lacking. Some evidence suggests that wetland loss has continued in the Canadian prairies, but there is currently no comprehensive inventory or periodic monitoring program (Dahl and Watmough 2007). In this study, I employed modern, rigorous estimation techniques in an effort to elucidate trends in impacts to Canadian prairie wetlands. Transition parameter estimates and incidence of wetland impacts clearly demonstrate high levels of wetland degradation across the entire Canadian PPR. Although impact rates on pristine wetland margins were different among provinces and ecoregions at the beginning of the study, they converged on similarly low rates by the mid-2000s after wetlands had attained a high percentage of degradation. Impacts to wetland basins fluctuated with precipitation throughout the study period. As well, ephemeral wetlands were most vulnerable to impact, and slowest to recover, and results also showed that a wetland's adjacent land use influenced impact rates.

The most parsimonious multistate model included effects of province and ecoregion, linear trends over time, pond density, land use, and wetland type to explain spatial and temporal variation in wetland impact rates. Generally, trends in estimates of transition parameters from the best approximating model were consistent with initial predictions. At the beginning of the study, incidence of wetland impacts was highest in Alberta, but impact rates were higher in Manitoba and Saskatchewan. Given that impact

rates on wetland margins were higher than recovery rates, I expected an increased incidence of degraded wetland margins over time, which was true for Manitoba and Saskatchewan. However, in Alberta, the incidence of margin impacts was initially high and subsequently declined to levels similar to those seen in the other prairie provinces. Even though recovery rates were lower than impact rates in Alberta, the high percentage of already-degraded margins meant there were more wetlands returning to a pristine state than were being modified to a partially degraded state. For all groups, impact rates on pristine wetland margins declined with time, and percentages of affected margins stabilized between 90% and 95% in the early 1990s and remained at those levels until the end of this study.

Throughout the study period, the incidence of basin impacts fluctuated more than the incidence of margin impacts. Estimates of impact and recovery rates for basins clearly demonstrate how basin impact rates are a function of spring water conditions. In wet springs (i.e., high pond densities), basin impact rates were low and recovery rates were high, and the converse was true in dry springs (i.e., low pond densities). The exception was Alberta grassland, where recovery rates exhibited a slight decline with an increase in pond density. Decreases in impact rates for wetland basins likely arose when pond densities were high because more basins were inundated with water, which made them less susceptible to activities like cultivation and grazing. Conversely, recovery rates increased when pond densities were high because basins re-flooded and then had opportunity to recover from impacts. Slopes for impact and recovery rates for basins in Saskatchewan grassland were higher than Saskatchewan parkland, suggesting that basin impacts in grassland were more sensitive to changes in pond density. Impact rates for Alberta grassland also had a steeper slope than Alberta parkland, but, as mentioned previously, the recovery rates in Alberta grassland were anomalous because they exhibited a slight decline with increased pond density. As such, it is not entirely clear that transition rates fluctuated more in grassland than in parkland regions, although some evidence is consistent with this possibility.

Generally, patterns in transition rates among different wetland types also conformed to predictions, with ephemeral and seasonal wetlands having higher impact rates. Pristine margins of streams and seasonal, permanent, and artificial wetlands all had

similar impact rates. Because margins are less prone to flooding than basins, they are likely subject to the same risk of agricultural impact regardless of wetland permanence. Pristine ephemeral wetlands had the lowest rate of impact to partially degraded wetlands, but their rate of impact directly to a fully degraded state was highest because ephemeral wetlands are shallowest and most prone to dry out completely in a single year. Pristine and partially degraded wetlands with higher degrees of permanence had lower rates of impact to fully degraded states. Pristine artificial wetlands had lowest rates of impact to fully degraded states, likely because deep basins, such as dug-outs and borrow-pits, are last on the landscape to go dry during periods of drought. Recovery rates to pristine states were equally low for all water bodies, which is consistent with the high incidence of wetland degradation observed throughout the study period.

As expected, impact rates were generally highest for wetlands in cultivated and pasture lands while recovery rates were highest for wetlands in more natural grass and wooded areas. Exceptions were transition parameters between partially and fully degraded wetlands where impact and recovery rates were almost equal among land use types. Impact rates in wooded and grassed areas may be lower because the land is agriculturally marginal and less profitable due to the added expense of conversion to “usable” land. Also, grassed lands may include areas that are under conservation covenants, where the land is to be managed as “native” prairie. Wetland recovery in natural areas may occur more quickly because these areas are not used for agriculture on an annual basis. In contrast, pasture and cultivated lands are routinely grazed and farmed, respectively, so wetlands in these areas have high impact rates and less opportunity to recover. Because transition parameters between partially and fully degraded wetlands varied by pond density, land use differences between impact and recovery rates should also vary with pond density. Saskatchewan parkland was relatively wet in 1995 (approximately 12 ponds / km²), which meant recovery rates were at their highest levels and impact rates were at their lowest levels. If I had used a drier year as my standard for land use comparisons, impact rates may have been higher than recovery rates for most land uses.

A potential criticism is that land use and wetland type were modeled as additive effects in the most parsimonious models, but no attempt was made to include these

individual covariates as multiplicative effects. However, I had no *a priori* expectation that trends among land uses or wetland types might vary spatially, and such complex relationships would be difficult to interpret. Another possible limitation was that I assigned a single dominant land use to wetlands when land uses can vary over time. On average, 8% of sample wetlands per year were surrounded by a land use that differed from their designated dominant land use. A possible solution may be to model land uses as time varying individual covariates. However, that approach would be impractical and difficult computationally in this case-study. Transition estimates of wetlands with different land uses were generally consistent with expectations, which led me to believe the estimates from land uses were defensible.

Although impact detection consistency between observers was high for basin and margin impacts in 2007, consistencies of 91% and 93% in 2006 for basin and margin impacts, respectively, may be considered low. However, because observers are arbitrarily assigned to survey wetlands, it is unlikely these types of discrepancies were biased towards particular wetlands in the dataset. Therefore, the observed level of misclassification of wetland states would not explain the directional trends exhibited in the transition rate estimates, and I felt confident with inferences.

2.4.1 Management Implications

In response to record low duck populations and intensified agriculture, the North American Waterfowl Management Plan (NAWMP) was established in 1986 to increase duck populations to average levels of the 1970s (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). To achieve this goal, NAWMP placed priority on preventing further habitat loss and degradation, and restoring habitat. To implement NAWMP strategies in the Canadian PPR, Prairie Habitat Joint Venture (PHJV) was created, and since its inception, PHJV has secured over 1.9 million ha of nesting and wetland habitat (North American Waterfowl Management Plan - <http://www.nawmp.ca/pdf/HabMat2007e.pdf>, *public communication*). Activities on these lands include enhancement, restoration, preservation, and land stewardship. Despite these activities, the present study demonstrates that wetlands across the region continued to be degraded. If I had solely examined impact rates on pristine wetlands, I might have inferred that conservation efforts are effective because rates decreased over

time. However, when impact rates are examined in conjunction with recovery rates and overall incidence of wetland impacts, it is evident that declining impact rates are a function of the decreasing number of pristine wetlands remaining on the landscape. More than 90% of wetlands had some form of visible agricultural degradation. I also caution that my estimates of recovery rates for wetlands may be high because wetland function was not quantified. It is possible, for instance, that reflooded wetlands, which appear to have recovered, may not be functionally equivalent to a truly pristine wetland. If other inputs, such as sedimentation or agricultural fertilizers and pesticides were considered, percentage of degraded wetlands would undoubtedly be even higher than estimates from this study (Houlahan and Findlay 2004, Voldseth et al. 2007), and the model framework I describe could be used to measure recovery and impact rates from such inputs in response to changes in policies or other intervention.

Conservation recommendations based on my results include placing priority on preserving remaining pristine wetlands because of high incidence of degradation and higher rates of impact than recovery. Protection of wetland margins could help to buffer basins against direct and indirect agricultural inputs, such as sedimentation, agrochemicals and pesticides, and elevated nutrient levels (Houlahan and Findlay 2004). Priority should also be given to ephemeral and seasonal wetlands, which generally had higher impact and lower recovery rates than wetlands with greater permanency. Adjacent land uses should also be considered in wetland conservation planning (Daniels and Cumming 2008). Wetlands in cultivated and pasture lands are at highest risk of impact, so efforts may be focused on wetlands in those land use areas. Additionally, if prairie climate becomes progressively drier as is projected (Johnson et al. 2005), it is likely basin impact rates will increase, and recovery rates will decline in the future. These points and recommendations should be considered in conjunction with other concerns, such as economies, wildlife requirements, endangered species, and ecosystem services when making conservation decisions.

Model comparisons in the present study indicated that spatial differences in estimated transition probabilities were a result of more than just differences in overall density of wetland basins between regions. Political, economic, or other environmental factors may also contribute to variation observed between groups. Agricultural subsidy

removal, such as elimination of Canadian grain transportation subsidies in 1995, may make farming marginal agricultural lands less profitable (Bradshaw and Smit 1997, Drever et al. 2007). Fluctuating commodity prices for agricultural products may similarly influence whether wetlands are degraded or not, and wetland size and distances to roads could also influence impact and recovery rates (Douglas and Johnson 1994, Daniels and Cumming 2008); these factors could be considered as covariates in future analyses of wetland impact and recovery rates. I defined transition states based on agricultural impacts, but wetland states could be defined based on other questions such as vegetative community structures, water nutrient and sedimentation levels, or invertebrate abundance (Dobkin et al. 1998, Gleason et al. 2003, Houlihan and Findlay 2004). If destruction events had occurred frequently in the dataset, I also could have estimated wetland "survival" (White et al. 2006).

In combination with previous work, this study demonstrates the potential utility of multistate models in producing credible estimates in diverse situations. Under conventional ecological applications, multistate models are used to estimate survival, re-encounter, and transition parameters of organisms. There is ongoing concern about the rate of degradation to the world's wetlands, forests, grasslands, coral reefs, and estuaries and other coastal habitats (Vitousek et al. 1997), and it is often unclear how interacting anthropogenic and natural inputs contribute to these degradations. Coupled with this issue of degradation is that of ecosystem resilience, and such questions as (1) do ecosystems have the capability to recover to their pristine (i.e., pre-impact or disturbance) states (Lindig-Cisneros et al. 2003, Suding et al. 2004), (2) are human restoration efforts required (Hobbs and Norton 1996), and (3) how long does a system need to recover from a disturbance (Dobkin et al. 1998, Driskell et al. 2001)? A multistate modeling approach could be modified to estimate rates for processes in other ecosystems, and test hypotheses about putative causes of habitat changes.

2.5 TABLES

Table 2.1 - Summary of wetland revisits during the Saskatchewan ground portion of the Waterfowl Breeding Population and Habitat Survey (2006 and 2007). Tabulated values are percentages of total assessments which differed between repeat observers for each factor listed. Basin and margin impact detection discrepancies refer to whether or not impacts were detected. If basin or margin impacts were detected, then impact types were examined to determine if the same types were identified. If the same types of basin or margin impacts were identified, then impact percentages were examined.

	2006 (<i>n</i> = 70)	2007 (<i>n</i> = 63)
Pond Type	1.4%	9.5%
Water Level	11.4%	17.5%
Basin Impact Detection Discrepancy	8.6%	3.2%
Basin Impact Type	1.4%	6.3%
Basin Impact Percent	0.0%	3.2%
Margin Impact Detection Discrepancy	7.1%	0.0%
Margin Impact Type	4.3%	12.7%
Margin Impact Percent	11.4%	7.9%
Margin Width	14.3%	7.9%
Upland Conditions	10.0%	9.5%

Table 2.2 – Multistate model selection results estimating transition probabilities for wetland impacts across the Canadian Prairie Pothole Region (1985-2005) in relation to spatial factors. The candidate set was used to determine how probabilities varied spatially with survival and recapture probabilities fixed at 1. Akaike’s Information Criterion was corrected for sample size and adjusted for overdispersion ($\hat{c} = 1.72$). Spatial models included: 1) no spatial variation (null), 2) ecoregional variation – grassland and parkland (ecoregions) 3) provincial variation - Alberta, Manitoba, and Saskatchewan (provinces), and 4) a combination of province and ecoregion (group).

Model	QAICc	ΔQAICc	QAICc weights	Number of parameters
group	78220.98	0.00	1.00	30
provinces	78362.33	141.35	0.00	18
ecoregions	79493.20	1272.22	0.00	12
null	79635.36	1414.38	0.00	6

Table 2.3 – Multistate model selection results for estimating transition probabilities of wetlands across the Canadian Prairie Pothole Region (1985–2005). Survival and recapture probabilities were fixed at 1. Results from the top-ranked 10 candidate models are displayed. Akaike’s Information Criterion results were corrected for sample size and adjusted for overdispersion ($\hat{c} = 1.72$).

Model^a	QAICc	ΔQAICc	QAICc weights	Number of parameters
group * T/PD + LAND + POND	72747.06	0.00	1.00	114
MPD * T/PD + LAND + POND ^b	72858.21	111.15	0.00	96
group + T/PD + LAND + POND	72901.84	154.78	0.00	90
group + T + LAND + POND	73362.36	615.29	0.00	90
group + PD + LAND + POND	73573.34	826.28	0.00	90
group + T + POND	74260.25	1513.18	0.00	60
group + CSM + LAND + POND	74303.42	1556.36	0.00	90
group * t	74453.06	1705.99	0.00	600
group + PD + POND	74525.88	1778.81	0.00	60
group + LAND + POND	74597.38	1850.32	0.00	84

^a model covariates and symbols: group = combination of provinces and ecoregions; MPD = maximum wetland basin density (constant); t = time-dependency (i.e., year-specific variation); T = linear-logistic trend over time; PD = annually varying pond density at group level; CSM = annually varying conserved soil moisture at group level; T/PD = 3 transition parameters constrained linearly with time, and 3 transition parameters and constrained by pond density; LAND = dominant land use (individual covariate); POND = dominant wetland type (individual covariate); ‘+’ indicates additive effects; ‘*’ indicates multiplicative effects.

^b a posteriori model

Table 2.4 – Estimates of transition probabilities (± 1 SE) for different wetland types in a cultivated landscape in Saskatchewan parkland, 1995. Estimates are derived from model (group * T/PD + LAND + POND). See Fig. 2.2 for further description of transition probabilities.

WETLAND TYPE	n_3	m_2	m_3	b_3	n_2	b_2
EPHEMERAL	0.04 \pm 0.01	0.01 \pm 0.00	0.31 \pm 0.02	0.02 \pm 0.00	0.14 \pm 0.02	0.00 \pm 0.00
SEASONAL	0.08 \pm 0.01	0.01 \pm 0.00	0.14 \pm 0.01	0.12 \pm 0.00	0.08 \pm 0.01	0.01 \pm 0.00
PERMANENT	0.09 \pm 0.01	0.02 \pm 0.00	0.05 \pm 0.00	0.11 \pm 0.01	0.05 \pm 0.01	0.00 \pm 0.00
ARTIFICIAL	0.09 \pm 0.01	0.02 \pm 0.00	0.02 \pm 0.00	0.19 \pm 0.02	0.02 \pm 0.01	0.01 \pm 0.00
STREAM	0.07 \pm 0.01	0.02 \pm 0.00	0.07 \pm 0.01	0.14 \pm 0.01	0.04 \pm 0.01	0.01 \pm 0.00

n_3 = rates of transition from wetlands with no visible impacts (pristine) to wetlands with margin impacts (partially degraded); m_2 = rates of transition from wetlands with margin impacts to wetlands with no visible impacts; m_3 = rates of transition from wetlands with margin impacts to wetlands with basin and margin impacts (fully degraded); b_3 = rates of transition from wetlands with basin and margin impacts to wetlands with margin impacts; n_2 = rates of transition from wetlands with no visible impacts to wetlands with basin and margin impacts; b_2 = rates of transition from wetlands with basin and margin impacts to wetlands with no visible impacts.

2.6 FIGURES

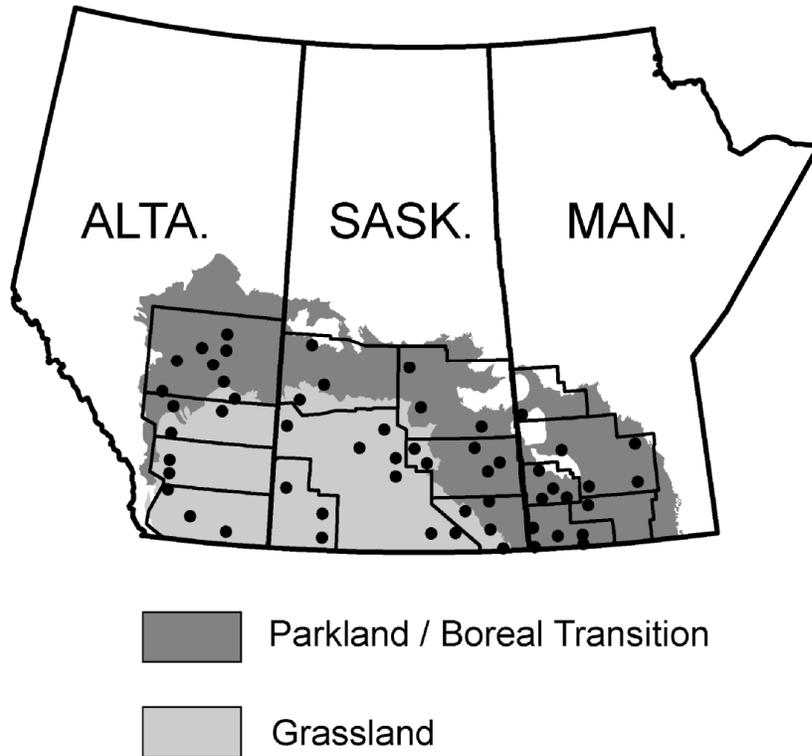


Figure 2.1 – Map of the Parkland/Boreal transition and Grassland ecoregions of the Canadian Prairie Pothole Region. Boundaries of prairie air-ground survey strata are represented by the polygons within the provinces, and solid circles signify the locations of survey segments (n = 56).

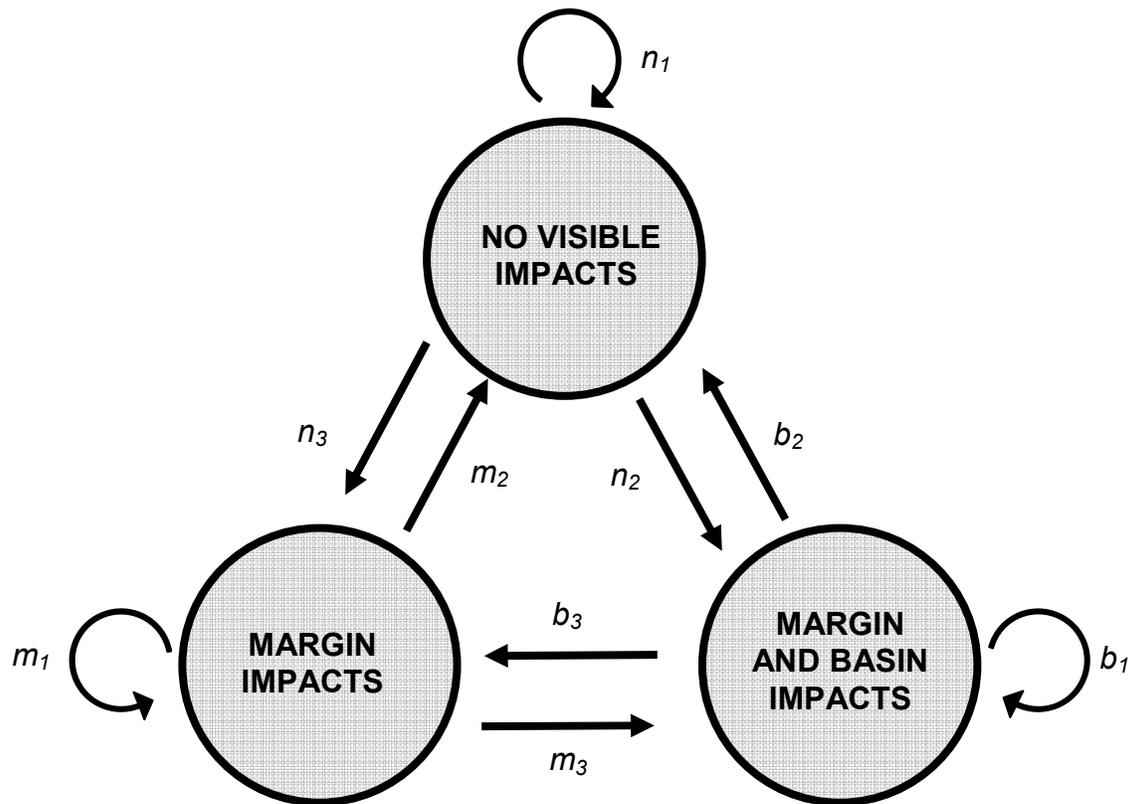


Figure 2.2 - Multistate framework depicting possible wetland states and transitions that can occur between years. n_1 = probability a wetland with no visible impacts will remain in that state; n_2 = probability a wetland with no visible impacts will shift to a wetland with margin and basin impacts; n_3 = probability a wetland with no visible impacts will shift to a wetland with margin impacts; m_1 = probability a wetland with margin impacts will remain in that state; m_2 = probability a wetland with margin impacts will revert to a wetland with no visible impacts; m_3 = probability a wetland with margin impacts will shift to a wetland with margin and basin impacts; b_1 = probability a wetland with margin and basin impacts will remain in that state; b_2 = probability a wetland with margin and basin impacts will revert to a wetland with no visible impacts; b_3 = probability a wetland with margin and basin impacts will revert to wetland with margin impacts.

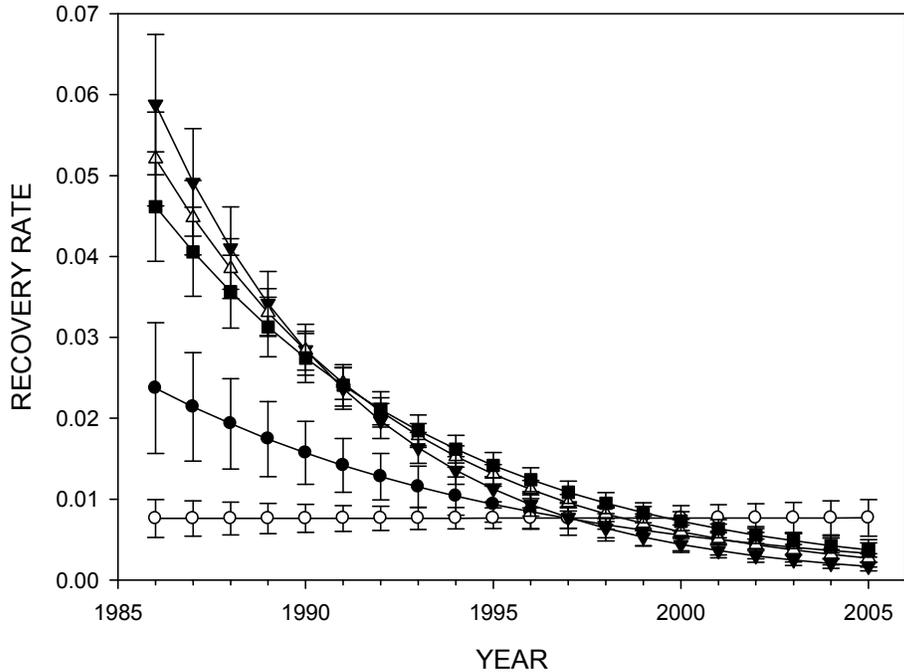
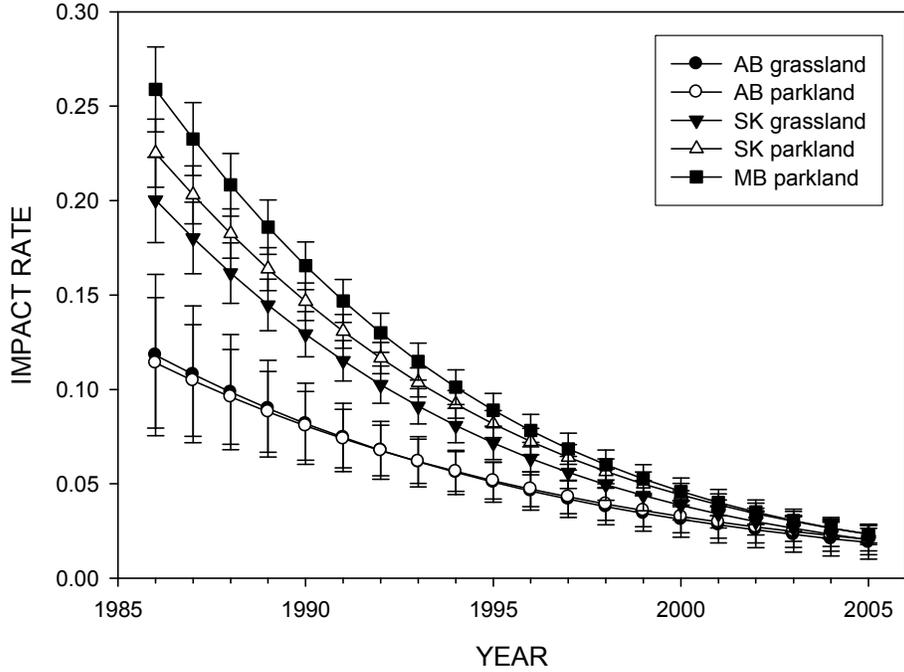


Figure 2.3 - Estimates of transition probabilities (± 1 SE) derived from model (group * T/PD + LAND + POND) for seasonal wetlands in cultivated landscapes, 1985-2005. Top: rates of transition from wetlands with no visible impacts to wetlands with margin impacts. Bottom: rates of transition from wetlands with margin impacts to wetlands with no visible impacts. Note that y-axis scales differ.

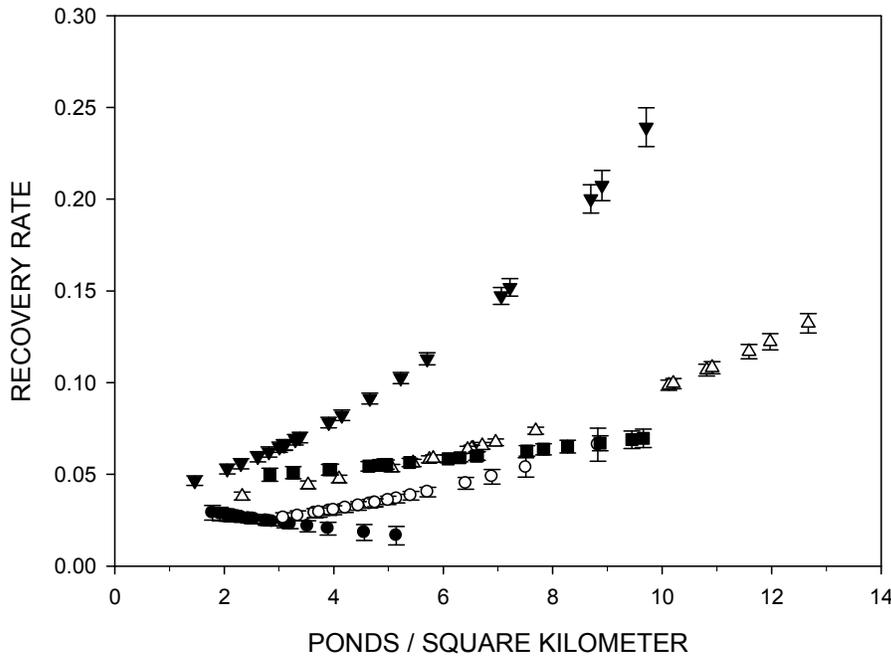
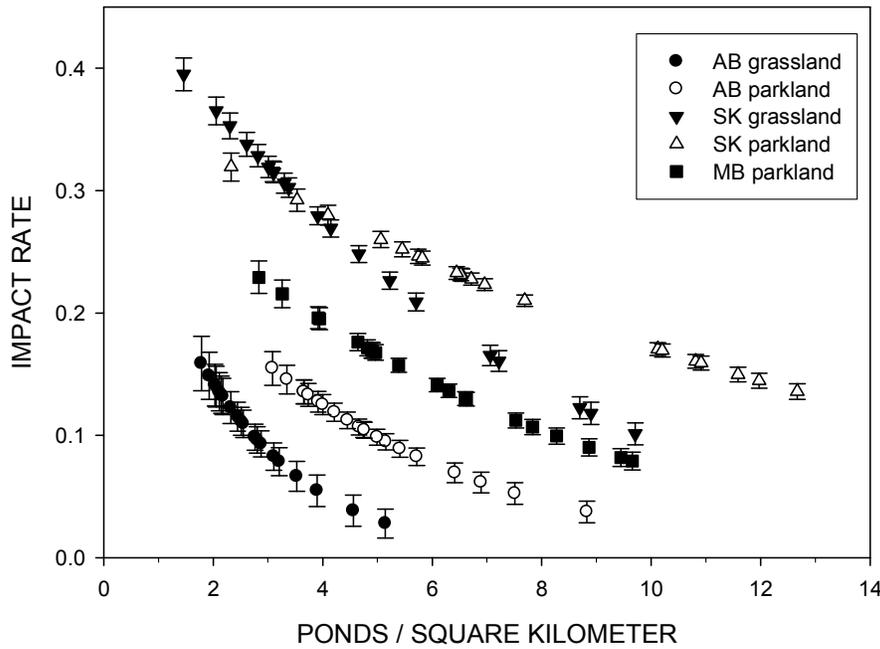


Figure 2.4 - Estimates of transition probabilities (± 1 SE) derived from model (group * T/PD + LAND + POND) for seasonal wetlands in cultivated landscapes relative to pond density, 1985-2005. Pond density was calculated from May pond estimates in the Waterfowl Breeding Population and Habitat Survey. Top: rates of transition from wetlands with margin impacts to wetlands with basin and margin impacts. Bottom: rates of transition from wetlands with basin and margin impacts to wetlands with margin impacts only. Note that y-axis scales differ.

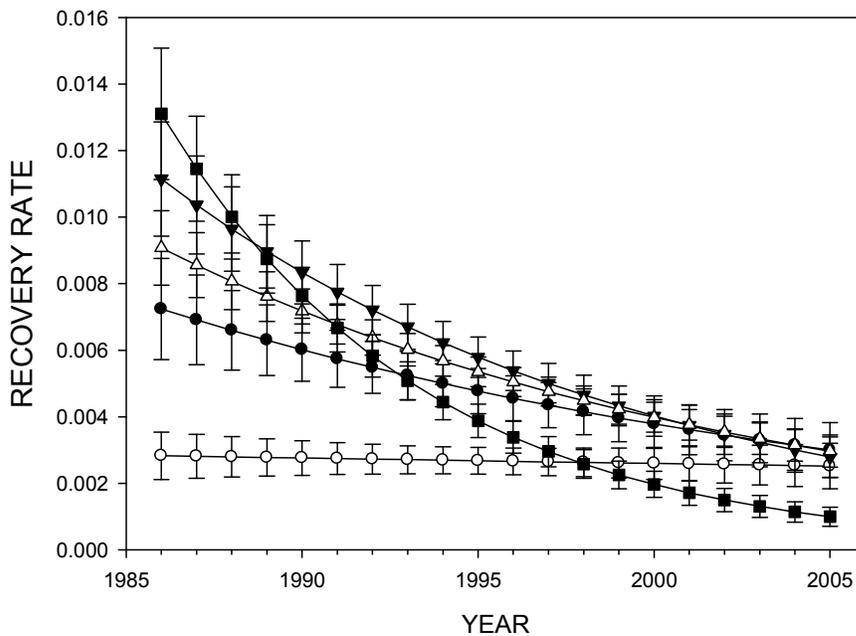
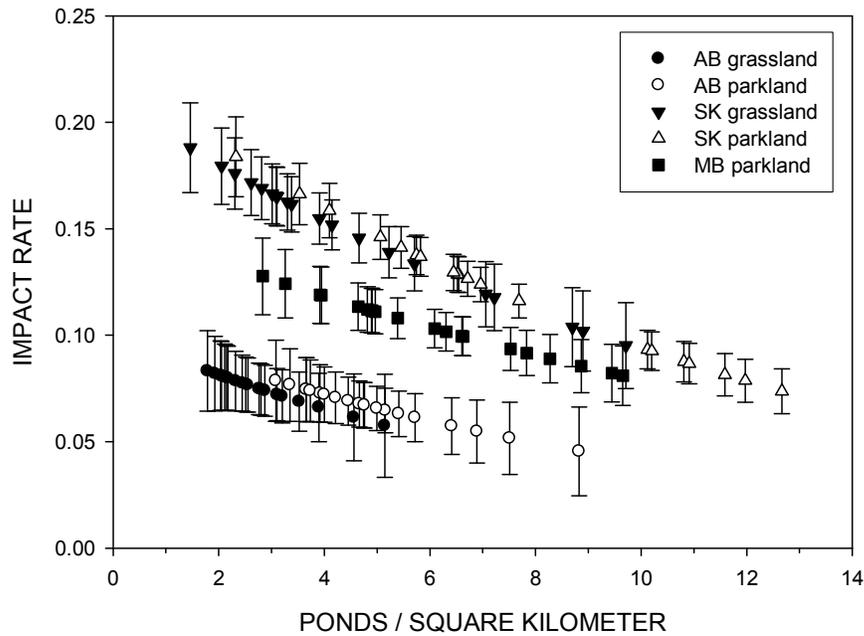


Figure 2.5- Estimates of transition probabilities (± 1 SE) derived from model (group * T/PD + LAND + POND) for seasonal wetlands in cultivated landscapes relative to time and pond density. Pond density was calculated from May pond estimates in the Waterfowl Breeding Population and Habitat Survey. Top: rates of transition from wetlands with no visible impacts to wetlands with basin and margin impacts relative to pond density. Bottom: rates of transition from wetlands with basin and margin impacts to wetlands with no visible impacts constrained to vary as a linear-logistic function of time. Note that y-axis scales differ.

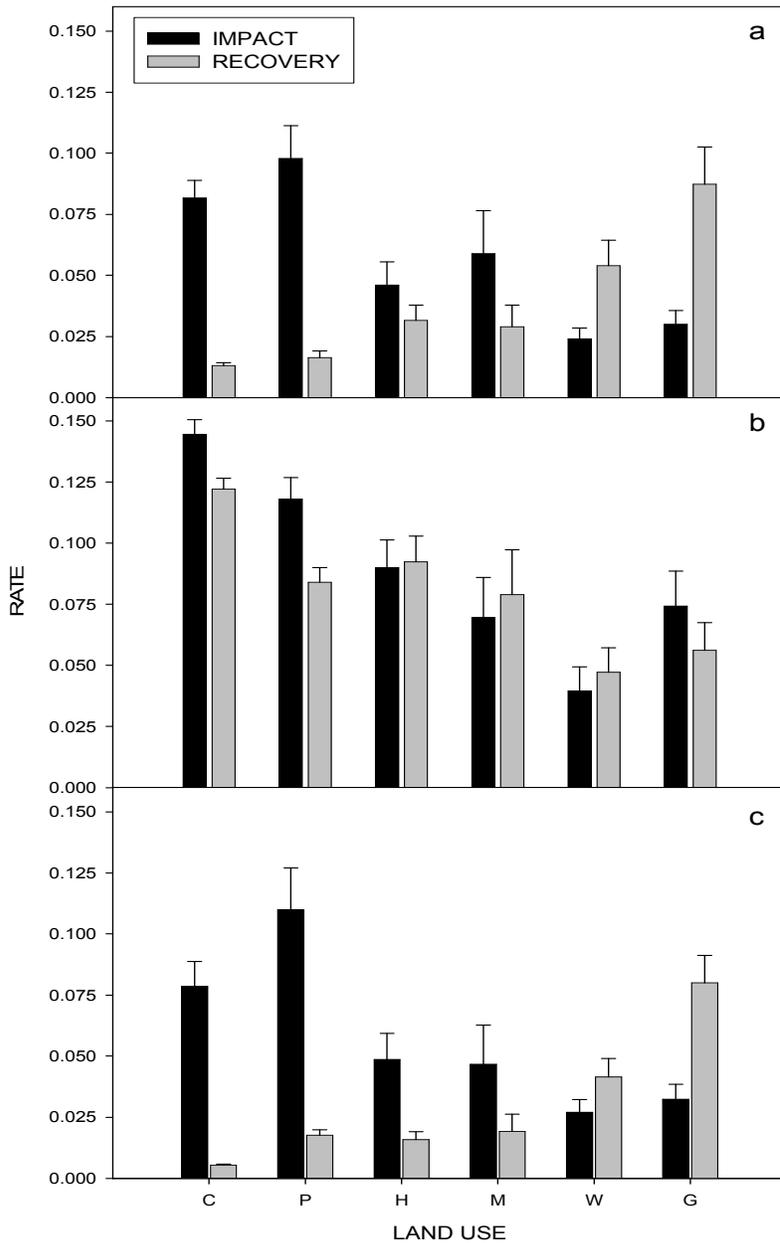
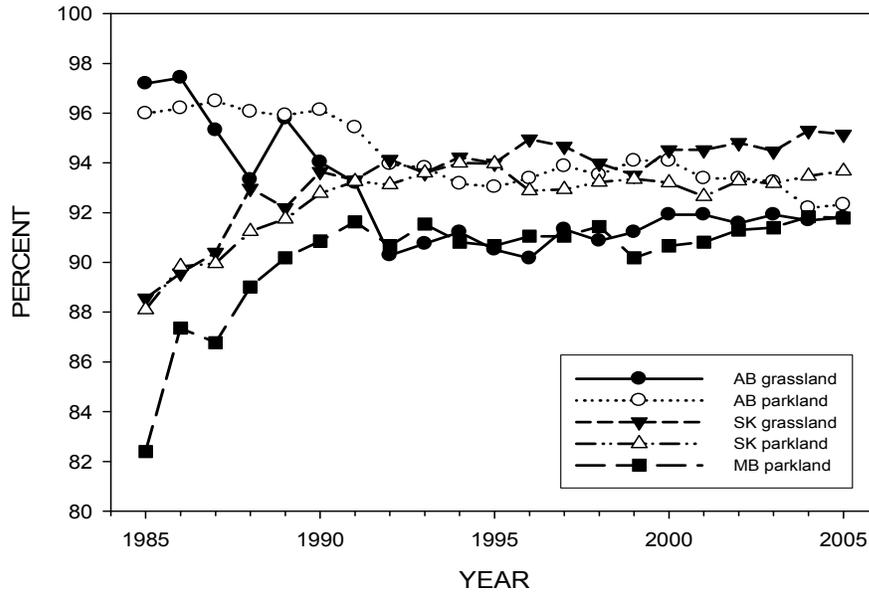


Figure 2.6- Estimates of transition probabilities (± 1 SE) derived from model (group * T/PD + LAND + POND) for wetlands surrounded by different land uses in Saskatchewan parkland, 1995. (a) Impact and recovery rates are estimates of transition probabilities between wetlands with no visible impacts and wetlands with margin impacts. (b) Impact and recovery rates are estimates of transition probabilities between wetlands with margin impacts and wetlands with basin and margin impacts. (c) Impact and recovery rates are estimates of transition probabilities of wetlands with no visible impacts and wetlands with basin and margin impacts. C = cultivation; P = pasture; H = hay / farmyard; M = mixed use; W = woodland; G = grassland (native and restored).

WETLAND MARGIN IMPACTS



WETLAND BASIN IMPACTS

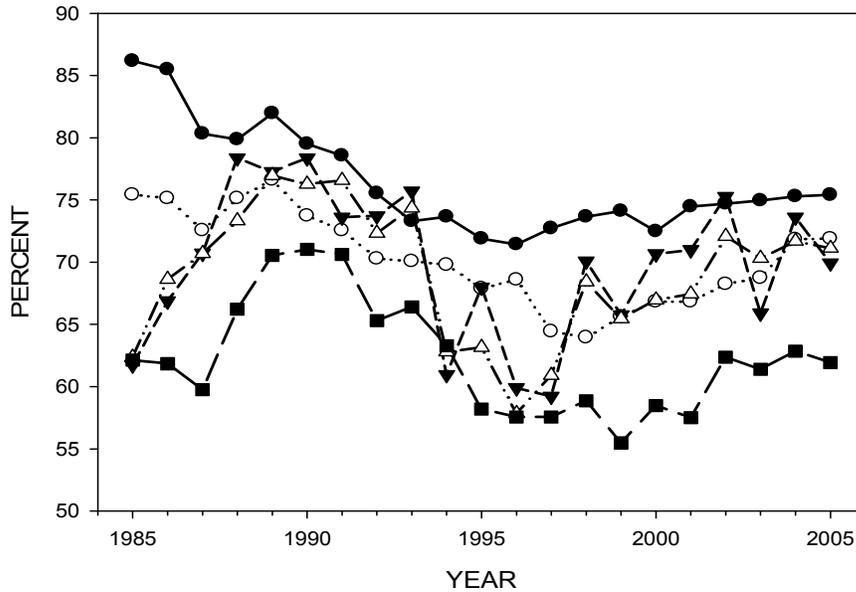


Figure 2.7 – Percent of degraded wetlands across the Canadian Prairie Pothole Region (1985-2005). Top: percent of sample with degraded margins. Bottom: percent of sample with degraded margins and basins.

CHAPTER 3 RELATIONSHIPS BETWEEN ABUNDANCE OF BREEDING DUCKS AND CHARACTERISTICS OF CANADIAN PRAIRIE WETLANDS

3.1 INTRODUCTION

The significance of wetlands to breeding ducks has been extensively documented throughout the world. In North America, a key breeding area for ducks is the Prairie Pothole Region (PPR) where there are millions of wetlands situated in post glacial depressions (Johnson et al. 1994, Greenwood et al. 1995). The PPR, approximately 780,000 km² in area and extending north from Iowa through the Dakotas and prairie Canada (Mitsch and Gosselink 2000), comprises only 10% of the continental breeding area but produces over 50% of North America's duck population (Crissey 1969, Greenwood et al. 1995). Although the relationship varies among species, there is generally a strong positive correlation between May wet pond densities and waterfowl abundance in a given area (Johnson and Grier 1988). Periodic drought and deluge conditions and regional climatic gradients produce spatiotemporal variation in wetland densities, in turn causing duck numbers to fluctuate (Johnson and Grier 1988, Austin 2002, Johnson et al. 2005).

Predictive models can facilitate management decisions by projecting how populations will respond to wetland conditions. In particular, based on models developed in the Dakotas, Cowardin et al. (1995) used a remote sensing based system to estimate the number and area of wetlands, sizes of breeding duck populations, and duck productivity for the PPR. Based on wet area of wetland basins (hereafter ponds; Cowardin 1982), the authors generated predictive regression models for abundance of breeding pairs of ducks (Cowardin et al. 1995). The relationship between breeding pair numbers and pond area was curvilinear, with a steep initial increase in the number of breeding pairs with an increase in pond area, followed by a gradual slowdown in rate of increase on larger wetlands. Cowardin et al. (1995) developed these models for numerous species, but their focus was on five major species of dabbling ducks (Anatinae), which are also the focus of this study: blue-winged teal (*Anas discors*), gadwall (*A. strepera*), mallard (*A. platyrhynchos*), northern shoveler (*A. clypeata*), and northern pintail (*A. acuta*). Although rates of increase and maximum densities varied

among species, they all exhibited the same curvilinear pattern. These models have been used to estimate breeding population numbers in specific areas based on wetland conditions (e.g., Austin et al. 2001, Devries et al. 2004). The use of wetland metrics based on remote-sensing data is advantageous because it provides a relatively simple, fast, and inexpensive means of measuring habitat over large and sometimes inaccessible areas (Cowardin et al. 1995, Cowardin et al. 1998).

Models developed for the Dakotas (hereafter Dakota models) have been applied to the Canadian prairies to estimate waterfowl carrying capacity (Devries et al. 2004), but it is unclear whether these models can accurately predict breeding waterfowl abundance in Canada. The Canadian portion of the PPR differs from the U.S. in terms of land use policies, economies, wetland density, duck community composition, and landscape conditions (Johnson and Grier 1988, Greenwood et al. 1995, Drever et al. 2007). These differences may be most apparent in the aspen parkland and boreal transition ecoregions of Canada (Marshall et al. 1999) because these regions have distinct vegetation, fauna, soil, water, climate, and physiography from the rest of prairie Canada and U.S. Other studies have shown that duck responses to environmental factors can vary in different portions of the PPR (e.g., Bethke and Nudds 1995, Miller 2000). Consequently, it may be unwise to assume that models developed in the Dakotas could be used to predict duck density and wetland area relationships in the Canadian parklands. Therefore, I evaluated the Dakota models with independent data collected in Canada. My general objectives were to: 1) assess how well the Dakota models performed in Canada, and 2) determine if models with improved predictive ability could be developed using data collected in Canada.

3.1.1 Hypotheses and Predictions

Blue-winged teal and gadwall have a primary breeding range situated in the Dakotas and southern Canadian prairies, whereas breeding ranges of mallards, pintails, and shovelers tend to be centered further north in the Canadian prairies (Johnson and Grier 1988). Based on historic core breeding ranges and densities (Johnson and Grier 1988), I anticipated that the Dakota models would over-predict breeding abundance of blue-winged teal and gadwall, but would under-predict abundance of mallards, northern pintails (hereafter pintails), and northern shovelers (hereafter shovelers). I anticipated

that pond area would still be an important predictor of duck abundance on Canadian ponds because of species basic food and breeding requirements, and varying degrees of tolerance towards conspecifics and other species (Titman and Seymour 1981, Nudds and Ankney 1982). Consequently, I expected that models derived from Canadian data would produce similar curvilinear trends to the Dakota models, but that the relationships would vary for each species: Canadian ponds would have lower densities of blue-winged teal and gadwall but higher densities of mallards, shovelers, and pintails. I also anticipated that variation in biotic and abiotic conditions could lead to variation within the Canadian PPR with respect to breeding pair to pond area relationships. As a test of this prediction, I examined the effect of two publicly available spatiotemporal variables (Migratory Bird Data Center - <http://mbdcapps.fws.gov/>, *public communication*): regional pond and duck densities calculated at the level of survey stratum (see Methods). I anticipated a higher abundance of breeding pairs per pond in regions of higher duck densities because ducks would be forced to crowd onto existing ponds. Conversely, there may be a lower abundance of breeding pairs on ponds in regions of higher pond densities because higher pond densities should allow ducks to distribute themselves across the landscape (Cowardin et al. 1998).

3.2 METHODS

3.2.1 Study Areas and Field Methods

3.2.1.1 *St. Denis National Wildlife Area*

St. Denis National Wildlife Area (hereafter St. Denis) is approximately 385 ha situated about 40 km east of Saskatoon in south-central Saskatchewan, Canada (52°12'N, 106°05'W; Fig. 3.1). In 2007 and 2008, waterfowl surveys were conducted at St. Denis on a weekly to biweekly basis from early May to early June. During surveys, observers cautiously approached each wetland, attempting not to disturb or flush birds. Wetlands were surveyed using binoculars and spotting scopes, and all visible waterfowl were counted and their social status recorded. Pond area measurements were also taken on 20-21 June 2007, and 5-6 May 2008 using handheld Global Positioning System (GPS) units. Each observer walked along the water's edge while holding a Garmin GPSmap 76CSx

unit; these were pre-set to save track points to a track log file every second. Observers walked completely around each pond, and ceased logging a track when moving between ponds. Consequently, the track log file consisted only of points pertaining to the perimeters of ponds. Using XTools Pro 5.0 in ArcGIS 9.2 (Environmental Systems Research Institute, 2006, Redlands, CA – <http://www.esri.com>), I converted the points into polygons representing individual ponds, and I calculated the area and perimeter of each polygon using Hawth's Analysis Tools 3.27 (Beyer 2006).

3.2.1.2 *Waterfowl Breeding Population Surveys and Wetland Areas*

The Waterfowl Breeding Population and Habitat Survey (WBPHS) has been conducted annually by the U.S. Fish and Wildlife Service and Canadian Wildlife Service since 1955 (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987). To estimate sizes of duck populations, aerial surveys are conducted over major breeding areas in Canada and the United States. These breeding areas are delineated into survey strata according to political boundaries, habitat conditions, and duck densities. Two-person aerial crews systematically survey 400 m-wide randomly-established transects within these strata. Where ground transportation networks and access are good, ground crews survey smaller segments (up to 29 km) within aerial transects with intent to obtain a complete survey of all ducks in segment boundaries; social status of observed ducks is also noted as described below. In addition to duck counts, Canadian ground crews visually assess habitat conditions at each wetland visited during surveys (Turner et al. 1987). Ground counts are then used to compute visibility correction factors which are applied to the aerial survey counts. Within the Canadian PPR, there are more than 120 air-ground comparison segments. Unlike the St. Denis surveys, margins are actively “beat-out” during the ground component of the WBPHS to ensure all waterfowl are counted. These surveys are only conducted once annually in May at each segment because of logistical constraints due to the much larger spatial extent of the WBPHS.

As part of a prairie wetland habitat monitoring program, 153 transects (including 65 air-ground segments) were established, and baseline habitat conditions were measured from aerial photography taken in May 1985 and re-measured *circa* 2001 (Millar 1987, Watmough et al. 2002). From this habitat study, Environment Canada (Mike Watmough, Canadian Wildlife Service, Edmonton, personal communication) provided wetland areas

and perimeters for 3,772 basins located on 59 air-ground segments across the Canadian PPR. From this sample, I selected only wetlands for which there were total area measurements, and I did not include basins that fell on air-ground transect or quarter section (64 ha) boundaries for which there were only partial area measurements. Another selection criterion was that wetland areas had not changed by more than 0.01 ha between assessments, so I could be confident that areas were applicable to the entire period between assessments. After I coupled the area and perimeter measurements of the selected wetlands to the corresponding WBPHS data (i.e., duck counts obtained from the ground component of each survey) from 1993-2002, I selected records of wetlands that had full or intermediate water level stage designations because the wet area of these ponds would most closely match with the basin areas provided by the habitat monitoring program. This selection process resulted in 3,550 individual records for 1208 unique wetlands on 57 air-ground segments (Fig. 3.1).

3.2.2 Analyses

For both datasets (St. Denis and Canadian PPR), I calculated estimated breeding pair abundance of ducks using tallying methods described by Cowardin et al. (1995), which were based on techniques developed by Dzubin (1969) and Hammond (1969). All pairs and each male in groups ≤ 5 were calculated as pairs, but for shovelers, only pairs and lone drakes were used in calculations. Because of multiple waterfowl surveys per spring at St. Denis, I selected survey dates that best matched breeding chronologies of the different species (Cowardin et al. 1995, Reynolds et al. 2006): 1) 9 May 2007 and 2 May 2008 for mallards and pintails, 2) 9 May 2007 and 13 May 2008 for shoveler, and 3) 24 May 2007 and 23 May 2008 for blue-winged teal and gadwall.

The following procedures were repeated for each duck species in each dataset unless otherwise stated. The first objective was to determine how well the Dakota models performed; to this end, I conducted linear regressions comparing observed number of breeding pairs of each species on a per pond basis to the number of pairs predicted by the Dakota models. I examined: 1) the coefficient of determination (R^2) to determine how much variation was explained by the predictive models, 2) the slope of the regression line to determine model consistency (slopes $\neq 1$ indicated inconsistency),

and 3) the intercept as an indication of model bias (intercept $\neq 0$ indicated bias; Pineiro et al. 2008).

After the evaluation process, I developed an *a priori* candidate set of models to explain breeding pair abundances on the basis of basic wetland metrics: wet area (area, in ha), square root of the wet area ($\sqrt{\text{area}}$, a proxy for shoreline length; Cowardin et al. 1995), wetland perimeter (perimeter, in m), and shoreline complexity. Shoreline complexity is the ratio of the actual perimeter of a water body to the circumference of a circle of equal area; a perfectly circular water body would have shoreline complexity = 1 (Hansson et al. 2005, Earnst et al. 2006). Along with a null model, I considered all single-factor models involving the explanatory variables, and I included additional two-factor models that combined wetland area with additive effects of each remaining variable. In addition, I developed one multiplicative model in which wetland area interacted with perimeter. Because square root of area serves as a proxy for perimeter, and shoreline complexity is a derivative of perimeter, these factors were never included together or with perimeter in the same model. As a result, the candidate set was composed of nine models for both datasets. To account for lack of independence from repeated measures on wetlands surveyed in multiple years, I used generalized least squares regression models in Program "R" Version 2.7.2 (Pinheiro and Bates 2000, R Development Core Team 2008). After extensive evaluation using standard techniques (Littell et al. 2000), a compound symmetry covariance structure was employed because it was deemed most appropriate for the data. Intercepts were not included in the models (i.e., regressions were forced through the origin) because there could be no breeding pairs on dry basins, i.e., at area = 0 and perimeter = 0, the number of breeding pairs must also equal 0. Although ducks are occasionally in fields or dry basins, survey protocols preclude assigning ducks to dry basins, and hence, ducks are assigned to the nearest wet basin (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987).

Model selection was based on an information-theoretic approach by calculating Akaike's Information Criterion (AIC) for all models (Burnham and Anderson 2002). AIC indicates a models' degree of parsimony, which represents a balance between model fit and precision of parameter estimates. Thus, models within each candidate set were ranked based on respective AIC values, with the lowest AIC indicating the most

parsimonious model. To aid in model selection, I also computed ΔAIC (AIC values expressed relative to AIC of the most parsimonious model) and AIC-based model weights (Burnham and Anderson 2002). Following Burnham and Anderson (2002), I considered all models with $\Delta\text{AIC} \leq 2$ as having substantial empirical support. I report parameter estimates from the most parsimonious model for each species in each dataset.

To evaluate how the most parsimonious models performed, I conducted a cross-validation procedure using 80% of observations (randomly selected) to generate parameter estimates for the most supported models (Snee 1977, Reynolds et al. 2006). I used those estimates to predict the number of breeding pairs for the remaining 20% of observations, and then conducted linear regression between observed and predicted pairs as with the Dakota model evaluation. For each model, I performed 1000 iterations, and I report the means of R^2 values, intercepts, and slopes computed over all iterations. For further evaluation of model performance, I applied estimates from one dataset to predict the number of breeding pairs for the other dataset and, as before, conducted a linear regression of observed to predicted breeding pairs. As a last form of evaluation for the Canadian PPR assessment, I summed the observed and predicted pairs of ducks per segment and year and again conducted linear regressions of observed to predicted breeding pairs.

A final objective was to determine whether the relation between duck abundance and wetland metrics was influenced by stratum-specific (i.e. regional scale) duck and pond densities. To address this objective, I used the Canadian PPR data set (1993-2002). First, I calculated annual duck (by species) and pond densities for each survey stratum by dividing the respective abundances by stratum area (km^2 ; Migratory Bird Data Center - <http://mbdcapps.fws.gov/>, *public communication*). I formulated a candidate set of four models for each species; first, the most parsimonious wetland metrics model served as a proxy null model to which I added either conspecific duck density ($\text{DD} \cdot \sqrt{\text{area}}$), pond density ($\text{PD} \cdot \sqrt{\text{area}}$), or duck and pond densities. The constitutive terms of the interactions, pond and duck density, were not included in analyses because all models regressed through the origin (i.e., at 0 ha of pond area, there are no breeding pairs). Inclusion of duck and pond density as additive terms could result in estimates of abundance $\neq 0$ at pond area = 0, which is inaccurate given the survey protocol.

3.3 RESULTS

3.3.1 Dakota Model Evaluations

The Dakota models explained more variation in duck abundance when applied to the St. Denis data set, but were more consistent and less biased when applied to the Canadian PPR (Table 3.1). With the exception of pintail, the Dakota models largely under-predicted numbers of breeding pairs at St. Denis (i.e., slope coefficients > 1 ; Table 3.1). For the Canadian PPR, the abundance of breeding pairs of mallards and shovelers were under-predicted by the Dakota models, but the breeding pair numbers for the other species were consistently predicted without bias (i.e. slope coefficients = 1, and intercepts = 0; Table 3.1).

3.3.2 Model Development from Canadian Data

For the Canadian PPR dataset, the proxy for shoreline length, $\sqrt{\text{area}}$, was included in the most parsimonious models for all species (Table 3.2). An additional parameter, area, was also included in the most supported models for blue-winged teal, gadwall, and pintail. Area, $\sqrt{\text{area}}$, or both were supported predictors for breeding pair abundance for all species at St. Denis (Table 3.3). Mallards were anomalous in that wetland perimeter was included in the most parsimonious model for St. Denis. With the exception of mallards, all species exhibited positive relationships between breeding pair numbers and variables in the most parsimonious models (Table 3.4). Mallard abundance was positively related to area and perimeter but had a negative relationship with the multiplicative term, $\text{area} \times \text{perimeter}$. The Dakota models consistently estimated fewer breeding pairs of mallards and shovelers, and more breeding pairs of gadwall, than the Canadian PPR models developed herein (Fig. 3.2). For blue-winged teal, and pintail, the Dakota models estimated slightly more breeding pairs at small pond sizes, but fewer breeding pairs at larger pond sizes than the Canadian PPR models (Fig. 3.2). Blue-winged teal generally had the highest breeding pair abundance, followed by mallards, whereas shoveler, gadwall, and pintail abundances were substantially less than the former two species (Fig. 3.2).

Cross-validation results indicated that the Canadian PPR models did not explain more variation than the Dakota models, but intercepts closer to zero and slope

coefficients closer to one suggested the new models were less biased and more consistent in predicting breeding pair abundance (Table 3.5; cf. Table 3.1). For St. Denis, the amount of variation explained by the most parsimonious models was slightly higher than the Dakota models for some species, but more notable differences were the intercepts being closer to zero and the slope coefficients being much closer to one (Table 3.5). When I used estimates from the newly developed models in one dataset to predict the number of breeding pairs based on the other dataset, the variation explained was similar to the Dakota models in both cases (Table 3.6). However, the St. Denis models generally over-predicted the number of breeding pairs for the rest of prairie Canada with the exception of pintail, and results were reversed when the Canadian PPR models were applied to St. Denis, as they under-predicted the number of breeding pairs of most species, but over-predicted pintail. When I scaled the analysis to the level of segment and year for the Canadian PPR (i.e., linear regressions conducted between observed and predicted abundances of breeding pairs, summed for each segment in each year; $n = 418$), the amount of variation explained by the models increased for blue-winged teal ($R^2 = 0.43$ vs. 0.06; Table 3.5), gadwall ($R^2 = 0.24$ vs. 0.03), mallard ($R^2 = 0.32$ vs. 0.03), pintail ($R^2 = 0.06$ vs. 0.02), and shoveler ($R^2 = 0.32$ vs. 0.03).

As an illustration of the potential effects of wetland loss and restoration on duck abundance, I performed a simulation exercise. First, I drew a random sample of 1000 wetlands (262.5 ha total wetland area) from the Canadian PPR data, and I estimated duck abundance using the Dakota and newly developed Canadian PPR models. The Dakota models estimated more gadwall and blue-winged teal, but fewer mallards and shovelers than the Canadian PPR models; pintail estimates were almost the same from either model (Table 3.7). Watmough and Schmoll (2007) reported a 5% wetland loss between 1985 and 2001 for the Canadian prairies; 0.10 ha was the median size of the lost wetlands. To simulate wetland loss, I randomly selected 25 wetlands ≤ 0.10 ha and 25 wetlands > 0.10 ha, and removed them from the sample, resulting in a loss of 7.8 ha total wetland area. Under both models, this loss of wetlands caused a decrease of approximately 4% for all species from the initial estimates, but the decreases in absolute numbers varied (Table 3.7). Then, as a restoration simulation, I "restored" 7.7 ha of wetland area. However, rather than restoring the original wetlands, I focused restoration on wetlands ≤ 0.10 ha

(123 wetlands \leq 0.10 ha were randomly selected). As a result, there was a net gain for each species of 2-3% relative to initial pair numbers even though there was slightly less total wetland area than was initially present (Table 3.7). This simple exercise demonstrated the potential effects of changes in wetland numbers on duck abundance, and how wetlands of different sizes can have different influences on abundance.

3.3.3 Effects of Variation in Regional Duck and Pond Density

When I examined how stratum-specific duck and pond density may affect the relationship between breeding pair abundance and wetland area, the models that included both parameters received full support for all species (AIC weight = 1.00; Table 3.8). Duck density was positively related, and wetland density inversely related, to breeding pair abundance per pond area for all species (Table 3.9). Thus, abundance on individual ponds increased with an increase in regional population density, but decreased with an increase in regional pond density. To illustrate the effects of changes in regional duck and pond density on breeding pair abundance, I chose to focus on mallards and blue-winged teal because they vary markedly in terms of morphology, reproductive strategies, and behaviour. Mallards are earlier nesters, larger bodied, more philopatric, and less territorial than blue-winged teal (Titman and Seymour 1981, Nudds and Ankney 1982, Titman 1983, Lokemoen et al. 1990). Blue-winged teal breeding pair abundance was equally sensitive to changes in duck and pond density (Fig. 3.3), whereas mallard breeding pair abundance was more sensitive to changes in pond density than changes in duck density (Fig. 3.4).

3.4 DISCUSSION

To effectively plan, deliver, and manage conservation programs for wildlife, it is critical to understand species' basic requirements in terms of habitat, food, and other biotic and abiotic factors. The reliance of breeding ducks on wetlands is well-documented, but critical knowledge gaps persisted. For instance, until now it was unclear whether predictive models developed for the Dakotas could be applied to the Canadian prairies to accurately predict breeding waterfowl abundance. The Dakota models explained more variation in breeding pair abundance when applied to data from St. Denis than when applied to the Canadian PPR, but estimates from these models were more

biased and less consistent for St. Denis. A likely explanation for low amount of variation explained when applied to Canadian PPR data set is the larger spatiotemporal scale of the Canadian PPR, as both duck and pond numbers varied greatly over the region and over the duration of this study (Wilkins et al. 2006). Some likely reasons the Dakota models largely under-predicted breeding pair abundance at St. Denis are (1) exceptional duck densities on and around the national wildlife area, (2) relatively pristine wetland conditions, and (3) ample suitable nesting habitat provided by idle and planted cover (Emery et al. 2005). In further support of exceptional conditions at St. Denis, the Canadian PPR models generally under-predicted breeding pair abundance at St. Denis, and the St. Denis models generally over-predicted breeding pair abundance for the Canadian PPR.

With exception of mallards at St. Denis, $\sqrt{\text{area}}$, which serves as a proxy for shoreline perimeter (Cowardin et al. 1995, Reynolds et al. 2006), was an important predictor for all species in both datasets. Dabbling ducks occur more frequently along shorelines of larger ponds because they utilize the shoreline for concealment against predators and conspecifics, and they rely on shallower water to feed (Kantrud and Stewart 1977, Nudds 1983, Reynolds et al. 2006). Interestingly, models that included perimeter or shoreline complexity (a derivative of perimeter) were not well supported by the data in most cases, which suggests the precise shapes and intricacies of shorelines are not as important as the approximate amount of shoreline available.

Although the models developed in this study generally did not explain more variation than the Dakota models, estimates from the newly developed models were less biased and more consistent. Also, when models derived from one data set were used to predict abundance in the other, unrelated data set, the amount of variation explained by the models was similar to the amount explained by the models that were actually developed from the unrelated data. In other words, when the Canadian PPR models, which explained low amounts of variation in the data set they were generated from, were applied to St. Denis, they explained almost as much variation in breeding pair abundance as the St. Denis models. Likewise, when the St. Denis models were applied to the Canadian PPR data, they explained nearly the same amount of variation in breeding pair abundance as the Canadian PPR models. These results suggest that R^2 may be

influenced by the scale at which the models are applied, and that using R^2 to evaluate model performance, in this instance, may not be useful. Therefore, I focus my evaluation of model performance on intercepts and slopes of the observed:predicted linear regressions (Pineiro et al. 2008), which suggests the models developed from independent data collected in Canada do perform better than the Dakota models.

This study also demonstrates that spatiotemporal variation in duck and pond density can influence the relationship between breeding pair abundance and pond area. As water conditions tend to be more stable in the northern parkland than the southern grassland (Bethke and Nudds 1993), the breeding pair to pond area relationships may fluctuate less in the north. However, drought-displaced waterfowl often redistribute to regions with more favourable water conditions (Johnson and Grier 1988, Hestbeck 1995), which could increase duck density in the north, and, thereby, alter the breeding pair to pond area relationships. Consequently, although habitat conditions may be more stable in the north, the relationships may fluctuate because of unstable conditions in the south. Different species had different levels of sensitivity to changes in duck and pond densities. For instance, mallard abundance appeared to be more sensitive to changes in pond density than changes in duck density, whereas blue-winged teal abundance appeared to be equally sensitive to changes in duck and pond density. Homing habits of species may, in part, explain the variation in response to duck and pond densities (Johnson and Grier 1988, Lokemoen et al. 1990). Mallards tend to be more philopatric and occupy their core breeding area (mainly the Canadian prairies) first, whereas blue-winged teal are more opportunistic and settle in suitable habitat as they encounter it (Johnson and Grier 1988). Perhaps, mallards may be more likely to return to an area and adapt to existing wetland conditions (Lokemoen et al. 1990). Other possible explanations for the varying responses are the species differences in territoriality and spacing behaviour. Mallards tend to be less territorial than blue-winged teal (Titman and Seymour 1981), and their tolerance of conspecifics can be more flexible; occupying smaller territories when they are under higher local population densities (Titman 1983). Therefore, mallards may be more likely to crowd onto remaining ponds when they encounter low pond densities, and blue-winged teal may be more likely to redistribute to areas of more favourable water conditions (Lokemoen et al. 1990).

One limitation associated with the Canadian PPR dataset was that I constrained the sample to include only ponds that had intermediate and full water level stages, so the basin areas would be closer to actual pond areas. However, breeding pair abundance to pond area relationships may vary slightly on ponds of different water levels (Bolduc and Afton 2008). Another potential criticism, which I have alluded to, is the inference of pond area from wetland basin area. I had to assume the provided basin areas were reasonable approximations of pond area. However, previous studies also did not use exact pond areas (Cowardin et al. 1995, Reynolds et al. 2006). Instead, observers carried maps with boundaries of all surveyed wetlands to visually estimate the percent of each wetland basin covered with water, and then this percentage was used to calculate the surface area of each pond (Reynolds et al. 2006). Further application of the Canadian PPR models to independent data consisting of spring duck surveys on ponds of known areas could help resolve these uncertainties. Another limitation of the present study may be the smaller distribution of pond sizes used to develop the Canadian PPR models relative to those used by Cowardin et al. (1995). However, other studies have shown the median wetland size is 0.15 ha for prairie Canada (Dahl and Watmough 2007), and work in the Dakota portion of the PPR suggests nearly 95% of all ponds are <2 ha (Cowardin et al. 1995). Because the median basin size in the Canadian prairie sample was 0.19 ha and the range was 0.02 ha to 2.32 ha, I suspect that the Canadian prairie sample is representative of the majority of prairie wetlands.

Unlike the WBPHS and Dakota surveys (Cowardin et al. 1995, Reynolds et al. 2006), the St. Denis surveys were more passive; field crews only recorded visible birds and did not actively "beat out" areas where birds may be obscured from observation. Although the different survey methods may lead to different estimated duck numbers, this would not explain why St. Denis had higher breeding pair abundance than the rest of the Canadian prairies. Indeed, one might have expected lower breeding pair abundance for St. Denis because of the more passive method of survey. Another potential source of error in the St. Denis data is that pond areas in 2007 were measured in June, after the waterfowl surveys. Ponds can recede as the summer season progresses, but water levels (i.e., depth) of all ponds at St. Denis were measured in the middle of May and June 2007. When I compared how many ponds had changed >10 cm between May and June

measurements, water levels dropped in 12 ponds, 8 ponds gained water, and 85 ponds did not change. Thus, wet area of most ponds likely did not change appreciably from May to June 2007.

3.4.1 Management Implications

This study suggests the application of Dakota models to estimate breeding pair abundance for blue-winged teal, gadwall, and pintails on Canadian prairie ponds may be reasonable, but Dakota models would underestimate breeding pair abundance of mallards and shovelers. Consequently, wetland loss or restoration in the Canadian prairies could have a more severe effect on mallards and shovelers than predicted previously by the Dakota models (Devries et al. 2004). Further caution against using the Dakota models for the Canadian prairies is suggested by the fact that St. Denis results, along with results from the Canadian PPR analysis, have demonstrated that relationships between breeding pair abundance and pond area can vary over time and space. Therefore, it may be more prudent to use parameter estimates from this study (or those based on further refinements), which are derived from data collected in Canada, and allow for regional and temporal variation in pond and duck densities.

This study also indicates the biggest change in breeding duck abundance occurs on smaller ponds (< 0.5 ha). In the wetland loss and restoration simulation, I demonstrated how restoration of smaller wetlands could increase duck abundance more than equivalent restoration of larger wetlands. Therefore, conservation of smaller wetlands is critical for maintaining and elevating breeding population levels of the species studied, yet these wetlands are currently most likely to be lost or degraded through agricultural impacts (Whigham 1999, Watmough et al. 2002, see also Chapter 2). Larger, more permanent wetlands may be important for brood-rearing and other waterbird use and should also be protected (Talent et al. 1982); however, these wetlands may be somewhat less threatened due to longer flooding duration (see Chapter 2).

The purpose of the models developed here was not to estimate abundance on individual ponds, as they would likely perform poorly, but to estimate the number of ducks in a given block or area based on its wetland conditions. The higher R^2 values obtained when I scaled the analysis up to the level of segment and year, as well as work conducted in the Dakotas (Reynolds et al. 2006), suggests these models may perform

reasonably well at predicting total duck abundance for given blocks with known pond areas. However, further confirmation is required by applying the models developed in this study to other data sources. A retrospective analysis of pre-existing duck and wetland data could be conducted or, preferably, entirely new data could be collected. Using similar methods to the ones I have outlined, ponds on entire quarter sections could be surveyed for ducks, and pond areas could be measured using similar techniques as those used at St. Denis. The total number of ducks could then be compared to the abundances predicted by these models.

I focused on five major species of dabbling ducks that occur in prairie Canada and that are of primary concern to waterfowl managers. However, several other species of dabbling ducks and some diving ducks (Aythyini and Oxyurini) rely on Canadian prairie ponds during the breeding season (Bethke and Nudds 1993). Although other dabbling species may exhibit similar patterns in the relationship between abundance and pond area, divers may exhibit a different relationship because they tend to utilize deeper, more-permanent ponds (Kantrud and Stewart 1977, Nudds 1983). To diver species, the amount of open water may be more important than the amount of shoreline. Therefore, further evaluation should be performed before applying these models to other duck species.

The ecological drivers of waterfowl distributions on ponds are complex. In addition to inter- and intraspecific interactions of ducks, proximate habitat factors such as surrounding land uses, a wetland's degree of degradation, and wetland permanency all likely have some influence on relationships between breeding pair abundance and pond area (Lindeman and Clark 1999, Drever 2006, Reynolds et al. 2006). However, if the models developed in this study reasonably approximate breeding duck abundance, then a remote sensing based system could be used to estimate abundance over large scales (Cowardin et al. 1995, Reynolds et al. 2006). Inclusion of other parameters would likely require additional on-the-ground assessments, and such assessments would require more resources, and, thus, limit the spatial extent of coverage. Therefore, further evaluation of models developed in this study should be pursued, as this approach provides a more cost-effective means of estimating duck numbers over large and, sometimes, inaccessible areas.

3.5 TABLES

Table 3.1 – Results of linear regressions comparing observed breeding pair abundance of ducks to pairs predicted by models developed for the Dakotas (Cowardin et al. 1995)^a. Canadian prairie data were from Waterfowl Breeding Population and Habitat Surveys (1993-2002), and wetland area measurements were provided by Environment Canada. St. Denis National Wildlife Area data were from 2007 and 2008 waterfowl surveys and wetland area measurements.

	<i>n</i>	<i>R</i> ²	intercept ± SE, (95%CI)	slope ± SE, (95%CI)
Canadian Prairies				
Blue-winged teal	3550	0.06	-0.07 ± 0.03, (-0.13 to -0.01)	1.09 ± 0.07, (0.95 to 1.23)
Gadwall	3550	0.02	0.00 ± 0.02, (-0.04 to 0.04)	0.82 ± 0.09, (0.64 to 1.00)
Mallard	3550	0.03	0.08 ± 0.03, (0.02 to 0.14)	1.81 ± 0.18, (1.46 to 2.16)
Northern pintail	3550	0.02	-0.01 ± 0.02, (-0.05 to 0.02)	1.11 ± 0.15, (0.82 to 1.40)
Northern shoveler	3550	0.03	0.01 ± 0.02, (-0.03 to 0.05)	1.53 ± 0.15, (1.24 to 1.82)
St. Denis, NWA				
Blue-winged teal	163	0.62	-0.49 ± 0.16, (-0.80 to -0.18)	4.21 ± 0.26, (3.70 to 4.72)
Gadwall	163	0.49	-0.15 ± 0.09, (-0.33 to 0.03)	3.89 ± 0.31, (3.28 to 4.50)
Mallard	164	0.39	-0.37 ± 0.15, (-0.66 to -0.08)	6.03 ± 0.59, (4.87 to 7.19)
Northern pintail	164	0.14	-0.03 ± 0.03, (-0.09 to 0.03)	0.97 ± 0.19, (0.60 to 1.34)
Northern shoveler	154	0.36	-0.08 ± 0.12, (-0.32 to 0.16)	6.16 ± 0.66, (4.87 to 7.45)

^a Dakota models: *Breeding Pairs* = $A \times \text{pond area} + B \times \sqrt{\text{pond area}}$ *A* and *B* are regression coefficients unique to each species

Table 3.2 – Model selection results of relationships between breeding duck abundance and wetland characteristics in prairie Canada (1993-2002). Models were developed using generalized least squares, and a compound symmetry covariance structure was employed to account for annual repeated measures from wetlands (3550 observations from 1208 wetlands). Results for models with $\Delta AIC \leq 2$ are displayed.

Model^a	AIC	ΔAIC	AIC weight	Number of parameters
Blue-winged teal				
area+ $\sqrt{\text{area}}$	8427.58	0.00	0.92	4
Gadwall				
area+ $\sqrt{\text{area}}$	3809.21	0.00	0.49	4
$\sqrt{\text{area}}$	3809.49	0.28	0.42	3
Mallard				
$\sqrt{\text{area}}$	8436.78	0.00	0.68	3
area+ $\sqrt{\text{area}}$	8438.31	1.53	0.32	4
Northern pintail				
area+ $\sqrt{\text{area}}$	3609.95	0.00	0.30	4
$\sqrt{\text{area}}$	3609.96	0.01	0.30	3
area+perimeter+area*perimeter	3610.47	0.51	0.23	5
area+perimeter	3611.28	1.32	0.16	4
Northern shoveler				
$\sqrt{\text{area}}$	4181.80	0.00	0.70	3
area+ $\sqrt{\text{area}}$	4183.51	1.71	0.30	4

^a model covariates and symbols: area = pond area; $\sqrt{\text{area}}$ = square root of pond area; perimeter = pond perimeter; '+' indicates additive effects; '*' indicates multiplicative effects.

Table 3.3 – Model selection results of relationships between breeding duck abundance and wetland characteristics at St. Denis Wildlife Area, Saskatchewan, Canada (2007 and 2008). Models were developed using generalized least squares, and a compound symmetry covariance structure was employed to account for annual repeated measures from wetlands (162 observations from 100 wetlands). Results for models with $\Delta AIC \leq 2$ are displayed.

Model^a		AIC	Δ AIC	AIC weight	Number of parameters
Blue-winged teal	area+ $\sqrt{\text{area}}$	580.55	0.00	0.96	4
Gadwall	area+ $\sqrt{\text{area}}$	413.30	0.00	0.86	4
Mallard	area+perimeter+area*perimeter	550.26	0.00	1.00	5
Northern pintail	area	29.16	0.00	0.26	3
	area+ $\sqrt{\text{area}}$	29.58	0.43	0.21	4
	$\sqrt{\text{area}}$	29.61	0.45	0.21	3
	area+shoreline complexity	29.93	0.77	0.18	4
	area+perimeter	31.05	1.90	0.10	4
Northern shoveler	$\sqrt{\text{area}}$	463.78	0.00	0.71	3
	area+ $\sqrt{\text{area}}$	465.57	1.80	0.29	4

^a model covariates and symbols: area = pond area; $\sqrt{\text{area}}$ = square root of pond area; perimeter = pond perimeter; '+' indicates additive effects; '*' indicates multiplicative effects.

Table 3.4 - Parameter estimates from the most parsimonious generalized least squares models used to predict breeding pair abundance of five duck species for prairie Canada (1993-2002), and St. Denis National Wildlife Area, Saskatchewan, Canada (2007 and 2008).

Species and Location	area ± SE	√area ± SE	perimeter ± SE	area*perimeter ± SE
Blue-winged teal				
Canadian Prairies	0.2359 ± 0.0901	0.4895 ± 0.0726		
St. Denis	0.4416 ± 0.1474	1.8595 ± 0.3071		
Gadwall				
Canadian Prairies	0.0740 ± 0.0490	0.1894 ± 0.0394		
St. Denis	0.1987 ± 0.0795	0.8539 ± 0.1655		
Mallard				
Canadian Prairies		0.6583 ± 0.0270		
St. Denis	1.0671 ± 0.0858		0.0032 ± 0.0011	-0.0059 ± 0.0011
Northern pintail				
Canadian Prairies	0.0708 ± 0.0499	0.1369 ± 0.0401		
St. Denis	0.0827 ± 0.0141			
Northern shoveler				
Canadian Prairies		0.3164 ± 0.0158		
St. Denis		1.2542 ± 0.1031		

Table 3.5 – Cross-validation results of linear regressions comparing observed breeding pair abundance of ducks to pairs predicted from most parsimonious generalized least squares models. The top subset was developed from data from prairie Canada (1993-2002), and the bottom subset was developed from St. Denis National Wildlife Area, Saskatchewan, Canada (2007 and 2008). R^2 , intercepts, and slopes are mean values computed from 1000 iterations.

	<i>n</i>	R^2	intercept \pm SE	slope \pm SE
Canadian Prairies				
Blue-winged teal	710	0.06	0.00 \pm 0.06	1.03 \pm 0.15
Gadwall	710	0.03	0.01 \pm 0.03	0.98 \pm 0.23
Mallard	710	0.03	0.07 \pm 0.07	0.84 \pm 0.19
Northern pintail	710	0.02	0.00 \pm 0.03	0.96 \pm 0.27
Northern shoveler	710	0.03	0.01 \pm 0.04	0.98 \pm 0.21
St. Denis, NWA				
Blue-winged teal	33	0.61	-0.11 \pm 0.30	1.07 \pm 0.15
Gadwall	33	0.49	-0.11 \pm 0.18	1.14 \pm 0.20
Mallard	33	0.39	-0.03 \pm 0.26	1.12 \pm 0.30
Northern pintail	33	0.21	0.03 \pm 0.05	1.35 \pm 0.48
Northern shoveler	31	0.46	-0.21 \pm 0.24	1.22 \pm 0.25

Table 3.6 - Results of linear regressions comparing observed breeding pair abundance of ducks to predicted pairs. St. Denis National Wildlife Area models were used to predict the number of breeding pairs for the Canadian prairies, and Canadian prairie models were used to predict the number of breeding pairs for St. Denis. Canadian prairie data were from Waterfowl Breeding Population and Habitat Surveys (1993-2002), and wetland area measurements provided by Environment Canada. St. Denis National Wildlife Area data were from 2007 and 2008 waterfowl surveys and wetland area measurements.

	<i>n</i>	<i>R</i> ²	intercept ±SE, (95%CI)	slope±SE, (95%CI)
St Denis models applied to Canadian Prairies				
Blue-winged teal	3550	0.06	-0.02 ± 0.03, (-0.06 to 0.03)	0.33 ± 0.02, (0.29 to 0.38)
Gadwall	3550	0.02	0.01 ± 0.01, (-0.01 to 0.03)	0.24 ± 0.03, (0.19 to 0.29)
Mallard	3550	0.02	0.43 ± 0.02, (0.41 to 0.47)	-0.08 ± 0.01, (-0.10 to -0.06)
Northern pintail	3550	0.03	-0.06 ± 0.01, (0.05 to 0.08)	2.49 ± 0.26, (1.98 to 3.00)
Northern shoveler	3550	0.03	0.00 ± 0.02, (-0.02 to 0.04)	0.25 ± 0.02, (0.20 to 0.30)
Canadian Prairie models applied to St. Denis, NWA				
Blue-winged teal	163	0.61	0.10 ± 0.13, (-0.06 to 0.36)	2.76 ± 0.17, (2.42 to 3.10)
Gadwall	163	0.48	-0.02 ± 0.08, (-0.11 to 0.15)	3.74 ± 0.30, (3.14 to 4.33)
Mallard	164	0.39	-0.41 ± 0.15, (-0.59 to -0.12)	2.89 ± 0.28, (2.34 to 3.45)
Northern pintail	164	0.14	0.00 ± 0.02, (-0.03 to 0.05)	0.56 ± 0.11, (0.35 to 0.78)
Northern shoveler	154	0.37	-0.16 ± 0.12, (-0.30 to 0.08)	4.39 ± 0.47, (3.48 to 5.31)

Table 3.7 – Simulation of the response of duck abundance to wetland loss and restoration. Duck abundance (i.e., breeding pairs) was estimated for a random sample of 1000 wetlands using estimates from the Dakota models (Cowardin et al. 1995) and Canadian PPR models (see Table 3.4). A stratified random sample of 5% of the wetlands (25 wetlands \leq 0.10 ha and 25 wetlands $>$ 0.10 ha) was removed, and an approximate total wetland area (7.69 ha) was then restored, but all restored wetlands were \leq 0.10 ha (123 wetlands). Values are predicted number of breeding pairs under each scenario.

Species	Dakota Models			Canadian PPR Models		
	Initial	5 % Loss	Restore	Initial	5 % Loss	Restore
Blue-winged teal	339	326	349	287	277	293
Gadwall	140	135	144	107	103	109
Mallard	136	131	140	303	291	311
Northern pintail	86	83	88	82	79	83
Northern shoveler	90	86	92	146	140	150

Table 3.8 - Model selection results for the influence of regional pond and duck densities on the relationships between breeding duck abundance and wetland characteristics in prairie Canada (1993-2002). Models were developed using generalized least squares, and a compound symmetry covariance structure was employed to account for annual repeated measures from wetlands (3550 observations from 1208 wetlands). Results for models with $\Delta AIC \leq 2$ are displayed.

Model^a	AIC	Δ AIC	AIC weight	Number of parameters
Blue-winged teal DD* $\sqrt{\text{area}}$ + PD* $\sqrt{\text{area}}$ + $\sqrt{\text{area}}$ + area	8335.70	0.00	1.00	6
Gadwall DD* $\sqrt{\text{area}}$ + PD* $\sqrt{\text{area}}$ + $\sqrt{\text{area}}$ + area	3741.49	0.00	1.00	6
Mallard DD* $\sqrt{\text{area}}$ + PD* $\sqrt{\text{area}}$ + $\sqrt{\text{area}}$	8342.81	0.00	1.00	5
Northern pintail DD* $\sqrt{\text{area}}$ + PD* $\sqrt{\text{area}}$ + $\sqrt{\text{area}}$ + area	3549.85	0.00	1.00	6
Northern shoveler DD* $\sqrt{\text{area}}$ + PD* $\sqrt{\text{area}}$ + $\sqrt{\text{area}}$	4082.79	0.00	1.00	5

^a model covariates and symbols: area = pond area; $\sqrt{\text{area}}$ = square root of pond area; DD = conspecific duck density at survey stratum level; PD = pond density at survey stratum level; '+' indicates additive effects; '*' indicates multiplicative effects.

Table 3.9 – Parameter estimates for breeding pair abundance of ducks in response to duck and pond density, and pond area in hectares for prairie Canada (1993-2002). Estimates were derived from the most parsimonious model for each species (see Table 3.8).

Species	duck density*$\sqrt{\text{area}}$ \pm SE	pond density*$\sqrt{\text{area}}$ \pm SE	$\sqrt{\text{area}}$ \pm SE	area \pm SE
Blue-winged teal	0.0777 \pm 0.0092	-0.0681 \pm 0.0073	0.7018 \pm 0.0961	0.1732 \pm 0.0889
Gadwall	0.0635 \pm 0.0095	-0.0199 \pm 0.0030	0.2392 \pm 0.0549	0.0166 \pm 0.0485
Mallard	0.0559 \pm 0.0106	-0.0630 \pm 0.0063	0.8595 \pm 0.0785	
Northern pintail	0.0419 \pm 0.0069	-0.0204 \pm 0.0030	0.2584 \pm 0.0521	0.0375 \pm 0.0486
Northern shoveler	0.0701 \pm 0.0074	-0.0290 \pm 0.0035	0.3437 \pm 0.0357	

3.6 FIGURES

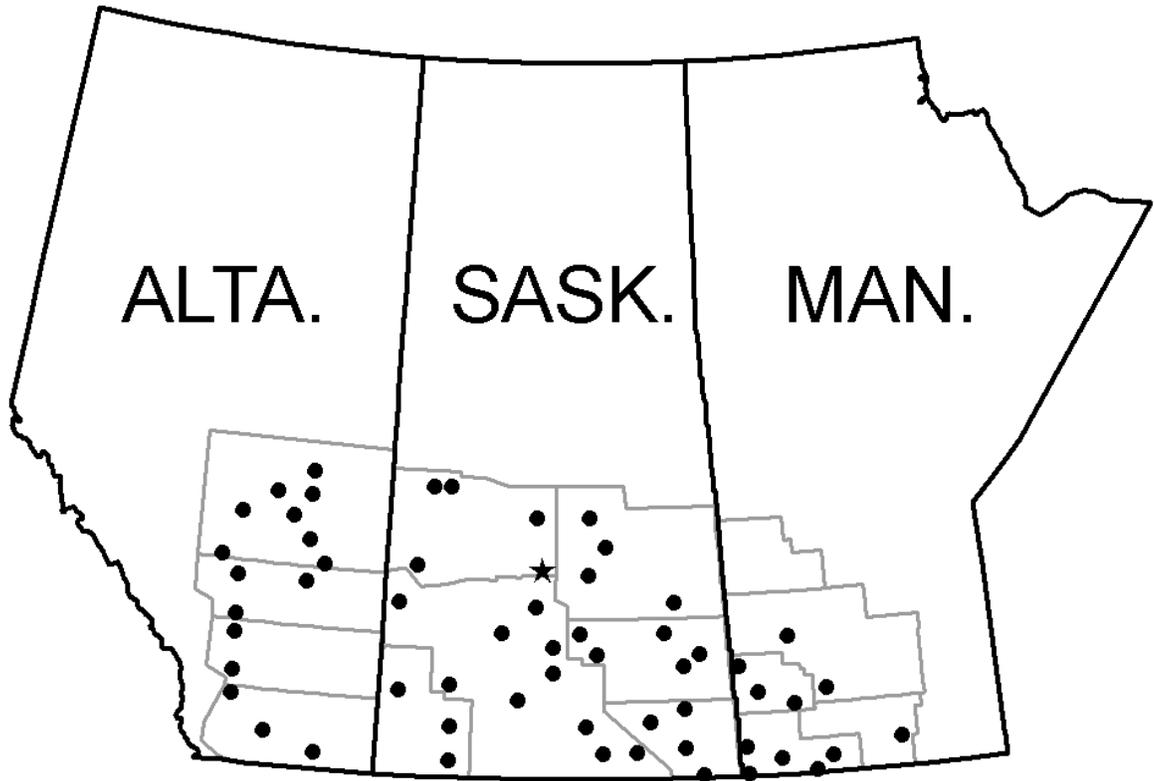


Figure 3.1 - Map of the Canadian prairie provinces with the delineated boundaries of the prairie Waterfowl Breeding Population and Habitat Survey strata. Solid circles signify the locations of the air-ground survey segments used in this study, and the star represents the location of the St. Denis National Wildlife Area.

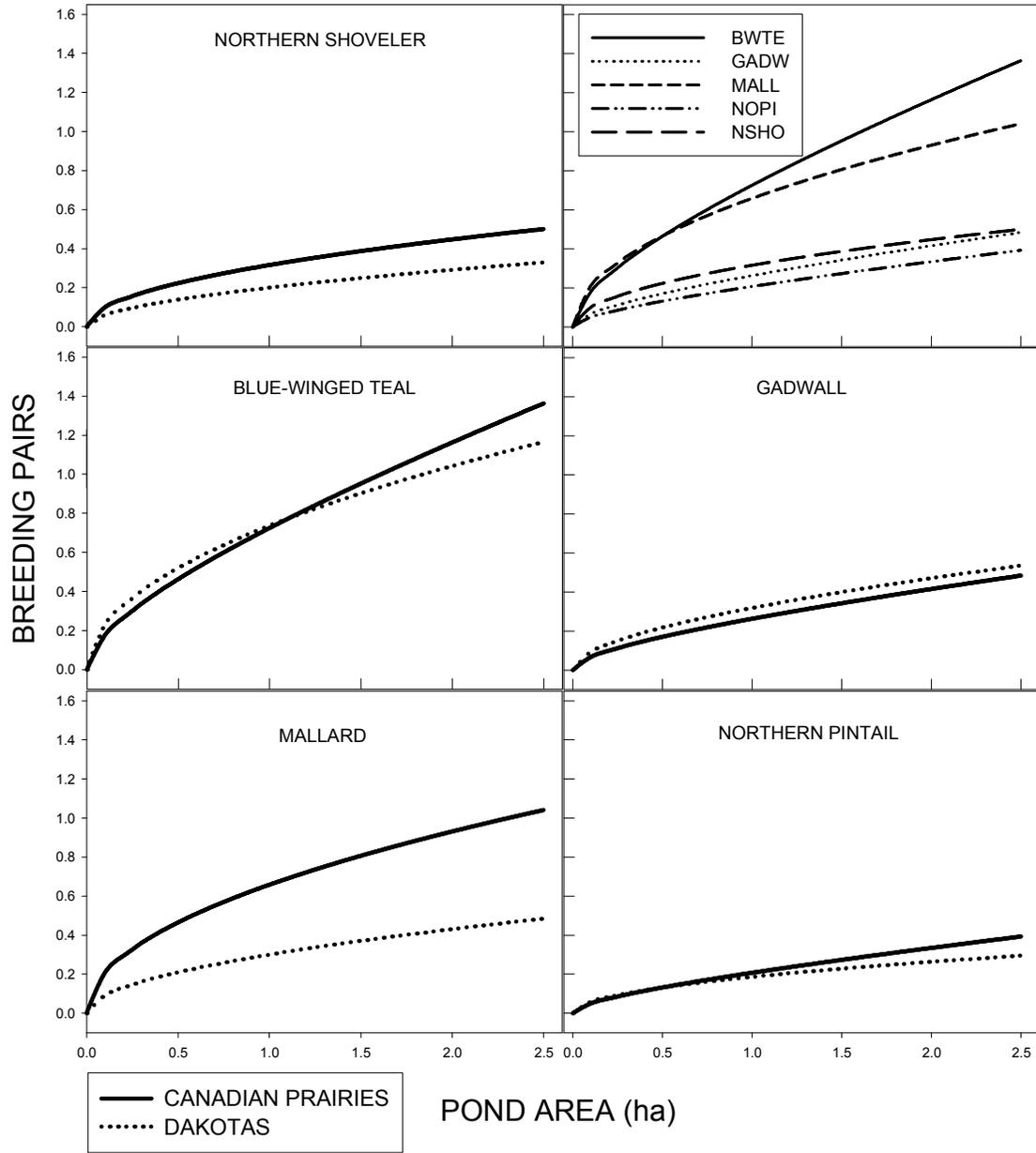


Figure 3.2 - Relationships between breeding pair abundance of ducks and pond area in prairie Canada based on models developed in the Dakotas and Canada. Estimates from the Canadian PPR (1993-2002) were derived from generalized least squares models. Upper right figure is a compilation of all 5 species from the Canadian PPR models.

BLUE-WINGED TEAL

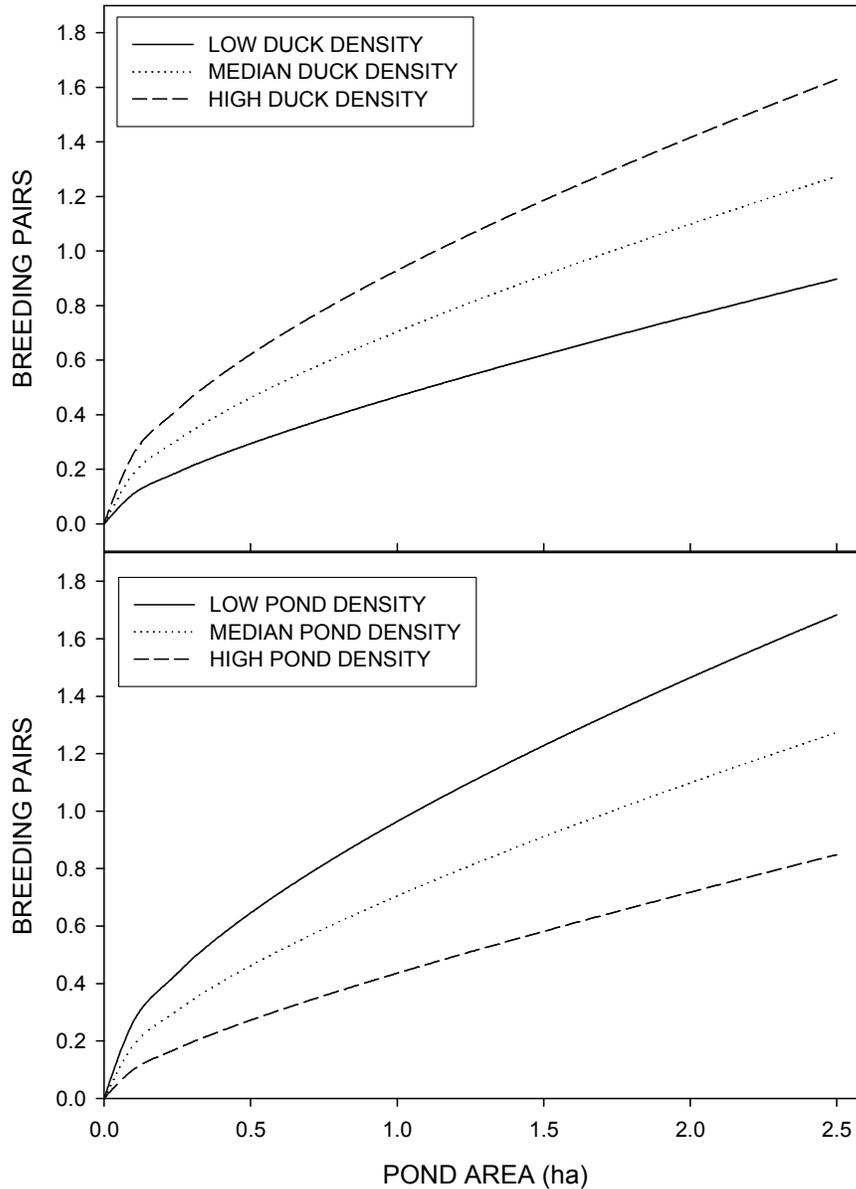


Figure 3.3 – Relationship of breeding pair abundance for blue-winged teal and pond area for prairie Canada (1993-2002) in response to varying regional duck and pond densities. Parameter estimates were derived from the most parsimonious generalized least squares model ($\text{duck density} \cdot \sqrt{\text{area}} + \text{pond density} \cdot \sqrt{\text{area}} + \sqrt{\text{area}} + \text{area}$). Duck and pond densities were calculated at the survey stratum level. Low, median, and high refer to the 25%, 50%, and 75% quartiles, respectively. Top: blue-winged teal density varies while pond density is fixed at the median. Bottom: pond density varies, while blue-winged teal density is fixed at the median.

MALLARD

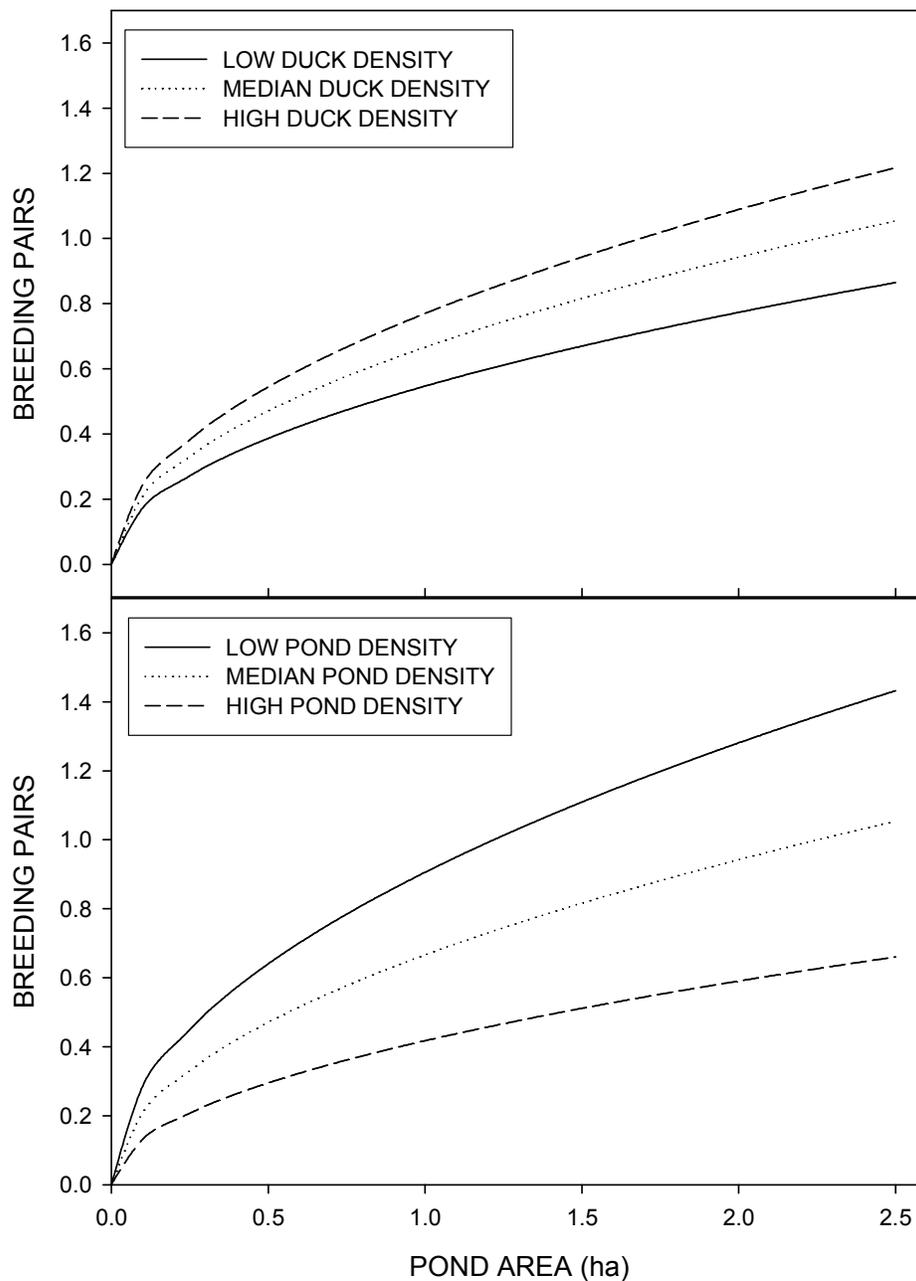


Figure 3.4 - Relationship of breeding pair abundance for mallards and pond area for prairie Canada (1993-2002) in response to varying regional mallard and pond densities. Parameter estimates were derived from the most parsimonious model (duck density* $\sqrt{\text{area}}$ + pond density* $\sqrt{\text{area}}$ + $\sqrt{\text{area}}$). Mallard and pond densities were calculated at the survey stratum level. Low, median, and high refer to the 25%, 50%, and 75% quartiles, respectively. Top: mallard density varies while pond density is fixed at the median. Bottom: pond density varies, while mallard density is fixed at the median.

CHAPTER 4 SYNTHESIS

Wetlands are a significant source of global biodiversity, yet over half have been lost, primarily to agricultural development, and the remainder have been degraded by some form of human activity (Mitsch and Gosselink 2000, Zedler and Kercher 2005). Wetlands of the Prairie Pothole Region (PPR) of North America have long been recognized for their importance to, and have largely been managed for, waterfowl (Crissey 1969, U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). As many duck populations were reaching record lows in the 1980s, the North American Waterfowl Management Plan (NAWMP) was developed to restore populations, and priorities were placed on habitat restoration and prevention of further habitat loss and degradation (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). Adaptive management strategies have been employed and routinely evaluated to assess the current impact of habitat programs and guide future program delivery. My research provides tools that could aid in future wetland and waterfowl management and conservation on the Canadian prairies.

Although some evidence suggested that wetland losses continued in the latter part of the twentieth century, there was scant information about trends in wetland degradation (Dahl and Watmough 2007). Consequently, in Chapter 2, I summarized the incidence of wetland degradation from, 1985-2005, and I then examined impact and recovery rates for wetlands of the Canadian prairies. I predicted that putative factors such as provincial and regional locations, surrounding land uses, wetland type, and regional moisture levels may affect impact and recovery rates. I used multistate models to estimate these rates and to model these rates in relation to the landscape factors mentioned above. I found that impact rates to wetlands' surrounding margins (natural vegetation around flooded basins) varied among provinces and ecoregions at the beginning of the study period, but then converged on similarly low impact rates for all regions. Margin recovery rates exhibited similar declines over time, but were at a much lower magnitude than impact rates, suggesting progressive degradation of wetlands over time. Examination of the incidence of margin degradation verified this suggestion, and also suggested that the decline in impact rates was likely attributable to a decline in unaffected wetland margins remaining on the landscape. Basin impact and recovery rates fluctuated with May pond densities

throughout the study period. In wet years, impact rates decreased and recovery increased, and in dry years, impact rates increased and recovery rates decreased. Wetlands in more agriculturally intensive areas, such as cultivated and pasture lands, had high impact and low recovery rates, but wetlands in more natural grass and wooded areas had low impact and high recovery rates. Finally, the effect of wetland type suggested more permanent wetlands had low impact and high recovery rates, and the shallower more temporary wetlands had high impact and low recovery rates.

In Chapter 3, I examined whether the characteristics of Canadian prairie wetlands could be used to accurately predict breeding duck abundance. In particular, I sought to determine how models based on pond area, which were developed in the Dakotas, performed in prairie Canada. In addition, I attempted to develop models with improved predictive capabilities with independent data collected in Canada. Evaluations showed that the Dakota models performed reasonably well for blue-winged teal, gadwall, and northern pintail, but under-predicted mallards and northern shovelers for the Canadian prairies. When I applied the Dakota models to a specific, intensively studied locale in south-central Saskatchewan (St. Denis National Wildlife Area), they under-predicted the abundance of all species except northern pintail. Possible explanations for the under-predictions at St. Denis include exceptional duck and pond densities on and around the National Wildlife Area, restrictive agricultural practices, and managed nesting habitat. For the most part, models developed from the Canadian data had the same explanatory variables as the Dakota models (pond area and the square root of pond area), but the regression coefficients were of different magnitudes. I also demonstrated that the relationship between duck abundance and pond area may be influenced by regional duck and pond density. Consequently, in years or locations of high duck densities, duck abundance per pond area may be greater. Conversely, in years or locations of high pond densities, duck abundance per pond area may be lower.

Persistent or permanent impacts to wetland margins and basins could irreversibly alter wetland functions (Chapter 2), and thereby, contribute to lower carrying capacities for ducks (Chapter 3). Impacts to wetland basins could have adverse effects on invertebrate egg and seed banks (Euliss and Mushet 1999, Gleason et al. 2003), and activities, such as filling and draining, could reduce wetland area. Impacts to wetland

margins could reduce the amount of cover available to conceal ducks from predators and conspecifics. Destruction of margins could increase geochemical inputs to wetlands (Houlahan and Findlay 2004) and allow farmers to gain access to wetland basins. In combination, these activities could reduce density of breeding pairs on ponds.

4.1 MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

To my knowledge, this is the first study to employ multistate models to estimate rates associated with changes in a landscape feature. The multistate model framework I have outlined could be modified to estimate rates associated with other landscape processes, such as forest succession or grassland conversion (Stephens et al. 2008). Analysis for wetland rates could be further extended to include effects of socioeconomic factors, such as commodity pricing, and agricultural subsidy implementation and removal. Use of multistate models would facilitate conservation planning by identifying habitat that was under greatest risk of being impacted and had the lowest chance of recovery, which, in the case of prairie wetlands, would be the shallow less permanent wetlands or wetlands situated in cultivated or pasture lands. Although a major objective of NAWMP was to prevent further habitat loss and degradation, this study indicated that wetland degradation still occurred at the regional scale. Also, any slowing of wetland impact rates likely occurred as a result of a diminishing number of pristine wetlands left on the landscape. Although many prairie waterfowl populations have recovered, some populations remain low, which may partly be a result of the persistence of highly degraded wetland habitat (Lindeman and Clark 1999, Podruzny et al. 2002).

Models predicting breeding pair abundance in relation to pond characteristics from this study may produce results that are less biased and more consistent than the Dakota models, but further evaluation is required. This study has demonstrated that relationships between abundance and pond characteristics can vary over space and time because analyses for St. Denis produced results distinct from the prairie-wide assessment and because models that allowed for variation by regional duck and pond density were well supported. Therefore, managers should consider that relationships between duck abundance and pond characteristics are neither spatially uniform nor temporally static. Often, management and conservation occur on a scale larger than individual ponds, for which models generated in this study need additional testing. Total abundance of ducks

in blocks or given areas containing an array of wetlands could be estimated from the study models, and then estimates could be compared to actual duck abundance. Such tests would give a sense of model performance at a scale most waterfowl managers are responsible for. Studies in the U.S. have shown that relationships between duck abundance and pond metrics can vary by wetland type (Cowardin et al. 1983, Reynolds et al. 2006), and, perhaps, the relationships could also vary by wetlands' states of impact, or wetlands' surrounding agricultural practices. These proximate factors could be included in future analyses, but they may be of limited use to waterfowl managers because they may require on-the-ground assessments of wetlands, which may be logistically unrealistic, whereas metrics such as pond area may be measured using a more feasible and efficient remote sensing based approach (Cowardin et al. 1995, Dahl and Watmough 2007).

A great deal of data preparation and compilation was required before the analyses involved in my project could proceed. Long-term data sets, such as the WBPHS data, contain a wealth of information that must be maintained, updated, and made readily available for analysis. Given current and anticipated threats to wetland systems and associated wildlife, it is imperative to use these data whenever appropriate to inform management decisions or to guide conservation programs and policies.

This study provides analytical tools that could potentially aid waterfowl and wetland management in the future. It also provides a broad scale, comprehensive assessment of wetland impact conditions on the Canadian prairies since the signing of NAWMP until 2005; such data were lacking before this study. As well, I have outlined a probability based framework that may be useful to those concerned with rates for other landscape processes in relation to multiple putative factors. Finally, I developed models that may be able to predict breeding duck abundance based on wetland characteristics. Such models are advantageous because they could potentially allow for estimates of populations over large areas using remote sensing based techniques. This study, in combination with previous and future work, will contribute to improvements in waterfowl and wetland conservation in the Canadian prairies.

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APPENDIX A. COMPLETE CANDIDATE SET OF MULTISTATE MODELS TESTED IN RELATION TO WETLAND IMPACT AND RECOVERY RATES

Multistate model selection results for estimating transition probabilities of wetlands across the Canadian Prairie Pothole Region (1985–2005). Survival and recapture probabilities were fixed at 1. Akaike’s Information Criterion results were corrected for sample size and adjusted for overdispersion ($\hat{c} = 1.72$).

Model^a	QAICc	ΔQAICc	QAICc weights	Number of parameters
group * T/PD + LAND + POND	72747.06	0.00	1.00	114
MPD * T/PD + LAND + POND ^b	72858.21	111.15	0.00	96
group + T/PD + LAND + POND	72901.84	154.78	0.00	90
group + T + LAND + POND	73362.36	615.29	0.00	90
group + PD + LAND + POND	73573.34	826.28	0.00	90
group + T + POND	74260.25	1513.18	0.00	60
group + CSM + LAND + POND	74303.42	1556.36	0.00	90
group * t	74453.06	1705.99	0.00	600
group + PD + POND	74525.88	1778.81	0.00	60
group + LAND + POND	74597.38	1850.32	0.00	84
group + t	75167.62	2420.56	0.00	144
group + CSM + POND	75256.75	2509.69	0.00	60
group + POND	75548.25	2801.18	0.00	54
group + T + LAND	75772.91	3025.85	0.00	66
group + PD + LAND	76075.91	3328.85	0.00	66
group + CSM + LAND	76775.12	4028.06	0.00	66
group + T	76906.11	4159.05	0.00	36
group + LAND	77034.43	4287.36	0.00	60
group + PD	77266.24	4519.17	0.00	36
group + CSM	77965.91	5218.85	0.00	36
group	78220.98	5473.91	0.00	30
provinces	78362.33	5615.27	0.00	18
ecoregions	79493.20	6746.14	0.00	12
null	79635.36	6888.30	0.00	6

^a model covariates and symbols: group = combination of provinces and ecoregions; MPD = maximum wetland basin density (constant); t = time-dependency (i.e., year-specific variation); T = linear-logistic trend over time; PD = annually varying pond density at group level; CSM = annually varying conserved soil moisture at group level; T/PD = 3 transition parameters constrained linearly with time, and 3 transition parameters and constrained by pond density; LAND = dominant land use (individual covariate); POND = dominant wetland type (individual covariate); ‘+’ indicates additive effects; ‘*’ indicates multiplicative effects. ^b *a posteriori* model. The bottom four models were considered independently of the rest of the models to determine which spatial factor (group) to include in the rest of the models.