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Research Papers

Agricultural Policy and Nest Success of Prairie Ducks in Canada and the United States

Politiques agricoles et succès de nidification des canards dans les Prairies canadiennes et états-uniennes

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ABSTRACT. The Prairie Pothole Region of North America has been modified by agriculture during the past 100 yr, resulting in habitat loss, fragmentation, and degradation that have reduced the abundance and productivity of many wildlife species. The 1985 U.S. Farm Bill provided economic incentives to agriculture that are considered by many to be beneficial to nesting waterfowl and other wildlife. Canada has not experienced an equally comprehensive legislative initiative, which would seem to indicate that benefits to waterfowl in Canada should lag behind those in the United States. However, with the removal of some agricultural subsidies in Canada during the 1990s, the amount of perennial cover in the Canadian prairies increased to levels similar to those of the 1970s. Therefore, it is unclear whether and how the U.S. and Canadian prairies might differ with regard to habitat quality for nesting waterfowl. We used historical and contemporary data to compare temporal trends in duck nest success between the United States and Canada and to assess how mean nest success varied with proportion of cropland and wetland density. The data best supported models with nonlinear temporal trends that varied between the two countries and suggested that mean nest success in Canada declined from its high point in 1930s and remained below the long-term value of 0.16 until the end of the time series in 2005. Mean nest success in the United States also declined from its high point in the 1930s, but increased to above the long-term value of 0.25 during the early 2000s. Mean nest success varied negatively with proportion of cropland in both the United States and Canada. Mean nest success was positively correlated with pond density at Canadian sites, but showed only a weak association with pond density at U.S. sites. All models explained the low proportions of the variation in nest success, suggesting that unmeasured factors such as the abundance and identity of nest predators may have strong effects on nest success. Nonetheless, these results support earlier suggestions that agricultural policy that encourages permanent cover positively influences duck reproductive success. We also found that, for reasons that are not entirely clear, nest success for the same intensity of row cropping was generally higher in the United States than in Canada. Further research is required to elucidate the exact nature of the composition, size, and distribution of permanent cover that coincides with greater average nest success by dabbling ducks in the United States. In addition, the data suggest that the benefits that might accrue from increases in the amount of perennial cover in Canada would be better realized if these efforts are accompanied by strong measures to conserve wetlands.

RÉSUMÉ. La région des cuvettes des Prairies nord-américaines a été altérée par l'agriculture au cours des 100 dernières années, menant à la perte, à la fragmentation et à la dégradation d'habitats, lesquelles ont contribué à diminuer l'abondance et la productivité de nombreuses espèces sauvages. Le Farm Bill états-unien de 1985 a fourni des incitatifs financiers aux agriculteurs qui auraient été bénéfiques à la nidification de la sauvagine et à d'autres espèces sauvages. Le Canada n'a pas adopté une politique aussi élaborée, ce qui suggère que les bénéfices pour la sauvagine devraient y être observés plus tard qu'aux États-Unis.

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Cependant, avec l'abolition de certaines subventions à l'agriculture durant les années 1990, le couvert de plantes vivaces dans les Prairies canadiennes a atteint des niveaux semblables à ceux des années 1970. Il n'est donc pas certain que la qualité de l'habitat de nidification de la sauvagine devrait différer entre les Prairies canadiennes et états-uniennes, ni dans quelle mesure elle pourrait différer, Nous avons utilisé des données historiques et contemporaines afin de comparer l'évolution temporelle des tendances du succès de nidification des canards entre les États-Unis et le Canada et de déterminer comment le succès de nidification moyen a varié en fonction de la proportion de terres cultivées et de milieux humides. Les données s'ajustaient le mieux aux modèles avec des tendances non-linéaires qui variaient entre les deux pays, et elles indiquaient que le succès de nidification moyen au Canada a décliné après son sommet dans les années 1930 et qu'il est demeuré en-deçà de la valeur à long terme de 0,16 jusqu'à la fin de la série temporelle en 2005. Le succès de nidification moyen aux États-Unis a également décliné à partir de son sommet dans les années 1930, mais il a augmenté, puis dépassé la valeur à long terme de 0,25 durant les années 2000. Le succès de nidification moyen était relié négativement à la proportion de terres cultivées, tant aux États-Unis qu'au Canada. Au Canada, cette variable était reliée positivement à la densité des étangs, mais cette corrélation était faible aux États-Unis. Tous les modèles ont expliqué la faible proportion de la variation du succès de nidification, ce qui suggère que des facteurs non quantifiés, comme l'abondance et la composition des assemblages de prédateurs de couvées, peuvent avoir des effets importants sur le succès de nidification. Néanmoins, ces résultats appuient les suggestions selon lesquelles les politiques agricoles qui encouragent un couvert végétal permanent influencent positivement le succès reproducteur des canards. Nous avons aussi trouvé, pour des raisons qui ne sont pas entièrement claires, que le succès de nidification était généralement plus élevé aux États-Unis qu'au Canada pour une même intensité agricole. Des travaux futurs devront être entrepris afin de déterminer quelles composition, étendue et répartition du couvert permanent correspondent au succès de nidification moyen le plus élevé des canards barboteurs aux États-Unis. De plus, nos données indiquent que les effets bénéfiques associés à l'augmentation de la quantité de plantes vivaces pourraient augmenter au Canada s'ils étaient accompagnés par une politique efficace de protection des milieux humides.

Key Words: *nest success; prairies; agricultural policy; United States; Canada; prairie ducks*

INTRODUCTION

The Prairie Pothole Region, an expansive complex of grasslands and wetlands spanning Canada and the United States in the mid-continent of North America, provides important breeding habitat for millions of waterfowl (Crissey 1969). Conversion of native grasslands to cropland has been a long-standing concern for wildlife managers, because cropland has been associated with reduced numbers and reproductive success of ducks (Higgins 1977, Boyd 1985, Greenwood et al. 1995, Bethke and Nudds 1995, Miller 2000). Indeed, Beauchamp et al. (1996*a*) have shown that nest success, i.e., the probability that a nesting attempt will produce ≥ 1 duckling, declined from an average of 0.30 in the mid-1930s to roughly 0.10 in 1992 in five species of dabbling ducks breeding across the Prairie Pothole Region: Mallard (*Anas platyrynchos*), Northern Pintail (*A. acuta*), Northern Shoveler (*A. clypeata*), Blue-winged Teal (*A. discors*), and Gadwall (*A. strepera*). This decline was consistent with the idea that there was general widespread erosion of the ability of the prairies to sustain successful nesting by ducks. However, an updated analysis over a longer time frame found that average nest success in the Prairie Pothole Region declined until the mid-1980s and then fluctuated widely (Drever et al. 2004); this analysis focused on the effects of duck density, wetland availability, and the abundance of nest predators as determinants of duck nest success. In addition to those factors, we examine the effects of landscape composition, with particular attention to the differences between Canada and the United States.

The 1985 U.S. Farm Bill and its subsequent reauthorizations provide programs that subsidize U. S. farmers for making land-use decisions that are widely perceived to benefit a broad range of wildlife (Haufler 2005). These programs include several provisions that provide habitat for upland-nesting ducks on agricultural land, e.g., the “Swampbuster” and “Sodbuster” provisions; one particularly important program of this type is the Conservation Reserve Program. It provides incentives to convert cultivated land to perennial cover and has resulted in extensive landscape-level change in habitat conditions for wildlife (Johnson and Schwartz 1993, Reynolds et al. 2001). From 1992 to 2005, approximately 1.9 million ha of cropland were converted to undisturbed grass cover in the Prairie Pothole Region of the Dakotas and northeast Montana (Reynolds 2005).

In contrast, Canada lacks a program of similar scope and magnitude. However, in the mid-1990s, the Canadian government adopted a policy of deregulation that led to the elimination of many subsidies, such as the annual subsidy to railways provided under the Western Grain Transportation Act (Bradshaw and Smit 1997). Subsequently, the area under tillage in Canada decreased to levels similar to those of the 1970s. Devries et al. (2004) estimate that, from 1971 to 2001, the agricultural landscape in the Canadian prairies changed as the amount of summer-fallowed land decreased by ~ 5.3 million ha, most of which is now cropped year round. This change was accompanied by an overall decrease of ~ 2.4 million ha in the total amount of tilled land since 1986, and by a decrease of ~ 0.8 million ha since 1971; these lands were converted mainly into pasture and hayland (Devries et al. 2004). As a result, it is unclear whether and how the different agricultural policies governing the the U. S. and Canadian prairies may have affected habitat quality and quantity for nesting waterfowl in the two countries.

Comparing temporal trends in nest success between the United States and Canada offers an opportunity to gauge the effect of agricultural policy on nesting waterfowl because habitat type and the extent of cropland are known to strongly affect nest success (Greenwood et al. 1995, Reynolds et al. 2001, Emery et al. 2005). However, the effect of habitat fragmentation on avian nest success can vary depending on spatial scale (Donovan et al. 1997, Howerter 2003, Stephens et al. 2003), so it is not certain that the patterns observed at the scale of individual study sites would be seen at larger scales. Further, the nest success of ducks may also be affected by climatic conditions (Stephens et al. 2005), which also vary regionally over time and may thus confound relationships between nest success and landscape attributes related to agriculture. Therefore, as well as examing differences in temporal trends in nest success between the United States and Canada, we incorporated information on agricultural practices from the quinquennial Census of Agriculture and information on wetland density from aerial counts of ponds from the May Breeding Waterfowl Survey (Smith 1995) to test directly whether these data supported correlations between nest success and proportion cropland and wetland density. We studied these relationships at the spatial scale of aerial survey strata. These strata are large survey units (~ 8000–65000 km²) that cover heterogeneous landscapes with different predator communities and grassland conditions, which may make the detection of patterns more difficult. However, an analysis at this large spatial scale is needed to evaluate the effects of national-level changes in landscape composition brought about by changes in agricultural policy.

METHODS

Historical trends in nest success

We used historical estimates of nest success available in published and unpublished studies that were compiled by Beauchamp et al. (1996*a,b*) and Drever et al. (2004). In addition, we added data from extensive recent studies of nesting ducks (PHJV 2002, Stephens et al. 2005, Emery et al. 2006; E. Loos, *unpublished data*; S. Stephens, *unpublished data*). The studies were carried out at locations in three Canadian provinces (Manitoba, Saskatchewan, and Alberta) and two U.S. states (North and South Dakota) in which no predator management activities took place (Fig. 1). We used estimates of nest success pooled among species, primarily Mallard, Northern Pintail, Northern Shoveler, Blue-winged Teal, and Gadwall. Some of the estimates in the studies by Emery et al. (2006) and unpublished data from the Department of Wildlife and Fisheries also included nests of Lesser Scaup (*Aythya affinis*) and Redhead (*Aythya americana*), but these were small fractions of the total sample. Although the use of pooled estimates may obscure important ecological differences among species and introduce some biases depending on species composition (see *Discussion*), by doing so we were able to acquire more data, because many studies provided only pooled estimates, and make our results comparable to the findings of previous studies. Following Beauchamp et al. (1996*a,b*), we excluded estimates based on < 10 nests or on multiple years or sites. In total, we had 507 estimates of pooled nest success, 206 from Canadian sites for the years 1935 to 2005 and 301 from U.S. sites from 1936 to 2006. The latitude and longitude for each nest success estimate were obtained from the original study or were provided by the authors. Units of longitude and latitude were decimal degrees such that the longitude for sites in the west is numerated as a larger negative number than for sites in the east. If otherwise unavailable, we assigned coordinates to each study site based on the location of nearby towns using the online query resources of the United States Census Bureau (U.S. Census Bureau 2002) and the Environmental Statistics Group at Montana State University (Environmental Statistics Group 2002) for sites in the United States and the Geographical Names Board of Canada for Canadian sites (Natural Resources Canada and Geomatics Canada 2002).

To examine trends in nest success over time, we used an information-theoretic approach (Burnham and Anderson 2002) to compare six general linear models that related nest success as a function of year of data collection, country (Canada vs. the United States) to location as denoted by the latitude and longitude of each study site (Table 1). We included the latitude and longitude of the study site in all six models to account for the broad spatial pattern in the nest success of ducks that occurs over the Prairie Pothole Region (Klett et al. 1988, Reynolds et al. 2001, Emery et al. 2006). The six models characterized six possible trends in nest success over time (Table 1). Model 1 was purely spatial, included only latitude and longitude, and assumed no trend over time, thus serving as a neutral model against which we compared models of greater complexity. In Model 2, nest success was allowed to vary between countries in addition to the spatial variation. Model 3 added the possibility that nest success varied linearly over time in the same way in both the United States and Canada, and Model 4 allowed the temporal linear trend to differ between the two countries. Model 5 included a quadratic term for year and portrayed the scenario in which nest success varied nonlinearly over time, e.g., in which nest success may have decreased over time and subsequently increased, in a similar manner in both countries. Model 6 was similar to Model 5 but allowed for the possibility that the nonlinear trends over time differed between the two countries. Models 5 and 6 were intended to portray the scenarios predicted by the hypothesis that landscape-level changes in habitat composition brought about by agricultural policies in Canada and the United States may have reversed the temporal trend in nest success observed by Beauchamp et al. (1996*a*,*b*). We evaluated the strength of evidence for each model by comparing the values of Akaike's Information Criterion corrected for small sample sizes (AICc) with Akaike weights (Burnham and Anderson 2002). In addition, we calculated model-averaged parameter estimates and their standard errors as weighted averages of the parameter estimates from all models, using Akaike weights (w_i) as weighting factors normalized to 1 for the subset of models in which that parameter appeared (Burnham and Anderson 2002). The proportion of total variance in nest success explained by each model was calculated as $r^2 = 1 - (\sigma^2/\sigma^2_0)$, where σ^2 is the variance of the residuals for each model, and σ^2_0 is the total variance in nest success (Xu 2003). Examinations of normal probability plots of residuals and plots of residuals vs. fitted values indicated that residuals were normally distributed and had homogenous variance.

We could not use model averaging to incorporate model selection uncertainty into the effect of year on nest success. The use of model averaging for β parameters can be problematic as a way to formally include model uncertainty when comparing linear and quadratic forms of the same variable (Blums et al. 2005). Therefore, we relied more heavily on the inferences available from model selection, rather than on model-averaging, to assess temporal trends in nest success. We also used a graphical approach to aid in interpretation. We calculated predicted values of nest success from all six models based on the mean values of latitude and longitude, and year values ranging from 1935 to 2006. These predicted values were then averaged over the six models, using w_i as weighting factors, and plotted against year.

Nest success, pond density, and proportion cropland

Using a geographic information system (Arcview 3.2, ESRI, Redlands, California, USA), we assigned each nest success estimate to a survey stratum of the May Breeding Waterfowl Survey conducted by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service. This systematic survey has been conducted since 1955 and provides counts of breeding waterfowl and wetlands from a large section of North America that extends from South Dakota to Alaska (Smith 1995). Once each estimate

Fig. 1. Locations of nest success estimates of dabbling ducks from the Prairie Pothole Region of North America, 1935–2006. The colors of the points indicate the time period during which data collection took place, and the lines indicate the state and provincial boundaries of the United States and Canada. The U. S./Canada border spans the 49th parallel.

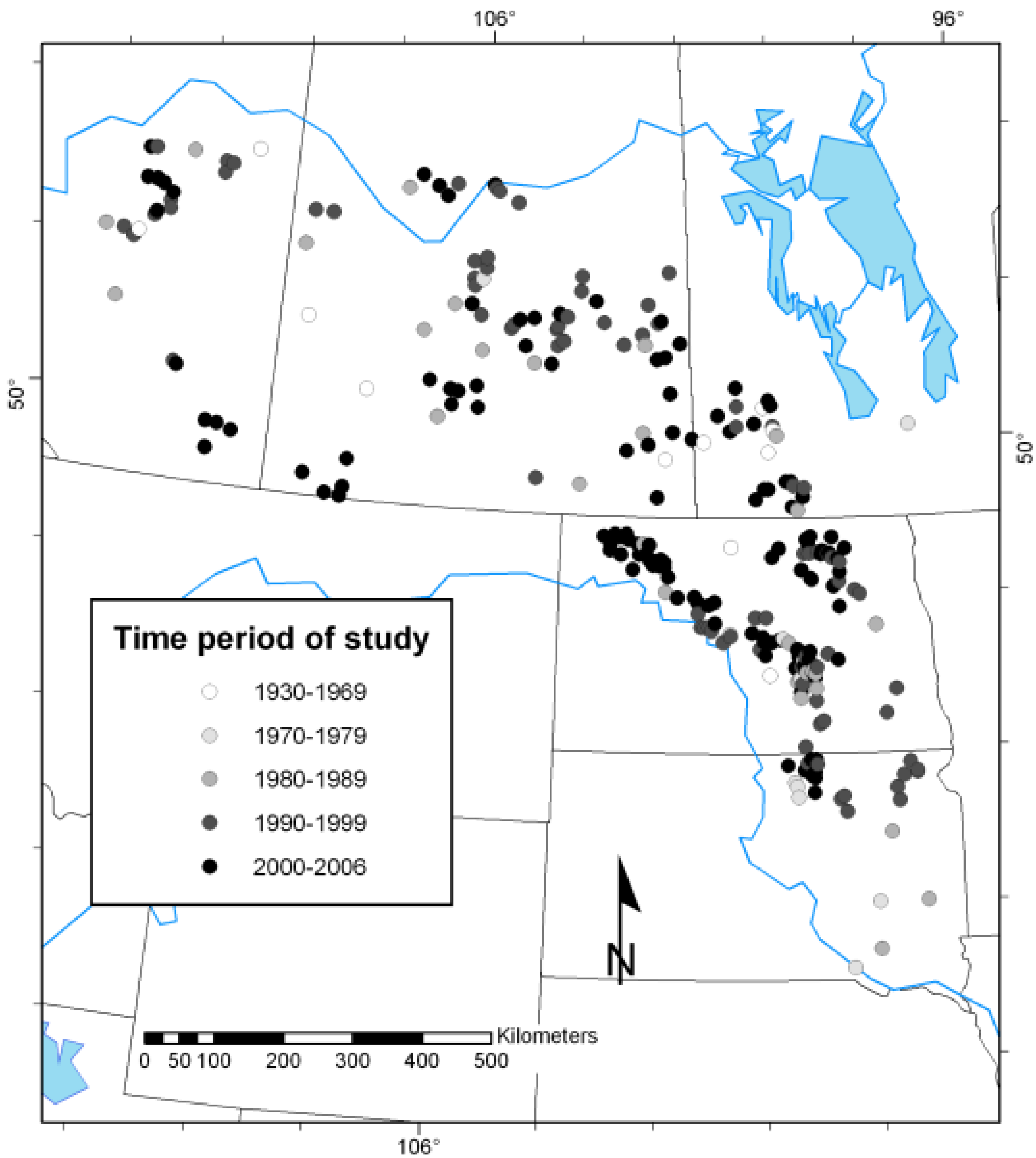


Table 1. Ranking of six general linear models relating temporal trends in nest success of dabbling ducks as a function of latitude, longitude of study site, country (Canada vs. United States), and year of study between 1935 and 2006. *n* = sample size; *K* = number of parameters; AICc = Akaike's Information Criterion, corrected for small sample sizes; ΔAICc = the difference in AICc between each model and the model with the minimum AICc; *w* = Akaike weight; and r^2 = the proportion of the total variation in nest success explained by each model (Xu 2003).

Model	Fixed effects	-2*LL	*n*	*K*	AICc	ΔAICc	*w*	r^2
1	Latitude Longitude	248.6	507	4	-489.0	26.8	0.00000	0.06
2	Latitude Longitude Country	253.0	507	5	-496.0	19.9	0.00003	0.08
3	Latitude Longitude Country Year	255.6	507	6	-499.0	16.9	0.0001	0.09
4	Latitude Longitude Country Year Country*Year	263.0	507	7	-511.7	4.2	0.07	0.11
5	Latitude Longitude Country Year Year²	264.7	507	7	-515.2	0.6	0.39	0.12
6	Latitude Longitude Country Year Year² Country*Year Country*Year²	267.1	507	9	-515.8	0.0	0.54	0.13

of nest success was assigned to a survey stratum, we were able to link the nest success data to estimates of wetland or "pond" density available online from the Migratory Bird Data Center (http://www.fws.gov/birddata/). Pond density served as a measure of environmental conditions and was estimated for each survey stratum by dividing the pond count for each year by the area of the stratum in square kilometers.

Miller (2000) obtained yearly estimates on the acreage of crops for the May Breeding Waterfowl Survey strata in the Prairie Pothole Region from 1961 to 1995 using data collected during the Census of Agriculture at the county level in the United States and at the level of the crop-reporting district in Canada. The Census of Agriculture is conducted every 5 yr, and Miller (2000) calculated yearly estimates by interpolating between censuses (Miller 1996, Miller 2000). These data were partitioned into yearly estimates of crop coverage for survey strata 26–35, 37–41, and 45–49, of the May Breeding Waterfowl Survey. Cropland estimates included areas covered by wheat (*Triticum* spp.), rye (*Secale cereale*), corn (*Zea maize*), oats (*Avena sativa*), barley (*Hordeum vulgare*), sorghum (*Sorghum* spp.), flaxseed (*Linum usitatissimum*), canola (*Brassica napus*), soybeans (*Glycine max*), mustard seed (*Brassica* spp.), sunflowers (*Helianthus annuus*), sugar beets (*Beta vulgaris*), potatoes (*Solanum* spp.), tomatoes (*Lycopersicon esculentum*), green peas (*Pisum sativum*), and lentils (*Lens culinaris*). We calculated proportion cropland as the area of land in each survey stratum covered by crops divided by the total acreage of each survey stratum. The agricultural data spanned a shorter time period than did the nest success data, so this second analysis was restricted to a smaller data set (*n* = 218) covering the years between 1964 and 1995.

We tested whether nest success varied as a function of proportion cropland and pond density, and whether this relationship varied between Canada and the United States, by comparing 12 linear mixed models (Pinheiro and Bates 2000) that considered different combinations of these variables and their interactions (Table 2). All 12 models included year and site nested inside survey stratum [site(stratum)] as random effects. The year random effect served as a temporally varying effect that acted independently of proportion cropland and pond density. Including site nested in survey stratum allowed us to account for persistent differences in nest success related to study site and to link the nest success data to the larger-scale pond density and proportion cropland data from Miller (2000). Model 1 included only an intercept, such that nest success had a mean value unaffected by country, proportion cropland, or pond density and provided a model against which to assess the effect of country alone. Subsequent models were progressively more complex. Model 2 allowed nest success to vary only as a function of country, which was intended to represent a geographic gradient in some unmeasured variable such as predator abundance and community composition or shape of wetland basins, as well as the country in which the study took place. Models 3–5 included combinations of country and pond density, but no terms for proportion cropland. Models 6–8 included the combinations of country and proportion cropland, but no terms for pond density. Model 9 included only main effects. Models 10 and 11 allowed nest success to vary with country, pond density, proportion cropland, and the interaction between country and proportion cropland or pond density. Model 12, the most parameterized model, included country, proportion cropland, pond density, and interactions that allowed the relationships of pond density and proportion cropland to vary by country.

We evaluated the strength of evidence for each model by comparing values of AICc and w_i and used model averaging to incorporate model selection uncertainty into parameter estimates for the effects of country, pond density, and proportion cropland (Burnham and Anderson 2002). Again, we calculated the proportion of variance explained by each model following Xu (2003) and used a graphical approach to aid in interpreting the effects of pond density and proportion cropland. To evaluate the effect of pond density, we calculated predicted values of nest success from all 12 models based on the mean value of proportion cropland and a range of observed pond density values. These predicted values were then averaged over the 12 models using w_i as weighting factors and plotted against pond density. To portray relations with cropland, we repeated this procedure using the mean value for pond density and a range of observed values of proportion cropland. We examined plots of residuals vs. fitted values and detected no evidence of heterogeneity of variance. Normal probability plots indicated that random effects were normally distributed, but residuals were skewed right. A natural log transformation of the nest success data provided models with normally distributed residuals but did not affect model rankings and overall conclusions. We therefore present the untransformed data for ease of interpretation.

RESULTS

Historical trends in nest success

Nest success over the period of study at Canadian sites averaged 0.16 (n = 206, SD = 0.13, CV = 76.7), whereas nest success at sites in the United States averaged 0.25 (n = 301, SD = 0.16, CV = 63.6). Nest success was negatively correlated with both latitude and longitude (Table 3). These negative correlations suggest that, for any given latitude, nest success tended to be lower at eastern sites relative to western sites and, similarly, that for a given longitude nest success tended to be lower at northern sites relative to southern sites, a spatial pattern in duck nest success similar to those found by Reynolds et al. (2001) and Emery et al. (2006).

The model that best explained temporal trends in nest success included parameters for the effects of country, year, quadratic year, and their interactions, i.e., Model 6 in Table 1, although this model explained only a small proportion of the total variance in nest success (r^2 = 0.13). The next best model, Model 5, included the same parameters as Model 6 but lacked the interaction terms. These two models had a combined Akaike weight of 0.91 (w_5 + w_6; Table 1), which suggests that the data best support a nonlinear temporal trend in nest success over the entire Prairie Pothole Region, and provide weaker support for the suggestion that this nonlinear trend differed between the two countries.

The model-averaged predicted values for mean nest success in Canadian sites show a decline from a predicted ~ 0.40 in the 1930s to a nadir of 0.14 in the early 1990s, and then a gradual return to its long-term mean value of 0.16 at the end of the time series in 2005 (Fig. 2). Model-averaged predicted values for mean nest success in sites in the United States show a decline from a mean of ~ 0.35 in the 1930s to a plateau that lasted through the 1970s until the early 1990s, when mean nest success rose above its long-term average and continued to increase until the end of the time series in 2006 (Fig. 2).

These results likely depended on the inclusion of nest success data from early studies, whose estimates may not be as reliable as those of later

Table 2. Ranking of 12 general mixed linear models relating the nest success of dabbling ducks as a function of country (Canada vs. United States), proportion cropland, pond density, and their interactions in North American prairies between 1964 and 1995. Each model had year and study site nested in survey strata as random effects. *n* = sample size; *K* = number of parameters; AICc = Akaike's Information Criterion, corrected for small sample sizes; ΔAICc = the difference in AICc between each model and the model with the minimum AICc; *w* = Akaike weight, and r^2 = the proportion of the total variation in nest success explained by each model (Xu 2003).

Model	Fixed effects	-2*LL	n	K	AICc	ΔAICc	*w*	r^2
1	Intercept only	-76.8	218	4	-68.6	14.81	0.00	0.02
2	Country	-79.6	218	5	-69.3	14.08	0.00	0.03
3	Pond Density	-79.1	218	5	-68.8	14.62	0.00	0.04
4	Country + Pond Density	-86.9	218	5	-76.6	6.77	0.01	0.09
5	Country + Pond Density + Country*Pond Density	-86.9	218	6	-74.5	8.88	0.00	0.09
6	Proportion Cropland	-92.5	218	6	-80.1	3.31	0.07	0.12
7	Country + Proportion Cropland	-92.7	218	7	-78.1	5.26	0.03	0.12
8	Country + Proportion Cropland + Country*Proportion Cropland	-92.7	218	7	-78.1	5.25	0.03	0.12
9	Country + Proportion Cropland + Pond Density	-96.0	218	7	-81.4	1.94	0.13	0.13
10	Country + Proportion Cropland + Pond Density + Country* Proportion Cropland	-96.0	218	8	-79.3	4.05	0.05	0.13
11	Country + Proportion Cropland + Pond Density + Country*Pond Density	-100.1	218	8	-83.4	0.00	0.35	0.15
12	Country + Proportion Cropland + Pond Density + Country*Pond Density + Country*Proportion Cropland	-102.1	218	9	-83.2	0.15	0.33	0.16

studies (Beauchamp et al. 1996*a*). We therefore repeated the analyses of temporal trends using only data collected after 1970. In this secondary analysis, the data best supported the same model as did the previous analysis, i.e., Model 6, which indicated a nonlinear trend differing between the countries, although support for this model was weaker (w_6 = 0.31). The next best models were Models 4 and 5 (w_4 = 0.21, w_5 = 0.17). Model-averaged predicted values for nest success at Canadian sites decreased from 0.18 in 1970 to about 0.16 in 1990, and gradually increased to 0.17 in 2005. Model-averaged predicted values suggest that nest success at U.S. sites was approximately 0.23 in 1970 and showed little change until 1985, when it increased gradually to 0.26 as of 2006. Thus, although the magnitude of the decline in mean nest success over time depended on whether data collected prior to 1970 were included, this reduced data set provided evidence that mean nest success showed a modest increase during the 1990s at sites in the United States but only a small increase at Canadian sites during the same period.

Nest success, pond density, and proportion cropland

Although mean nest success was negatively associated with proportion cropland in both the

Table 3. Model-averaged parameter estimates based on six general linear models relating the nest success of dabbling ducks as a function of latitude and longitude, country (Canada vs. the United States), and year in the North American Prairie Pothole Region between 1935 and 2006. SE refers to standard error, and *t* = estimate/SE. Parameters in which *t* > 1.96 have 95% confidence intervals that do not include 0.

Parameter	Estimate	SE	*t*
Intercept	247.5	132.2	1.87
Latitude	-0.01	0.007	-1.91
Longitude	-0.01	0.003	-2.84
Country	115.7	122.0	0.95
Year	-0.25	0.13	-1.88
Year*Country	-0.19	0.20	-0.94
$Year^2$	0.00007	0.00004	1.88
$Year^2$*Country	0.00005	0.00006	0.93

United States and Canada, the relationship of nest success to pond density varied between the two countries. Model 11, which included parameters for country, proportion cropland, pond density, and the country*pond density interaction, was ranked most parsimonious (Table 2). This model ($w_i = 0.35$) had similar support as the next best model, Model 12, with an Akaike weight of 0.33. Models 11 and 12 were very similar and differed only by the inclusion of the interaction effect between country and proportion cropland, suggesting that support for the inclusion of this interaction effect is weak. Similarly, the third best model, Model 9, included only main effects, suggesting that the evidence for including any interaction effects may be weak. The parameters for proportion cropland appeared in all the models with Δ AICc < 4, suggesting that the data provided strong support for an effect of proportion cropland on nest success. Overall, models explained low proportions of the total variance in nest success, with r^2 values ranging between 0.02 and 0.16.

Model-averaged parameter values and predicted values support the strong effects of country, proportion cropland, and the interaction between country and pond density on duck nest success, as parameter values for these effects had 95% confidence intervals that did not encompass 0 (Table 4). Overall, mean nest success was lower in Canada than in the United States (Fig. 2, Table 4). Mean nest success varied negatively with proportion cropland (Fig. 3), and the 95% confidence interval for the interaction effect between country and proportion cropland encompassed 0, indicating that nest success varied negatively with proportion cropland in a similar way in both countries. In contrast, the 95% confidence interval for the interaction parameter between pond density and country did not encompass 0 (Table 4), suggesting that the relationship between nest success and pond density varied between the two countries. Model-averaged parameter values and predicted values indicate that nest success varied positively with pond density at sites in Canada and had a slightly negative relationship with pond density in the United States (Table 4, Fig. 3).

DISCUSSION

Our results suggest that previously reported declines in duck nest success in the Prairie Pothole Region may have been reversed or at least halted, and that

Fig. 2. Temporal trends in nest success in the Prairie Pothole Region of (A) Canada and (B) the United States. Nest success estimates were collected from studies based at sites in Alberta, Saskatchewan, Manitoba, North Dakota, and South Dakota from 1935 to 2006. The solid lines in panels A and B indicate the model-averaged predicted values from a series of models depicting nest success as a function of latitude, longitude, country (Canada/United States), year, year as a quadratic term, and the interactions of the above. Thin horizontal lines represent the mean value of all nest success estimates for each country (0.16 in Canada, 0.25 in the United States).

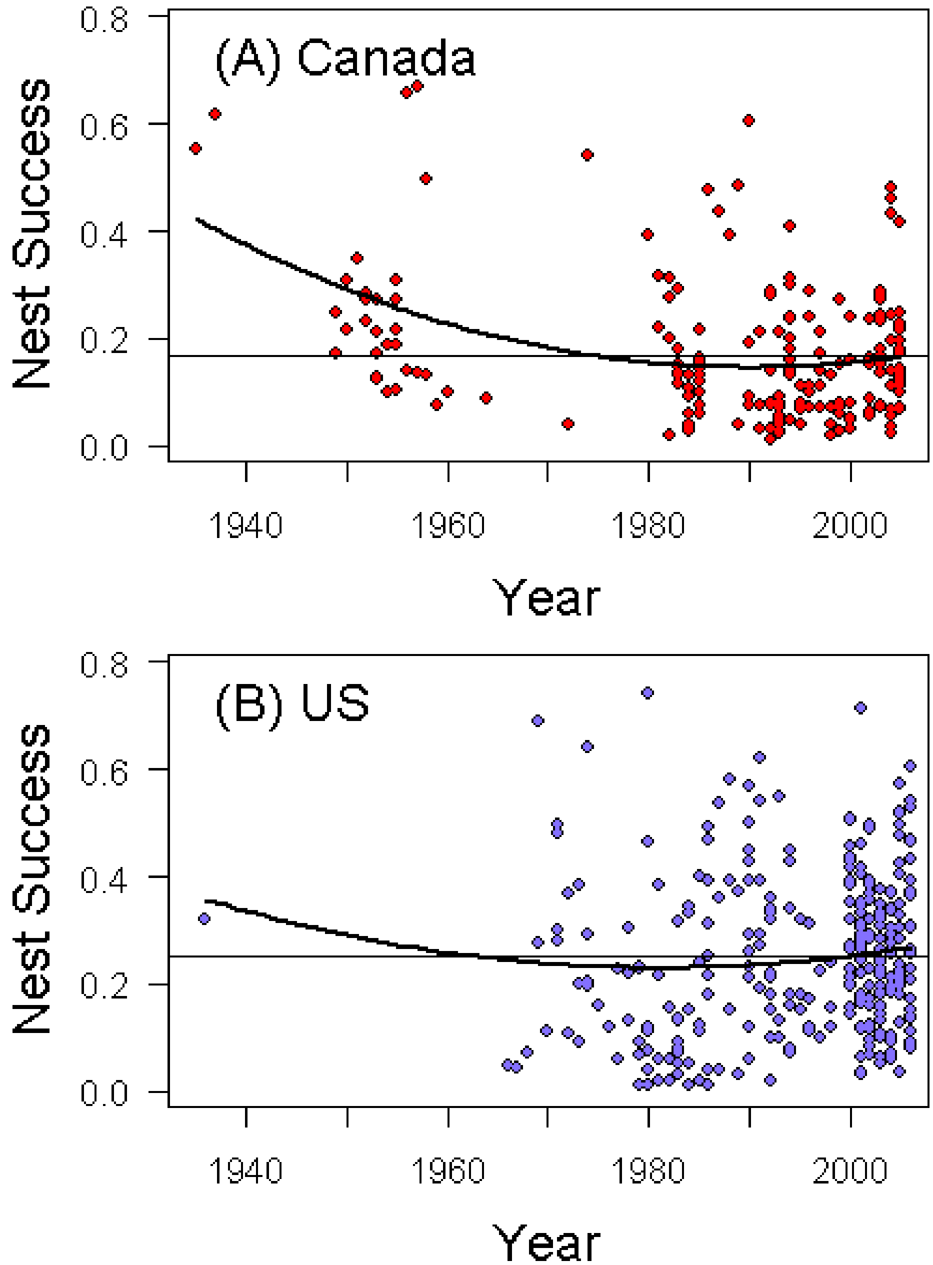
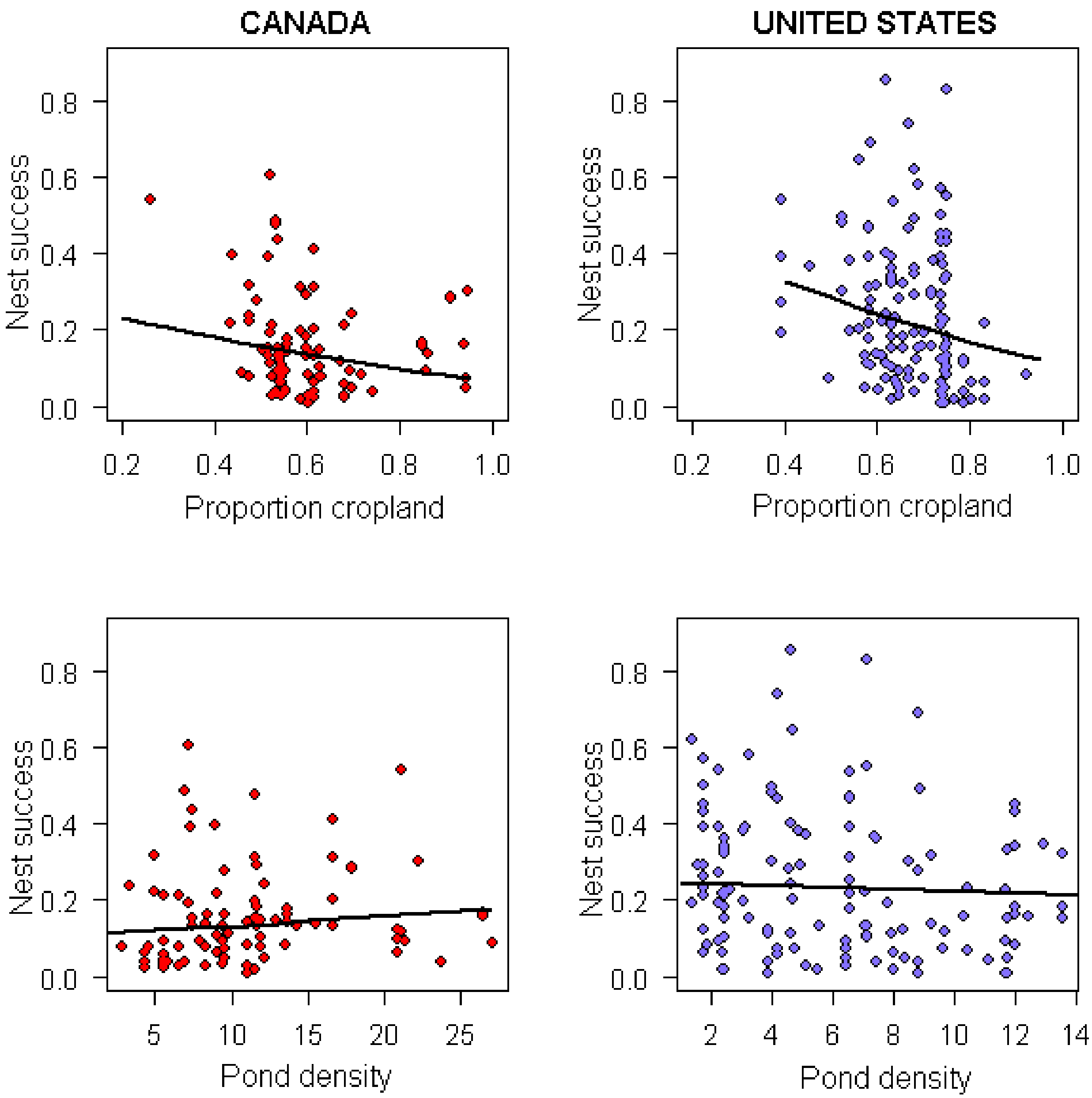


Table 4. Model-averaged parameter estimates based on 12 general mixed linear models for nest success of dabbling ducks as a function of country, proportion cropland, pond density, and interactions in the North American Prairie Pothole Region between 1964 and 1995. SE refers to standard error, SD to standard deviation, and t = estimate/SE. Parameters in which $t > 1.96$ have 95% confidence intervals that do not include 0.

Parameter	Estimate	SE	*t*
Fixed effects			
Intercept	0.84	0.11	7.52
Country: Canada	-0.37	0.12	-3.18
Proportion Cropland	-0.49	0.17	-2.89
Proportion Cropland*Country Interaction (Canada)	0.43	0.27	1.60
Pond Density	-0.01	0.01	-1.82
Pond Density*Country Interaction (Canada)	0.02	0.01	2.66
Random effects		SD	
Site(Stratum)		0.004	
Year		0.001	
Residual		0.019	

these trends may be in part related to landscape-level changes in the proportion of land under cultivation. We found that nest success was negatively associated with proportion cropland in the United States and Canada, a pattern consistent with other extensive studies of landscape effects on nest success of ducks (Greenwood et al. 1995, Reynolds et al. 2001). Nests in cropland may be lost directly to agricultural practices such as plowing and seeding operations (Bellrose 1980, Sugden and Beyersbergen 1985, Klett et al. 1988) or, more importantly, nest success can be affected indirectly through the effects of landscape change on predator communities (Sargeant et al. 1993, Phillips et al. 2003). According to Sargeant et al. (1993), the expansion of agriculture in the prairies coincided with an increase in the abundance and distribution of medium-sized predators such as red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and American crow (*Corvus brachyryhynchos*). The fragmentation of upland nesting habitat is thought to enhance the foraging efficiency of predators, which visit small isolated tracts of grassland more frequently and search them more thoroughly than larger tracts of grassland (Clark and Nudds 1991, Sovada et al. 2000, Phillips et al 2003). Although consistent with these interpretations, our results do not enable us to directly distinguish how landscape composition affects nest success. Nevertheless, these results are consistent with the hypothesis that landscape-level changes brought about by the U.S. Farm Bills have resulted in an increase in the average nest success of ducks breeding in the U.S. portion of the Prairie Pothole Region (Reynolds et al. 2001). In addition, we found that nest success varied weakly with pond density in the United States. This result may have

Fig. 3. Mean nest success of dabbling ducks as a function of proportion cropland and pond density in the Pothole Prairie Region of Canada and the United States, 1964–1995. Nest success estimates were collected from published and unpublished studies. Agricultural data are from the Census of Agriculture collated by Miller (2000) and represent the proportion of strata from aerial waterfowl surveys (Smith 1995) covered in row crops. Lines indicate the model-averaged predicted values from 12 general linear mixed models depicting possible relationships between nest success, country, proportion cropland, and pond density. Note differences in the *x*-axes between countries with respect to pond density.



resulted from the large variation in estimated nest success in the United States (Fig. 3), although Reynolds et al. (2001) and Stephens et al. (2005) also found that nest success in the U.S. portion of the Prairie Pothole Region varied weakly or even negatively with the abundance of wetlands. This difference in response to wetland abundance may result from the reduced potential for variation in the wetland base in the United States relative to Canada (see the range of wetland densities in Fig. 3), as suggested by Miller and Nudds (1995). The stronger relationship between pond density and nest success seen in Canada may also be driven by the severe droughts of 1988–1993 and 1999–2003. Although the mechanism is unclear, the reduced effect of wetland abundance in the United States suggests that trends in mean nest success in this country may be more strongly associated with trends in proportion of cropland than with trends in wetland abundance.

Although the overall effect of the farm bills has been to reduce the proportion of cultivated land in the United States, it is clear that locally, i.e., at the site level, ducks nest across similarly variable conditions with respect to the proportion of cropland in both countries. Thus, the effects of legislative differences between countries are almost certainly more complex than simply reducing the amount of cropland and thereby generating an increase in nest success. Rather, the effect appears to emerge at the larger scale, as reflected in the consistent differences in mean nest success between countries. In other words, it appears that there must be a further qualitative difference among sites in different countries with similar low proportions of cropland. Whether this is because of the spatial configuration or composition of noncropland habitats between the countries, e.g., the planted dense nesting cover characteristic of former cropland converted to the Conservation Reserve Program in the United States vs. alternative permanent cover types in Canada (see below), should be a topic for future investigations, because an examination of this issue might provide some insights into the actual mechanism by which differences in nest survival arise.

Mean nest success in the Canadian portion of the Prairie Pothole Region is a function of both proportion cropland and wetland density. Thus, agricultural policies that promote conversion of cropland to perennial cover will best benefit nesting ducks if they include provisions to reduce wetland loss. Potential benefits to nesting ducks resulting from the conversion of previously tilled land to hayland and pasture in the Canadian prairies may have been offset by wetland loss and the further breaking of new native prairie (Devries et al. 2004), which has continued to occur (Watmough et al. 2002). Continued wetland loss may thus have contributed to the differences in temporal trends between the United States and Canada. Alternatively, the different trends may reflect a potentially important difference in the decreases in cropland between the two countries. Cropland in Canada was primarily converted to pasture and hayland (Devries et al. 2004), whereas cropland in the United States was converted to undisturbed planted cover. Nest success varies among cover types according to their abilities to provide security from predators (Greenwood et al. 1995), and thus the differences in temporal trends in nest success between the two countries may reflect the differences in cropland, hayland, pasture, and undisturbed planted cover.

The nest success estimates used in this study came from sites of different sizes and in different habitats, and were collected using different methods, e.g., nest searching, telemetry. In addition, the data on pond density and agricultural cover likely contained unquantified errors during collection and interpolation. Although we have attempted to account for spatial variation in nest success through the inclusion of latitude and longitude and the use of site as a random effect in our models, sources of variation such as these contributed to the magnitude of the overall unexplained variation in nest success, as indicated by the low r^2 values (Tables 1 and 2). Although the broad patterns we observed, e.g., spatial gradients in nest success, negative effect of agricultural cover, and weak effect of wetland abundance in the United States, have been documented in studies with more consistent methodology but covering smaller spatial and temporal scales (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005), these low r^2 values suggest that unmeasured processes may have strong effects on these estimates of nest success. We have focused on the indirect effects of predation as modulated by landscape composition, but predation rates will also vary strongly with predator abundance and composition (Johnson et al. 1989). Abundances of the various nest predators have fluctuated over time for many reasons, including changes in predator control, disease, and complex interactions among predator species (Greenwood and Sovada 1998). Therefore, including some measure of predator abundance could perhaps reduce this unexplained variation.

Nest success has shown consistent differences among the duck species considered in this study. Gadwall, Blue-winged Teal, and Northern Shoveler typically have higher nest success than Mallard and Northern Pintail (Klett et al. 1988, Beauchamp et al. 1996*a*). The relative abundances of these species have varied spatially and temporally over the Prairie Pothole Region (Bellrose 1980, USFWS 2006). We accounted for persistent spatial effects by incorporating latitude and longitude into our analyses, However, this temporal variation in species distributions may complicate the interpretation of temporal trends based on estimates of nest success pooled among species, because these estimates may simply reflect the changing composition of the component duck species. Our results must thus rest on the assumption that the nest successes of these species have co-varied in synchrony. We lack the data to compare temporal trends separately by species and test this assumption. However, Beauchamp et al. (1996*a*) found that the linear trend they observed using nest success estimates pooled among species was supported in analyses in which species were considered independently, which made us more confident that the pooled estimates we used reflected trends in the component species.

It is clear, however, that large-scale agricultural policies that promote the conversion of cropland to perennial cover through the provision of economic incentives or the removal of subsidies can have positive effects on duck nest success. Although largely motivated by issues of erosion control and surplus production, the 1985 Farm Bill, which brought the Conservation Reserve Program into existence, was the first to have a specific title devoted to conservation (Cain and Lovejoy 2004). The farm bills thus serve as examples of how the merging of commodity support policy and resource conservation policy has a powerful potential to affect change in agricultural practices and the composition of upland habitats. In Canada, these benefits will be best realized if significant attention is also paid to the challenge of stemming the continued loss of wetlands.

Responses to this article can be read online at:
http://www.ace-eco.org/vol2/iss2/art5/responses/

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