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Jane Austin

USGS Northern Prairie Wildlife Research Center, jaustin@usgs.gov

Thomas K. Buhl

USGS Northern Prairie Wildlife Research Center, tbuhl@usgs.gov

Glenn R. Guntenspergen

USGS Northern Prairie Wildlife Research Center

Wayne Norling

USGS Northern Prairie Wildlife Research Center

H. Thomas Sklebar

USGS Northern Prairie Wildlife Research Center

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DUCK POPULATIONS AS INDICATORS OF LANDSCAPE CONDITION IN THE PRAIRIE POTHOLE REGION*

JANE E. AUSTIN*, THOMAS K. BUHL, GLENN R. GUNTENSPERGEN**¹, WAYNE
NORLING**² and H. THOMAS SKLEBAR

*U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota,
U.S.A.*

(* author for correspondence, e-mail: jane_austin@usgs.gov)

(** Present addresses: ¹ U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, U.S.A.;

² U.S. Geological Survey, National Wetlands Research Center, Lafayette, Louisiana, U.S.A.)

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Abstract. The Prairie Pothole Region of the northern Great Plains is an important region for waterfowl production because of the abundance of shallow wetlands. The ecological significance of the region and impacts from intensive agriculture prompted the U.S. Environmental Protection Agency to select it as one of the first areas for developing and evaluating ecological indicators of wetland condition. We examined hypothesized relations between indicators of landscape and wetland conditions and waterfowl abundance on 45 40 km² study sites in North Dakota for 1995–1996. Landscape condition was defined *a priori* as the ratio of cropland area to total upland area surrounding wetlands. Measures of waterfowl abundance included estimated numbers of breeding pairs (by species and total numbers) and γ , a species-specific correction factor which effectively adjusts breeding pair estimates for annual or area-related differences in pond size. Landscape indicators and waterfowl measures varied among regions. Results indicated that most areas in the Coteau region are of much higher quality for ducks than those in the Drift Plain, and areas in the Red River Valley are of the poorest quality for ducks. Regression models demonstrated the impact of agricultural development on breeding duck populations in the Prairie Pothole Region. The most consistent landscape indicators of waterfowl abundance were percent of cropland and grassland. Models were inconsistent among years and species. The potential biotic indicators of landscape and wetland condition examined here would be appropriate for temporal trend analyses, but because of inherent geographic variability would not be appropriate for single-year geographic trend analyses without more extensive evaluations to improve explanatory models.

Keywords: dabbling duck population, indicator, landscape condition, North Dakota, prairie pothole region, wetlands

1. Introduction

The Prairie Pothole Region (PPR), located in north-central United States and south-central Canada, is characterized by a high density of shallow, productive wetlands that support an abundance of waterfowl and other water birds (Kantrud *et al.*,

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1989). Ducks traditionally have been considered one of the most important wild-life resources of the region. Of the surveyed population of all breeding ducks in North America, 51% occur in the PPR, and 67% of the continental mallard (*Anas platyrhynchos*) population is found in this region (Batt *et al.*, 1989). The portion of the PPR in the United States accounts for 15% of mallards surveyed in North America (Batt *et al.*, 1989). Ducks rely on wetlands for food resources and security, and most dabbling ducks (*Anas* spp.) use uplands for nesting habitat. Their numbers, therefore, may furnish an integrated measure of landscape condition. Ducks furnish the values of biological integrity and harvestable productivity described by Peterson (1994) for the PPR.

Agriculture is the predominant factor affecting the landscape in the PPR (Kantrud *et al.*, 1989). Wetland quality and function are degraded primarily by agricultural activities associated with annual crops, including drainage, cultivation of wetland basins, siltation due to soil erosion from adjacent cropland, and agricultural chemicals (Kantrud *et al.*, 1989). Agricultural activities affecting upland habitats also affect duck populations (Bethke and Nudds, 1995) and production (Johnson *et al.*, 1987) at local and landscape scales. Most dabbling ducks nest in grasses, forbs, or shrubs, and the success of their nesting effort is affected by the availability and type of cover (Johnson *et al.*, 1987; Klett *et al.*, 1988). Perennial grassland habitat has been lost and what remains is fragmented in areas where cropland is abundant. Greenwood *et al.* (1995) found that duck nest success in the Canadian PPR was negatively correlated with the amount of cropland present.

In 1989, the U.S. Environmental Protection Agency (EPA) initiated the Environmental Monitoring and Assessment Program (EMAP) to provide quantitative assessments of the status and long-term trends in the condition of ecological resources on a regional and national scale (Peterson, 1994). The ecological significance of the PPR and the stress imposed on this ecosystem by conversion of grassland to cropland was the reason the EPA selected the PPR for development and evaluation of ecological indicators to monitor wetland condition (Cowardin and Peterson, 1997). The first stage of EMAP (Prairie Pothole Pilot I Study) evaluated the performance of selected landscape- and field-level variables as indicators of environmental quality of wetlands and as tools to discriminate between wetlands in highly disturbed (crop agricultural) and less disturbed (grassland) landscapes (Peterson *et al.*, 1997). One component of the Pilot I study evaluated estimated numbers of breeding ducks as an indicator of landscape conditions (i.e. wetland basin conditions and upland habitat availability; Cowardin and Sklebar, 1997). In that study, habitat data derived from aerial video and counts of ducks were used as input to models to predict the annual combined breeding population of five species of dabbling ducks: mallards, blue-winged teal (*Anas discors*), gadwalls (*A. strepera*), northern shovelers (*A. clypeata*), and northern pintails (*A. acuta*). The definition of landscape condition was dependent on the ratio of cropland area to total upland area; poor-condition areas had high ratios of cropland to upland area (median value = 91%) and almost no grassland cover. This definition, established

for the Pilot I study, was based on the perception that wetlands in a complex containing predominantly cropland would probably be in a more degraded state than those containing predominantly grassland (Cowardin, 1997: 11–12).

The Pilot I study showed that the estimated combined breeding population of the five duck species was an indicator that could separate two extremes in landscape condition (high vs. low ratio of cropland to total area of upland; Cowardin and Sklebar, 1997). More ducks were calculated on grassland-dominated study areas than on cropland-dominated study areas ($P = 0.0038$, 1992 and $P < 0.001$, 1993). The differences between the two extreme landscape conditions were apparent despite the fact that Cowardin and Sklebar (1997) observed no association between duck pairs and number of wetland basins as would be expected. Numbers of breeding pairs therefore showed promise as an indicator of landscape condition.

Our study is the next stage of EMAP studies, Prairie Pothole Pilot II. We used a larger data set to build upon the results of the Pilot I studies and to test hypothesized relations between indicators of landscape and wetland condition and waterfowl abundance (an indicator for bird communities). Our objective was to evaluate the use of duck numbers as indicators of landscape condition, where landscape condition is defined as the ratio of cropland area to total upland area.

2. Selection of Study Areas

EMAP systematically divided North America using a grid of 40 km² hexagons. From this sample universe, we selected as study areas 45 hexagons in North Dakota east of the Missouri River using systematic sampling (Figure 1). The study areas were post-stratified into three regions (Red River Valley, Drift Plain, and Coteau) based on maps by Kantrud *et al.* (1989).

3. Methods

Base Mapping and Landscape Analyses. Original base maps and geographic information coverages obtained from EPA included National Wetlands Inventory (NWI) wetland and upland data for 1979–1982. These coverages were updated using 1995–1996 aerial photography, ground truthing, and data from the Department of Agriculture's Natural Resources Conservation Service. The area and extent of water in sampled wetland basins were evaluated from aerial photography taken for each study area in May of 1995 and 1996 using the feature map process of TNTMIPS (MicroImages Inc., Lincoln, NE). Wetland basins were classified to wetland regime following Cowardin *et al.* (1979).

Landscape-level indicators of condition used in the analysis followed those recommended by Cowardin and Sklebar (1997) and included: (1) cropland as a percentage of total upland habitat (PERCROP); (2) grassland as a percentage of

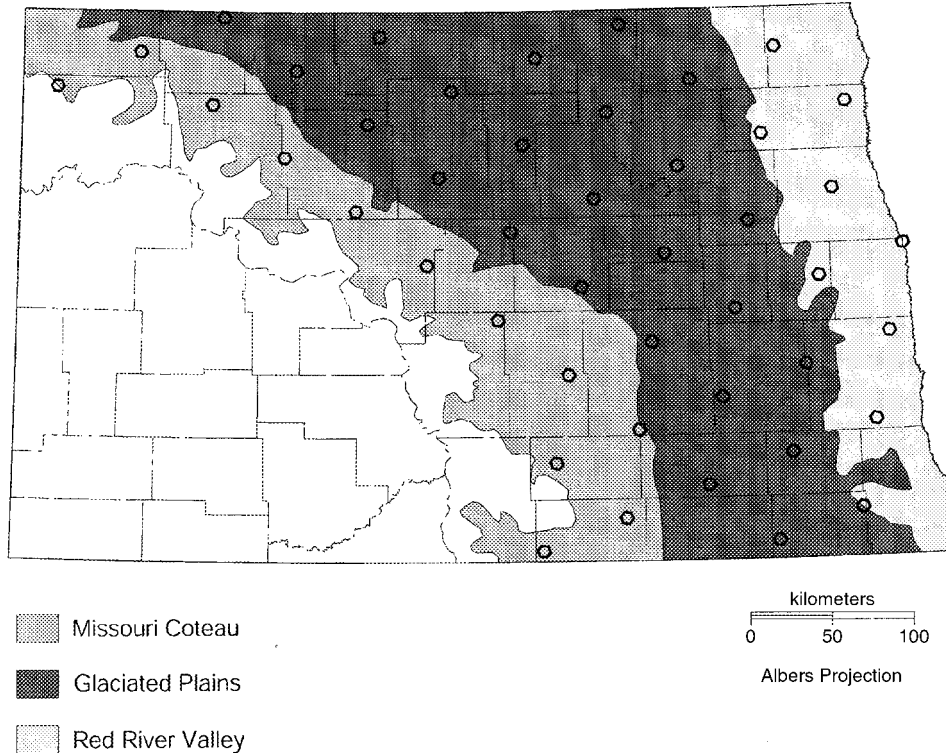


Figure 1. Location of 45 40 km² study areas in North Dakota used to examine duck populations as indicators of landscape condition, 1995–1996.

total upland habitat (PERGRASS); (3) proportion of basins modified by drainage (PCTNMOD); (4) total linear drainage length (m), an indicator of drainage intensity (TOTDRAIN); (5) percent of cropland adjacent to all temporary, seasonal, and semipermanent basins (ALLADJC); and (6) percent of grassland adjacent to all temporary, seasonal, and semipermanent basins (ALLADJG). TOTDRAIN and PCTNMOD were derived from original NWI data and photointerpretation of 1996 aerial photography.

Other landscape variables used included total basin area (BASAREA (ha), as determined from GIS coverage), total number of basins (TOTBASIN), and indices in the change in wet area, indicating seasonal water loss for semipermanent basins (SEMICID), seasonal basins (SEASCID), and temporary basins (TEMPCID) between May and July. These indices were included because Cowardin and Sklebar (1997) found the indices were able to discriminate between extremes in landscape condition and were more sensitive than the raw data. We calculated the change index (CI) for area of water in each study area between May and July 1996 using the following formula (Cowardin and Sklebar, 1997):

$$CI = |(May - July)/NWI|$$

where

- May = wet area of sampled basins in May;
- July = wet area of sampled basins in July;
- NWI = area of sampled basins from GIS coverage.

CI was calculated for each basin class across each study area.

3.1. DUCK POPULATIONS

Roadside transects were located along all roads drivable in May in each study area. Wetland basins observable from the road right-of-way constituted the sample of wetland basins in each study area for pair counts. In 1995, the roadside transect and associated wetland basins available for sampling included everything 402 m (0.25 mi) on either side of the center of the road; in 1996, this width was reduced to 201 m (0.125 mi) to improve observability. A random subsample of 100 basins from the transect area was selected proportional to the area and frequency of each basin class. If there were less than 100 basins in the transect, all basins were sampled. All permanent basins within the transect were sampled. When we were unable to view a basin, we replaced it with a basin of the same wetland regime which was located within the transect area.

Three technicians conducted duck counts from vehicles along the right-of-way. For each basin, we recorded number of ducks by social groups (Cowardin *et al.*, 1995), the proportion of the basin that could be observed, the proportion of the basin that was not obstructed by emergent vegetation, basin cover type (relative distribution of open water and emergent vegetation in the basin; Stewart and Kantrud, 1971), and areal percent of basin holding water. Ducks counted were later adjusted for visibility using the first 2 wetland measures and followed the assumption that ducks were dispersed equally across the basin.

Two counts were conducted each year: early counts were conducted during 1–15 May and late counts were conducted during 20 May–5 June. Data from early counts were used to estimate breeding pairs of mallards and pintails whereas data from late counts were used to estimate breeding pairs of blue-winged teal and gadwalls (Cowardin *et al.*, 1988b). Breeding pairs of northern shovelers were estimated from the count occurring nearest 15 May. Numbers of breeding pairs were determined from social groups as described by Cowardin *et al.* (1995).

Numbers of breeding pairs were extrapolated from the adjusted duck counts to the entire study area using previously developed regression models that related estimated breeding pairs to pond area (area of the basin containing water; Cowardin *et al.*, 1995). A correction, γ , for temporal and spatial variation was calculated as the ratio of observed to predicted pairs for the sampled basins. The estimate from the regression model for all basins on a study area was corrected by multiplying the regression estimate by γ . This method does not require the assumption that

duck density on the sampled basins represents density on the entire study area. We assumed that the difference between observed pairs and pairs predicted by the regression for the sampled basins was representative of the unsampled basins within the study area.

Data Analyses. We used analysis of variance (ANOVA) techniques to assess differences in estimated numbers of breeding pairs, γ 's, and landscape variables among three regions. Landscape variables changed very little between years, so only one value was used for both years. To achieve normality and constant variance, TOTDRAIN was transformed using a square root ($Y+0.5$) transformation, and TEMPCID, SEASCID, and SEMICID were transformed using an inverse transformation of ($Y+1$). The least squares means procedure (SAS Institute, Inc., 1997) was used to estimate parameters; LSMEANS reported here are back-transformed values.

We used ANOVAs to assess the potential influence or relationship of the explanatory variables (landscape variables) to the indicated pair counts and estimated γ . We dichotomized each explanatory variable into low and high categories using their respective medians as the dividing point. Following methods described in Milliken and Johnson (1992), we conducted a factorial ANOVA with main effects and two-way interactions to determine potential factors to use in a multiple regression analysis. We used 0.2 as a significance level for the screening process, but used 0.05 as a significance level for reporting mean comparisons. We then followed model selection methods described in Myers (1990) and Neter *et al.* (1990) to develop regression models and their explanatory capabilities towards the response variables. ANOVAs were conducted using the mixed model procedure (PROC MIXED) of SAS (SAS Institute, Inc., 1997), with mean separations for significant effects in the ANOVAs being done with Fisher's protected LSD criteria (Milliken and Johnson, 1992). Regression analyses were conducted using the regression procedure (PROC REG) of SAS (SAS Institute, Inc., 1997). ANOVAs were done separately for each duck species and their respective γ , and for each year because of differences in sampling design between years. Landscape parameters did not differ between years, but four study areas were censored from 1995 analyses because no duck counts were conducted.

We included γ as a response variable to assess the effect of landscape variables because γ adjusts for a variety of effects such as geographic within-year and/or year effects. In the calculation of γ , predicted numbers (the denominator) is based on water available in each basin. We examined various regression models using PROC GLM (SAS Institute, Inc., 1997), incorporating PERCROP, PERGRASS, TOTDRAIN, and PCTNMOD.

TABLE I

Analysis of variance results and least squares means (LSMEANS) estimates of landscape variables among 45 study areas in the Coteau, Drift Plain, and Red River Valley regions of North Dakota, 1995–1996. LSMEANS within species for each year having the same letter superscript are not different ($P > 0.05$)

Variable	F	P	LSMEANS		
			Coteau	Drift Plain	Red River
PERCROP (%)	4.29	0.02	53.5 ^a	69.9 ^b	78.7 ^b
PERGRASS (%)	14.29	<0.01	42.0 ^c	22.4 ^b	7.9 ^a
TOTDRAIN* (m)	5.63	0.01	3416 ^a	11848 ^b	7931 ^{ab}
PCTNMOD (%)	3.63	0.04	0.038 ^a	0.103 ^b	0.122 ^b
TOTBASIN (no.)	15.93	<0.01	507.0 ^a	764.4 ^b	128.6 ^c
BASAREA (ha)	7.97	<0.01	334.8 ^b	412.9 ^b	127.7 ^a
TEMPCID*	6.37	<0.01	0.14 ^a	0.40 ^b	1.18 ^a
SEASCID*	5.84	0.01	0.39 ^a	0.51 ^a	0.17 ^b
SEMICID*	0.38	0.69	0.37	0.43	0.30
ALLADJC (%)	11.46	<0.01	34.1 ^a	62.4 ^b	43.0 ^a
ALLADJG (%)	23.37	<0.01	57.4	26.9	20.1

* Back-transformed LSMEANS.

4. Results

4.1. LANDSCAPE VARIABLES

All landscape variables except SEMICID and ALLADJG varied significantly among regions ($P < 0.05$) (Table I). Most measures of wetland basins and upland habitat indicated that study areas in the Red River Valley had the most disturbed and the Coteau the least disturbed conditions. The Red River Valley had the lowest TOTBASIN and BASAREA and also a high level of modification to basins (PCTNMOD, TOTDRAIN); however, neither of the latter variables differed between the Red River Valley and the Drift Plain, and TOTDRAIN actually was highest in the Drift Plain. PERCROP declined from the Red River Valley to the Coteau, whereas PERGRASS increased across these regions. ALLADJC did not follow the pattern for PERCROP as expected; it was higher in the Drift Plain than in the other two regions.

4.2. ESTIMATED BREEDING PAIRS

Estimated numbers of breeding pairs also differed among regions each year, and differences were similar between years (Figure 2). Estimated numbers of all species combined (expressed as LSMEANS) were highest in the Coteau (1404 and 1233

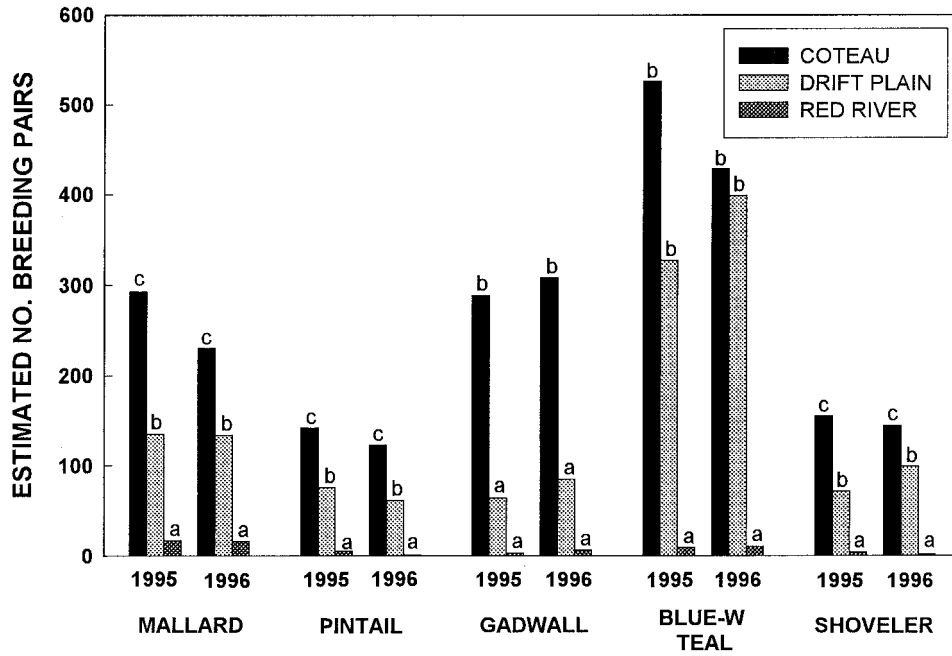


Figure 2. Least squares means (LSMEANS) for estimated numbers of breeding duck pairs among 45 study areas in the Coteau, Drift Plain, and Red River Valley regions of North Dakota, 1995–1996. LSMEANS within species for each year having a different letter label are significantly different ($P > 0.05$).

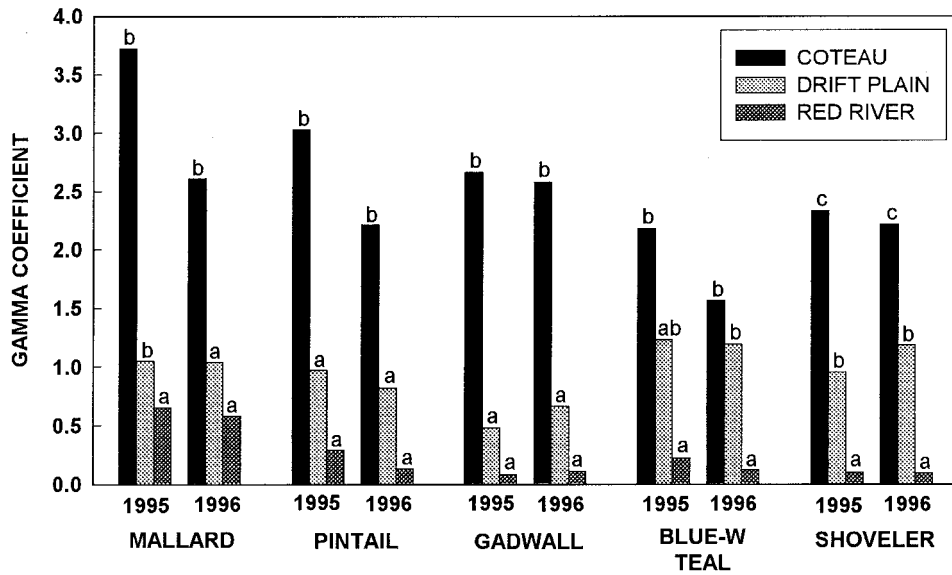


Figure 3. Least squares means (LSMEANS) for gamma (γ) coefficients among 45 study areas in the Coteau, Drift Plain, and Red River Valley regions of North Dakota, 1995–1996. LSMEANS within species for each year having a different letter label are significantly different ($P > 0.05$).

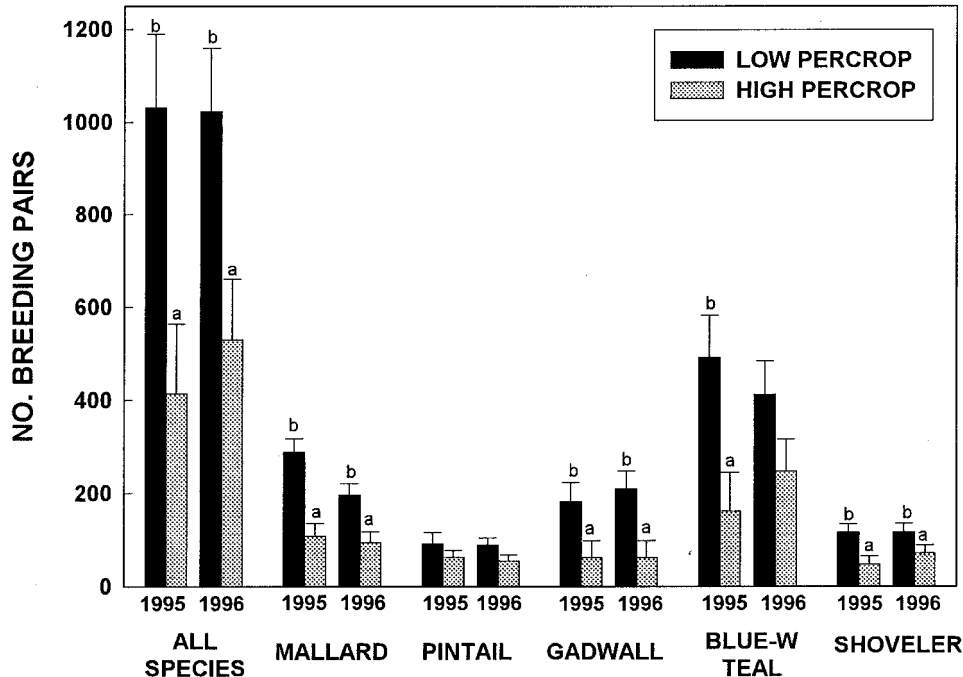


Figure 4. Effects of high or low levels of cropland, as a percentage of total upland habitat (PERCROP), on estimated numbers of breeding pairs in 45 study areas in North Dakota, 1995–1996. Median value of PERCROP was 71.45 (1995) and 73.18 (1996); study areas having less or more PERCROP than the median value were classified as Low or High, respectively. LSMEANS within species for each year having a different letter label are significantly different ($P > 0.05$; see also Table II).

in 1995 and 1996, respectively), intermediate for the Drift Plain (618 and 778), and lowest in the Red River Valley (35 in both years) ($P < 0.01$). Except for blue-winged teal, estimated numbers of pairs were usually twice as high in the Coteau than in the Drift Plain, while estimated numbers in the Red River Valley were <12% of estimated numbers in the Drift Plain (Figure 2). Similar patterns were found for γ , with the highest values in the Coteau and the lowest values in the Drift Plain (Figure 3).

PERCROP was a significant factor affecting estimated numbers of pairs for most species and years, but it often interacted with other factors (Table II, Figure 4). It was not a significant factor for estimated numbers of pintails (both years), blue-winged teal (1996), or shovelers (1996). PERCROP was the single landscape variable affecting estimated number of pairs in 1995 for all species combined, blue-winged teal, and shovelers. Estimated numbers for these species were consistently higher with low PERCROP than with high PERCROP (Figure 4).

Interactions were detected between PCTNMOD and PERCROP for mallards (both years) and between PCTNMOD and TOTDRAIN for pintails in 1996 (Table

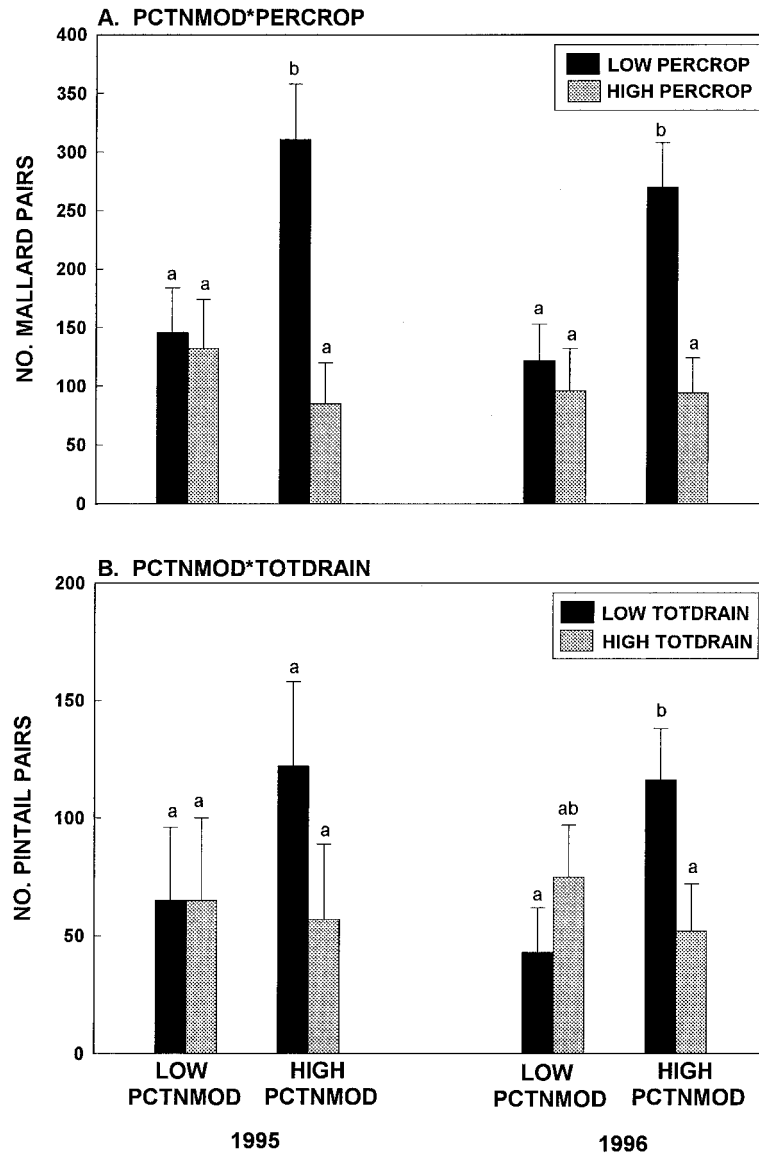


Figure 5. Interactions between percent of modified wetlands (PCTNMOD) and (A) percent of total upland habitat (PERCROP) for number of mallard pairs and (B) between PCTNMOD and total number of wetlands drained (TOTDRAIN) for number of pintail pairs. Median values used to determine high and low categories of landscape variables were: 0.063 for PCTNMOD; 71.45 (1995) and 73.18 (1996) for PERCROP; and 7409 for TOTDRAIN. LSMEANS within species for each year having a different letter label are significantly different ($P > 0.05$; see also Table II).

TABLE II

Analysis of variance results (*P* values) of the effect of three landscape variables on estimated numbers of breeding pairs and gamma (γ) coefficients for 45 study areas in North Dakota, 1995–1996

Response variable	Year	PCTN-MOD	PER-CROP	TOT-DRAIN	PCTNMOD* PERCROP	PCTNMOD* TOTDRAIN	PERCROP* TOTDRAIN
<i>Estimated number of breeding pairs</i>							
All species	1995	0.53	< 0.01	0.86	0.72	0.20	0.15
	1996	0.10	< 0.01	0.92	0.23	0.34	0.05
Mallard	1995	0.15	< 0.01	0.17	0.02	0.35	0.05
	1996	0.04	< 0.01	0.58	0.03	0.49	0.11
Pintail	1995	0.46	0.41	0.33	0.86	0.34	0.11
	1996	0.24	0.10	0.45	0.29	0.03	0.22
Gadwall	1995	0.40	0.03	0.18	0.14	0.13	0.04
	1996	0.13	< 0.01	0.15	0.16	0.19	0.05
Blue-winged teal	1995	0.78	0.01	0.20	0.66	0.66	0.94
	1996	0.26	0.11	0.40	0.74	0.94	0.20
Shoveler	1995	0.93	< 0.01	0.75	0.62	0.06	0.10
	1996	0.42	0.09	0.77	0.37	0.21	0.04
<i>Gamma coefficients</i>							
Mallard	1995	0.48	0.51	0.09	0.18	0.43	0.72
	1996	0.72	0.04	0.17	0.12	0.64	0.50
Pintail	1995	0.49	0.66	0.18	0.79	0.74	0.39
	1996	0.87	0.11	0.55	0.35	0.52	0.85
Gadwall	1995	0.84	0.09	0.13	0.21	0.43	0.12
	1996	0.27	< 0.01	0.11	0.11	0.28	0.13
Blue-winged teal	1995	0.88	0.03	0.18	0.14	0.67	0.37
	1996	0.62	< 0.01	0.34	0.67	0.78	0.34
Shoveler	1995	0.36	0.02	0.59	0.50	0.45	0.70
	1996	0.55	0.08	0.86	0.29	0.49	0.22

PCTNMOD = proportion of basins modified and/or drained, an indicator of partially or wholly drained basins. PERCROP = cropland as a percentage of total upland habitat. TOTDRAIN = total linear drainage length, an indicator of drainage intensity.

II, Figure 5). Estimates of mallard pairs were higher with high PCTNMOD and low PERCROP in both years, but there was no difference by PERCROP when PCTNMOD was low (Figure 5a). The interaction of landscape factors was more complex for pintails (Figure 5b). In 1996, estimates of pintail pairs were higher

TABLE III

Interactions between total drainage length (TOTDRAIN) and percentage of total upland habitat (PERCROP) for number of breeding pairs. Median values used to determine high and low categories of landscape variables were 71.45 (1995) and 73.18 (1996) for PERCROP; and 7409 for TOTDRAIN. LSMEANS within species for each year having the same letter superscript are not significantly different ($P > 0.05$). Only those species and years in bold had significant interactions (see Table II). Sample sizes noted for All species remained the same for individual species

Interaction	PERCROP	TOT- DRAIN	1995		1996	
			LSMEAN	SE (n)	LSMEAN	SE (n)
All species	Low	Low	1215 ^b	205 (13)	1223^c	174 (14)
		High	846 ^b	245 (7)	824^{bc}	213 (8)
	High	Low	269 ^a	233 (8)	351^a	201 (9)
		High	559 ^a	183 (13)	710^{ab}	166 (14)
Mallard	Low	Low	299^b	38	233 ^b	31
		High	158^a	47	159 ^b	38
	High	Low	95^a	44	76 ^a	36
		High	122^a	33	113 ^a	30
Pintail	Low	Low	136 ^a	31	110 ^a	19
		High	47 ^a	39	68 ^a	23
	High	Low	52 ^a	36	49 ^a	22
		High	74 ^a	27	59 ^a	18
Gadwall	Low	Low	275^b	48	302^b	49
		High	89^a	63	116^a	60
	High	Low	41^a	56	47^a	57
		High	82^a	46	77^a	47
Blue-winged teal	Low	Low	409 ^b	110	436 ^a	92
		High	575 ^b	141	388 ^a	112
	High	Low	89 ^a	125	140 ^a	106
		High	236 ^a	105	357 ^a	88
Shoveler	Low	Low	135^b	23	141 ^b	24
		High	100^{ab}	28	93 ^{ab}	30
	High	Low	23^a	27	39 ^a	28
		High	73^a	21	103 ^{ab}	23

when TOTDRAIN was low and PCTNMOD was high but the pattern was reversed for high PCTNMOD.

Interactions also were detected between PERCROP and TOTDRAIN for all species combined (1996), mallards (1995), gadwalls (both years), and shovellers (1996) (Table III). Estimated numbers of pairs of all species combined was lowest with high PERCROP and low TOTDRAIN, and highest with low PERCROP.

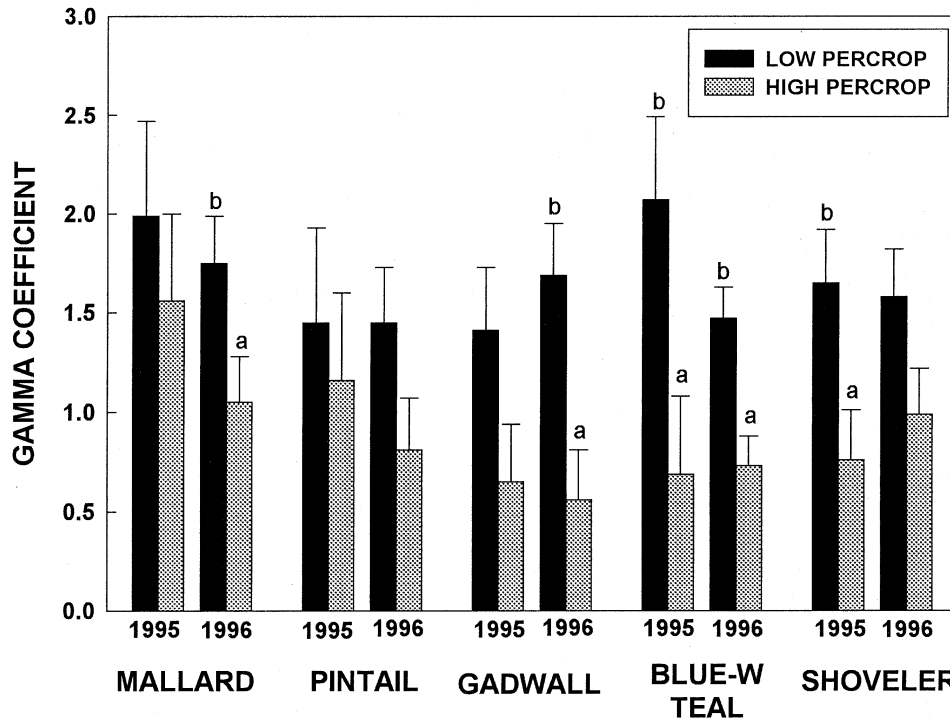


Figure 6. Effects of high or low levels of cropland, as a percentage of total upland habitat (PERCROP), on gamma (γ) coefficients, on 45 study areas in North Dakota, 1995–1996. Median value of PERCROP was 71.45 (1995) and 73.18 (1996); study areas having less or more PERCROP than this median value were classified as Low or High, respectively. LSMEANS within species for each year having a different letter label are significantly different ($P > 0.05$; see also Table II).

Estimates of mallard and gadwall pairs were highest with low PERCROP and low TOTDRAIN but TOTDRAIN did not affect estimates when PERCROP was high.

Only PERCROP affected γ , and the results were inconsistent among years and species. The effect of PERCROP was significant for mallards and gadwalls in 1996, blue-winged teal in both years, and shovelers in 1995. No interactions were significant. Values of γ were consistently higher when PERCROP was low (Figure 6).

We examined various regression models to predict number of breeding pairs or γ using four landscape variables (PERCROP, PERGRASS, PCTNMOD, and TOTDRAIN) for each year separately. Most models yielded $R^2 < 0.20$ (Table IV). Models for estimated numbers of breeding pairs of all species yielded R^2 of 0.20–0.22. The strongest model for any single species was that for shovelers in 1995 ($R^2 = 0.38$). Model results for breeding pairs were inconsistent between years except for gadwall. Model results for γ were more consistent, with PERGRASS predominating as the single factor contributing to all models except for mallards in 1995.

TABLE IV

Regression models to explain number of breeding pairs and gamma coefficient (γ) based on four landscape variables (percentage of total upland habitat (PERCROP), percentage of total upland habitat (PERGRASS), total number of wetlands drained (TOTDRAIN), and percent of modified wetlands (PCTNMOD)). For each year, only the models yielding the highest R^2 values are given

Response variable	Year	Terms in model	Unadjusted R^2
<i>Estimated numbers of breeding pairs</i>			
All species	1995	PERGRASS, TOTDRAIN, PERGRASS*TOTDRAIN	0.29
		PERGRASS	0.29
	1996	PERGRASS, PCTNMOD	0.22
Mallard	1995	PERGRASS, PCTNMOD, TOTDRAIN, PERGRASS*PCTNMOD, PERGRASS*TOTDRAIN	0.32
	1996	PERGRASS, PCTNMOD, PERGRASS*PCTNMOD	0.17
Pintail	1995	PERGRASS	0.10
		PERGRASS, PCTNMOD, TOTDRAIN, PCTNMOD*TOTDRAIN	0.10
Gadwall	1995	PERGRASS, TOTDRAIN, PERGRASS*TOTDRAIN	0.29
		PERGRASS, TOTDRAIN, PERGRASS*TOTDRAIN	0.30
Blue-winged teal	1995	PERGRASS	0.16
		PERGRASS, TOTDRAIN, PERCROP*TOTDRAIN	0.11
Shoveler	1995	PERGRASS, PCTNMOD, TOTDRAIN, PERGRASS*TOTDRAIN, PCTNMOD*TOTDRAIN	0.38
		PERGRASS, TOTDRAIN, PERGRASS*TOTDRAIN	0.15
	1996	PERGRASS, TOTDRAIN, PERGRASS*TOTDRAIN	0.15
<i>Gamma coefficient</i>			
Mallard	1995	TOTDRAIN	0.12
		PERGRASS, PCTNMOD, PERGRASS*PCTNMOD	0.18
Pintail	1995	PERGRASS	0.08
		PERGRASS	0.07
Gadwall	1995	PERGRASS	0.25
		PERGRASS, PCTNMOD, PERGRASS*PCTNMOD	0.32
Blue-winged teal	1995	PERGRASS	0.10
		PERGRASS	0.32
Shoveler	1995	PERGRASS	0.36
		PERGRASS	0.22

5. Discussion

Both estimated numbers of pairs and γ indicate most areas in the Coteau are more attractive to breeding ducks than areas in the Drift Plain, followed by areas in the Red River Valley. Regional differences were present in both response and explanatory variables. Geographic differences in soils and climate contribute to regional differences in the landscape variables by their influences on agricultural activities and landowners' ability to drain wetlands. However, regional differences in estimated numbers of pairs should be interpreted with caution. The distributions of some species, most notably pintail, gadwall, and shoveler, display an east-west trend which likely relates to a complex interaction of geologic and wetland features. Cowardin and Sklebar (1997) anticipated this interaction of duck numbers with geography. Thus within-year analyses using estimated numbers of pairs as an indicator of landscape condition probably are not appropriate, but comparisons among years for a specific area as part of a long-term monitoring program should not be influenced by geographic differences in duck distribution.

Regression models demonstrated the impact of agricultural development on breeding duck populations in the PPR. PERCROP and PERGRASS were included in most models, as suggested by the exploratory ANOVA tests, but models were inconsistent among years and species. These results suggest there are landscape effects on waterfowl breeding pairs, but the relations are more complex than we were able to examine here. Models using numbers of pairs or γ may be improved with the incorporation of other factors not considered in this study, such as habitat fragmentation.

PERCROP significantly affected total number of duck pairs as anticipated (more ducks were present when PERCROP was low) and contributed to the best regression models. In 1996, this relation was complicated by an interaction with TOTDRAIN. The response of individual species was more complex and, except for blue-winged teal, included interactions with PCTNMOD and TOTDRAIN. Cowardin and Sklebar (1997) noted species differences but did not conduct tests to compare among species. Differences in species biology and habitat selection contribute to these differences among species and the greater complexity in response. The lack of a significant effect of PERCROP for pintails may reflect the greater use of cropland by nesting pintails (Greenwood *et al.*, 1995) or be confounded by the east-west trend noted above. Annual differences in significant effects within species makes it difficult to explain interactions and reduces our confidence in using species-specific measures as good indicators of landscape condition. A longer study may clarify what other factors are contributing to these patterns or the nature of the relations among these variables.

We included γ as a response variable in our analyses as an alternative measure of duck response to landscape conditions. Cowardin *et al.* (1995) developed baseline regression equations for the five duck species to predict breeding pairs as a function of pond size, based on data collected in the Arrowwood Wetland

Management District under moderate water conditions. The correction factor, γ (the ratio of observed to predicted number of ducks), allows for adjustment of these original regressions for each area and year. Because 'predicted' breeding pairs is based on ponds by size in the study area that year, γ effectively adjusts for annual or area-related differences in the response of duck pairs to ponded wetlands by area. Where γ is <1 , as found consistently in the Red River Valley and many Drift Plain study areas, fewer ducks are present in an area than predicted given those wetland conditions. This would suggest other factors are contributing to the relative lack of ducks, such as landscape factors or wetland regime. The magnitude of γ therefore may provide a useful measure of the landscape condition for ducks, given those wetland conditions. However, of the landscape variables examined, only PERGRASS showed any significant effect, and the results were not consistent among species or years. The curvilinear relation between mallard pairs and pond area varies with wetland regime (Cowardin *et al.*, 1988a), suggesting that better results might be obtained if γ specific to seasonal wetlands were used rather than γ 's from all wetland regimes combined, as used here.

Under the systematic sampling scheme used here, the distribution of landscape variables tended to be clumped toward one end of the range. For example, the median of PERCROP in this study was 73.2%, and only four study areas had $<33\%$ of upland habitat in cropland. In comparison, the Prairie Pothole Pilot Study I used study areas specifically selected to provide two non-overlapping extremes: the median value of cropland in cropland-dominated areas was 91.5% whereas that for grassland-dominated areas was 23.9% (Cowardin and Sklebar, 1997). Although it would have been desirable to have better representation of grassland-dominated areas in this study, the systematic sampling results reflect the dominance of annual-crop agriculture in the entire glaciated region of North Dakota. To better examine the relation between landscape variables and duck numbers, we need to select areas which would provide a more uniform distribution of the landscape variables of interest. The split of landscape variables into high versus low values in our analyses was artificial but allowed exploratory analyses of relations between estimated numbers of pairs and the selected explanatory variables.

Before the results of this study are used for monitoring landscape condition, several caveats should be considered. First, the study was conducted during two wet years, when number of basins holding water and basin size were high compared to the average. In 1996, the Palmer Hydrological Drought Index averaged 4 (on a scale of -8 to $+8$, 0 being normal) (National Climate Data, 1998), and May pond numbers in the north-central U.S. in 1995 and 1996 were at record highs (U.S. Fish and Wildlife Service, 1997). We anticipate that the relations found here would differ under different water conditions, particularly in dry years. Other waterfowl studies that have categorized years as wet, moderate, or dry have found breeding duck responses differ relative to water conditions (e.g., Sorenson, 1991; Serie *et al.*, 1992; Anderson *et al.*, 1997). Second, numbers of breeding pairs available to settle in an area can be constrained by the population available. Johnson (1996)

found numbers of blue-winged teal and pintails in a North Dakota area were correlated to their continental breeding population. Populations of prairie-breeding ducks change over time and, for some species, recent population changes have been dramatic. Gadwall numbers increased >200% and pintail numbers declined by 40% over the past 10 yr (U.S. Fish and Wildlife Service, 1997). Such changes likely influence the numbers of pairs present annually on specific areas. Comparisons of estimated duck numbers among areas within a single year would not be affected by this, but it would be a factor in temporal trend analyses. Our understanding of how changes in the continental population influence local numbers, and at what scale such an effect can be detected, is poor and those relationships likely vary with species.

Naugle *et al.* (1999) demonstrated that life history characteristics also should be taken into account when considering wetland species as indicators of local or landscape-level conditions. Black terns (*Chlidonias niger*), a mobile species that forages in multiple wetlands, had smaller area requirements in heterogeneous than in homogeneous landscapes and were more likely to occur in landscapes where grasslands had not been tilled for agricultural production. In contrast, the occurrences of two sedentary species that forage largely or entirely within their nesting wetlands (pied-billed grebe (*Podilymbus podiceps*) and yellow-headed blackbird (*Xanthocephalus xanthocephalus*)), were explained solely by within-patch variation in wetland measures. Average home ranges and habitat use patterns for ducks also vary among species due to differing life-history characteristics. The scale of measurements likely will affect the relationships between duck occurrence and landscape measures, but this issue has not been adequately addressed. Biologists need to consider the significance of life-history characteristics, and the scale at which those characteristics are expressed, when selecting species to include in studies monitoring wetland conditions. Multispecies approaches should consider including species representing a range of characteristics appropriate to the scale of interest.

The intent of this study was to test whether waterfowl breeding populations could be used as a biotic indicator for monitoring the status and long-term trends of ecological resources in the region (Peterson, 1994). Resources needed to monitor either landscape features or waterfowl, following methods used here, include acquisition of aerial photographs each spring and extensive GIS processing; waterfowl monitoring also requires support of field personnel during May. Although it may appear to be more cost-effective to simply monitor the percentage of cropland in upland habitat, we estimate GIS processing effort for water data, needed to extrapolate duck counts from the roadside transect surveys, is approximately 5–6 times lower than the effort needed to determine the percentage of cropland in upland habitat. This savings more than outweighed the costs associated with field work. Thus using waterfowl as an indicator remains a more cost-effective approach.

In conclusion, our results suggest there are landscape effects on waterfowl breeding pairs but the relations are complex. Our results are confounded by the geo-

graphic differences in upland habitat which are largely the result of geologic and climatic factors. Percentage of cropland in upland habitat, originally considered a proxy to wetland habitat condition, does have the most consistent effect on the waterfowl measures examined, but this variable is among the most strongly influenced by geographic location. Most of the potential biotic indicators of wetland condition examined here would be appropriate for temporal trend analyses, but because of inherent geographic variability would not be appropriate for single-year geographic trend analyses with out more extensive evaluations to improve explanatory models.

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