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Waterfowl–wetland relationships in the Aspen Parkland of British Columbia: comparison of analytical methods

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Abstract

We explored the relationships between aquatic bird abundance and various pond features (physical and chemical) using data from 112 ponds located in the Aspen Parkland of British Columbia. As expected, pond size was the most important factor influencing the number of aquatic birds present. Total dissolved nitrogen, conductivity and calcium were positively associated with the abundance of several species whereas chloride tended to be negatively associated. The abundance of dabbling ducks was positively associated with turbidity and total dissolved nitrogen and negatively with percent of forested shoreline, percent of marsh and chloride. The abundance of diving ducks was associated positively with pond depth, conductivity and total dissolved nitrogen and negatively with percent of marsh and phosphorus levels. Pond area influenced more the abundance of diving ducks than dabbling ducks. Relationships between bird density and pond features were affected significantly by the area unit used to calculate density. For example, the density of Bufflehead (*Bucephala albeola*) was correlated positively with pH and conductivity when expressed per area of water 0–2 m deep but negatively when expressed per total area of pond. Results highlight the problems associated with interpreting correlative type studies especially the difficulties in assessing the biological significance of the observed correlations. It underscores the urgent need for experimental approaches to bird-habitat studies.

In recent years progress has been made in our understanding of the relationships between habitat features and bird diversity and abundance in aquatic systems (Patterson, 1976; Danell & Sjobert, 1978; Nilsson & Nilsson, 1978; Mack & Flake, 1980; Godin & Joyner, 1981; Tallent *et al.*, 1982; Mulhern *et al.*, 1985). However, most of these studies dealt with only a few species of dabbling ducks and occurred mostly in prairie potholes. Information of habitat relationships and abundance of aquatic birds in the Aspen Parkland of Canada is limited, especially regarding diving ducks. Such information is needed to develop habitat evaluation models for assessment, acquisition and management purposes (Larson, 1976; Reppert *et al.*, 1979).

From 1980 to 1986, during an intensive study of the ecology of Barrow's Goldeneye (*Bucephala islandica*) (Savard, 1987, 1988a, b), data were collected on the abundance of aquatic birds and the physical characteristics of 112 ponds in the Aspen Parkland of British Columbia. Although incidentally collected, these data permitted an exploratory analysis of the relationships between pond features and waterfowl abundance. The data collected has been presented in several technical reports (Boyd & Savard, 1987, Boyd & Smith, 1989; Boyd *et al.*, 1989; Savard, 1991). In this paper we pursue further the analysis, exploring the relationships between aquatic birds and pond features and comparing some analytical techniques. We focus especially on the effect of the area unit used to express bird density on the relationships with habitat features, and highlight the interpretation problems related to correlative studies.

Methods

Study area

The study area is located in the Cariboo Parklands biotic area (Munro, 1945; Munro & Cowan, 1947) located in the Interior Douglas Fir zone of British Columbia (Krajina, 1965), one of the most productive regions for waterfowl in the province (McKelvey & Munro, 1983). The 112 ponds surveyed are located within a 150 km^2 area near Riske Creek on the Fraser plateau in south-central B.C. This region is characterized by severe winters and warm summers ranging from daily means of −11.6 °C in January to 13.7 °C in July (Topping & Scudder, 1977). Vegetation is typically open grassland with mixed stands of Douglas fir, lodgepole pine and aspen (Munro, 1947).

The ponds surveyed differed greatly in size and chemical composition (Table 1). Topping & Scudder (1977) present a detailed chemical analysis of 12 of these ponds, and Boyd & Savard (1987) and Boyd *et al.* (1989) summarized the most important chemical and physical factors of all 112 ponds. All ponds are devoid of fish and most support high densities of invertebrates (Scudder, 1969; Reynolds, 1979; Boyd & Smith, 1989).

Table 1. Range of values between ponds of the variables measured.

	Minimum	Maximum
Maximum pond depth	0.5 m	5.3 m
% marsh	0%	88%
% forest	0%	93%
Conductivity (COND)	42 μmhos	17050 μmhos
Ph	7.0	10.1
Hardness (TALKA)	11 ppm	4830 ppm
Nitrogen (NN)	0 ppm	0.13 ppm
Total dissolved nitrogen (TDNIT)	0.1 ppm	18.4 ppm
Calcium (CAL)	0 ppm	563 ppm
Phosphorus (TPHOS)	0.03 ppm	19.4 ppm
Sulphur	0.2 ppm	19100 ppm
Magnesium	2 ppm	1130 ppm
Chloride	0.3 ppm	690 ppm
Turbidity (TURB)	0.5 units	67 units
Total pond area	0.2 ha	10.16 ha
Area 0–1 m	0.2 ha	22.92 ha
Area 0–2 m	0.2 ha	22.92 ha

Physical characteristics

Depth profiles were determined for all wetlands in 1983, an average year in terms of precipitation. Water depth was determined from a canoe, along grids or to/from prominent shoreline features using a weighted rope calibrated every 10 cm. Distance from shore was estimated using canoe lengths. These transects were used to derive contour maps (Boyd & Savard, 1987). Areas for all contour intervals were calculated. Colour airphotos (Scale 1:5000) taken in September 1983 were used to calculate marsh area and to quantify surrounding upland vegetation.

Chemical characteristics

Water samples were collected from 92 of the 112 wetlands in July 1982, June 1983 and August 1983. Samples were taken at waist depth by immersing plastic bottles 10 cm under the water surface and were analyzed in the field within 48 hours. Conductivity and salinity were determined using a S-C-T Meter (Yellow Springs Instrument Co.) and calcium, sodium and pH using a Specific Ion Meter (Orion Research Inc.). In September 1984, we collected water samples from the same wetlands, using sterilized bottles. Those samples were shipped on ice to the Inland Waters Directorate laboratory (Environment Canada, N. Vancouver, B.C.) where they were analyzed, using standard methods, for the following: hardness, magnesium, chloride, sulphate, nitrate nitrogen, total dissolved nitrogen, total phosphorus and turbidity.

Bird surveys

Surveys were conducted from April to August 1980 to 1986. To minimize bird movements among ponds, adult counts were done from vantage points and no efforts were made to flush birds concealed in vegetation. Most ponds (>90%) lacked or had only a narrow (<1 m) zone of emergent vegetation which greatly facilitated counts. The frequency and intensity of counts varied among years (Savard, 1991). Fluctuations in the number of males was used to determine, for each species, the counts that best represented the breeding population of the area, (Savard, 1991). Only these counts were used to calculate the average number of birds seen on a given pond. Because of different breeding phenologies, sample sizes differed among species, ranging between 4 and 15 counts. Because waterfowl counts on given ponds are more variable between years than chemical and topographic features we use an average estimate (over 5 years) of bird use to compare with our unique measurement of habitat features taken on an average year.

Analysis

In an earlier analysis (Boyd *et al.*, 1989), we used principal components and multiple regression to tease out relationships between bird abundance and pond features. There was, as expected, a strong area effect for all species and there was indication that some of the relationships were not linear. It is clear from the data that the factor most affecting bird abundance is the size of the pond. To study the relationship between bird abundance and other habitat variables, we must account for the effect of size. Unfortunately, the determination of other bird-habitat relationships is to some extent dependent upon how we account for dependence on size.

Density measures

To compare the effect of different measures of density on the results, we expressed bird density using four different measures of area: 1) area of water between 0 and 1 m in depth; 2) area of water between 0 and 2 m in depth; 3) area of water between 0 and 3 m in depth; and 4) total area of open water. We then ran Pearson's correlations between bird densities and physical and chemical pond characteristics (Table 2).

Multiple stepwise regression

With regression analyses we used two techniques to account for the size of the wetland. First, we computed bird density based on area, and then regressed this on the habitat variables. This method removes the effect of area by division. Second, we included area as one of the habitat variables and forced it into the regression first using the actual number of birds as the dependent variable. This removes the effect of area by subtraction.

The next question is the measure of size we use? We tried two measures. The first was total area of the pond. The second was area of water less than 1 m deep for dabbling ducks, and less than 2 m deep for diving ducks, coots and grebes. Marsh area was not included in these area measurements.

In the following section, only the variables that met the minimum entry tolerance of 0.01 are presented up to a maximum of four (Table 3–5). Rarely was there more than four significant.

Bird density-pond feature relationships: ranking

Dabbling duck densities were expressed as number of birds per area of water less than 1 m in depth and diving duck densities in number of birds per area of water less than 2 m in depth, as we considered those depths as the most meaningful from an ecological point of view. We then ranked ponds according to bird density and divided them into 3 to 5 groups depending on the range in bird density. We calculated for each group the average value of each physical and chemical variable and its standard error and

Table 2. Correlations between various bird density estimates[1] and selected physical and chemical variables. (Samples size indicated in parentheses.)

Area used	Mean depth (112)	pH (112)	Cond (112)	CAL (112)	TALKA (92)	NN (92)	TDNIT (92)	TPHOS (92)	TURB (92)
Mallard									
0–1 m	0.18*[2]	0.04	−0.08	0.01	−0.09	−0.00	0.03	−0.15	0.11
0.2 m	−0.01	−0.12	−0.16*	0.01	−0.13	−0.04	−0.00	−0.13	0.14
0–3 m	−0.19**	−0.18*	−0.26**	−0.04	−0.21**	−0.07	−0.03	−0.12	0.13
T area	−0.26**	−0.44**	0.25**	−0.04	−0.22**	−0.09	−0.09	−0.12	0.07
Blue-winged Teal									
0–1 m	0.12	0.07	−0.12	−0.05	−0.18	0.04	0.01	−0.07	0.12
0–2 m	0.01	0.01	−0.18*	−0.06	−0.21**	0.05	−0.00	−0.02	0.17
0–3 m	−0.10	−0.02	−0.22**	−0.09	−0.24**	0.01	−0.01	0.00	0.17
T area	−0.28**	−0.32**	−0.30**	−0.10	−0.28**	−0.02	−0.08	−0.04	0.10
Barrow's Goldeneye									
0–1 m	0.40**	0.13	0.12	−0.09	0.12	−0.02	0.06	−0.07	−0.05
0–2 m	0.40**	0.14	0.13	−0.07	0.14	−0.04	0.05	−0.07	−0.03
0–3 m	0.39**	0.13	0.09	−0.08	0.09	−0.04	0.08	−0.08	−0.03
T area	0.16*	0.13	−0.00	−0.01	−0.03	−0.05	0.13	−0.10	0.02
Bufflehead									
0–1 m	0.53**	0.22**	0.25**	−0.19**	0.37**	−0.02	−0.03	−0.06	−0.21**
0–2 m	0.47**	0.16*	0.19**	−0.19**	0.32**	−0.04	−0.07	−0.05	−0.20*
0–3 m	0.37**	0.09	0.08	−0.17*	0.20*	−0.04	−0.10	−0.06	−0.22**
T area	−0.05	−0.25**	−0.18*	−0.06	−0.11	−0.04	−0.18*	−0.11	−0.21**

[1] Density estimates are based on all birds observed on the ponds divided by the area of water.
[2] * $P<0.10$; ** $P<0.05$. (These P values were not adjusted for multiple comparisons.)

looked for any patterns related to the density gradient. In Tables 6 to 8 we present the most significant variables for each species.

Results

Density measures

We present correlation results for four species and nine variables (Table 2). The significance, magnitude and direction of the correlations between the four density measures used and pond characteristics varied with the density unit used. With Mallards (*Anas platyrhynchos*) there was only one significant correlation when using 0–1 m and 0–2 m area but four when using 0–3 m and total area. Total area yielded the most significant correlations for Blue-winged Teal but the least for Bufflehead. Mallard and Blue-winged Teal densities were positively associated with water depth when expressed per 0–1 m area but negatively when expressed per 0–3 m or per total area. Similarly, Bufflehead density was positively associated with pH when expressed per 0–1 m or 0–2 m area, but negatively when expressed per total area. In other cases the strength of the correlation changed but not the direction.

These results underscore the importance of the unit selected to express density and also the difficulty associated with assessing the biological significance of the correlations observed. Total area of a pond or a lake is the most commonly used unit to express waterbird density as it is easily measured. It may be useful in comparing densities between areas but it may be inappropriate when trying to relate bird densities to pond features. For example, would a Mallard be influ-

Table 3. Stepwise multiple regression on dabbling ducks ($n = 92$ ponds). Only variables meeting the minimum entry tolerance of 0.01 are presented up to a maximum of four (area not counted as a variable). Each numerical entry in the table represents the percent of the total variance that each variable explained when it entered into the regression equation. The sign (+ or −) indicates whether the regression coefficient was positive or negative.

Area of water 0–1 m deep		Area of open water	
Density	Area forced[3]	Density	Area forced
Green-winged Teal	(area 19)		(area +18)
% Marsh −2	% Marsh −6	Depth −17	Phosphorus +4
pH −5	Calcium −2	pH −8	
Tdisnitr. +3	Conductivity +2		
Sulphur −5	pH −3		
Mallard	(area +30)		(area +41)
Phosphorus −6	Depth +12	Depth −27	Phosphorus −4
% Marsh −5	Phosphorus −4	pH −9	Turbidity +2
pH −4	Turbidity +4	Phosphorus −5	Turbidity +2
Turbidity +2	pH −1	% Forest +1	
Northern Pintail	(area +15)		(area +13)
% Marsh −14	% Marsh −7	Magnesium −15	Turbidity +10
Turbidity +6	Turbidity +5	Forest −9	Forest −3
% Forest −2	Forest −2	Calcium −6	Nitrogen −2
Depth +2		Chloride −2	
Blue-winged Teal	(area +18)		(area +16)
Chloride −13	Chloride −5	Depth −22	Chloride −8
% Forest −5	Conductivity +5	Conductivity −	% Forest −9
Depth +5	% Forest −4		Tdisnitr. +3
Tdisnitr +3	Depth +5		
Northern Shoveler	(area +32)		(area +23)
Tdisnitr. +18	Phosphorus +15	Depth −20	Phosphorus +21
% Forest −7	Tdisnitr. +6	Nitrogen −6	Tdisnitr. +5
% Marsh −4	Forest −2	Forest −7	Depth −4
	Conductivity +2	Calcium −4	% Forest −2
Gadwall	(area +10)		(area +11)
Tdisnitr. +18	Tdisnitr. +17	Depth −6	Tdisnitr. +17
Magnesium −5	Magnesium −9	% Marsh −5	Calcium −14
Nitrogen +4	Calcium −5	Forest −8	Forest −2
% Marsh −2	Hardness +4		
American Wigeon	(area +10)		(area +19)
% Marsh −10	Marsh −15	Depth −9	% Marsh −7
Chloride −6	Tdisnitr. +3	Conductivity −3	Tdisnitr. +3
Tdisnitr.[1] +3	Phosphorus −2		Chloride −3
	Calcium −2		Calcium −2
Total dabbling ducks	(area +34)		(area +36)
Chloride −5	% Marsh −10	Depth −36	Turbidity +6
Tdisnitr. +8	Tdisnitr +2	Conductivity −5	% Forest −2
Depth +6	Chloride −2	Chloride −2	Chloride −3
% Forest −2	Depth +2	Tdisnitr. +5	Tdisnitr +3

[1] Tdisnitr. = Total dissolved nitrogen.

[2] Nitrogen = nitrate nitrogen.

[3] Actual number of birds used as dependent variable

Table 4. Stepwise multiple regression on diving ducks ($n = 92$ ponds). Only variables meeting the minimum entry tolerance of 0.01 are presented up to a maximum of four (area not counted as a variable). Each numerical entry in the table represents the percent of the total variance that each variable explained when it entered into the regression equation. The sign (+ or −) indicates whether the regression coefficient was positive or negative.

Area of water 0–2 m deep		Area of open water	
Density	Area forced	Density	Area forced
Canvasback	(area +8)		(area +7)
% Marsh +3	% Marsh +5	% Forest −8	% Marsh +7
pH +6	pH +4	pH +3	pH +5
Depth +4	% Forest −2		% Forest −2
% Forest −4	Depth +3		Chloride −5
Redhead	(area +7)		(area +6)
% Marsh +3	% Marsh +4	% Marsh +12	% Marsh +6
Depth +4		Calcium +4	
% Forest −3			
Lesser Scaup	(area +30)		(area +38)
% Forest −9	Conductivity +7	Calcium +5	% Forest −7
Depth +9	Depth +4	% Forest −3	Calcium +2
Calcium +2	% Forest −6		
Turbidity +3	Chloride −2		
Barrow's Goldeneye	(area +25)		(area +48)
Depth +21	Depth +26	% Marsh −7	Depth +8
Tdisnitr.[1] +6	Conductivity +9	Calcium +3	Conductivity +6
Nitrogen[2] −3	Nitrogen −3		Phosphorus −2
Phosphorus −2	Phosphorus −4		Turbidity +3
Bufflehead	(area +41)		(area +58)
Depth +17	Depth +14	pH −4	Turbidity −4
Hardness −3	Chloride +3		Tdisnitr +1
Magnesium +2	Turbidity −3		Hardness −1
	Hardness −2		Conductivity +2
Ruddy Duck	(area +11)		(area +10)
% Forest −11	% Forest −10	% Marsh +10	% Forest −9
Turbidity −6	% Marsh +4	% Forest −6	% Marsh +7
Tdisnitr. +4	Depth +3	Depth +6	Tdisnitr. +3
Depth +2	Tdisnitr. +4	Calcium +2	Chloride −4
Total diving ducks	(area +47)		(area +66)
Depth +18	Depth +16	Calcium +6	Tdisnitr. +5
Tdisnitr. +6	Conductivity +6		Depth +3
Phosphorus −6	Tdisnitr. +1		Phosphorus −1
	Hardness −1		Conductivity +1

[1] Tdisnitr = Total dissolved nitrogen.
[2] Nitrate = Nitrate nitrogen.

enced by water areas that are deeper than 1 m, as they feed mostly in shallow water? Also, most waterfowl species defend territories associated with shorelines, *i.e.* it is rare to see a pair defend a territory solely surrounded by open water. Thus, biologically speaking, breeding dabbling ducks

Table 5. Stepwise multiple regression on American Coot and grebes ($n = 92$ ponds). Only variables meeting the minimum entry tolerance of 0.01 are presented up to a maximum of four (area not counted as a variable). Each numerical entry in the table represents the percent of the total variance that each variable explained when it entered into the regression equation. The sign (+ or −) indicates whether the regression coefficient was positive or negative.

Area of water 0–2 m deep		Area of open water	
Density	Area forced	Density	Area forced
Pied-billed Grebe	(area +2)		(area +1)
% Marsh +27	% March +25	% Marsh +29	% Marsh +26
Conductivity +3	Calcium +7	Conductivity +4	Calcium +27
Chloride −2		Calcium +2	
Horned Grebe	(area +14)		(area +20)
Calcium −7	Depth +7	Calcium −10	Phosphorus −4
Depth +7	Chloride +2	% Marsh +10	Chloride +3
Phosphorus −4	Phosphorus −5	Phosphorus −5	Hardness −2
Sulphur +5	Calcium −3	Sulphur +4	Magnesium +2
Eared Grebe	(area +22)		(area +17)
Phosphorus +14	Phosphorus +12	Calcium −7	Phosphorus +14
Calcium −4	Calcium −4	Conductivity +9	Calcium −4
Hardness +9	Magnesium +6		Magnesium +6
Turbidity −4	Turbidity −2		Turbidity −2
American Coot	(area +4)		(area +1)
% Marsh +32	% Marsh +24	% Marsh +35	% Marsh +24
Nitrogen[1] +7	Nitrogen +6	Calcium +6	Nitrogen +6
Magnesium +4	Magnesium +3	% Forest −3	Magnesium +3
Turbidity −4	Turbidity −1	pH +2	pH +1

[1] Nitrogen = Nitrate nitrogen.

should respond mostly to the areas of water between 0–1 m, whereas breeding diving ducks should be influenced by areas of deeper water, up to 2 m in depth.

Multiple stepwise regressions

All four analyses yielded similar results for species not strongly associated with pond size (American Wigeon, Gadwall, Redhead, Canvasback, Ruddy Duck, Coot and Pied-billed Grebe). The same variables were generally highlighted by the four analyses (Tables 3–5). Results for other species whose numbers were more correlated with pond size (Mallard, Barrow's Goldeneye, Bufflehead) often differed considerably depending on the analytical technique used. Use of density expressed per total area of water revealed a strong negative association with depth for most dabbling ducks. As most large ponds tended to be deeper than small ones, dividing by total lake area may have been too drastic a way of removing size effect. When density was expressed per area of water less than 1 m deep, depth was positively associated with the density of dabbling ducks. With diving ducks, use of density expressed per total area of water explained most of the variability of the data set and thus identified the fewest number of associations with other variables. Using multiple regression to remove area effect when using total pond area was better in terms of the number of other variables identified.

These attempts at removing the effect of lake size to identify the variables associated with waterfowl abundance, affected the results. The dif-

Table 6. Mean value (±SE) of selected physical and chemical pond variables in relation to density of dabbling ducks expressed per area of water between 0 and 1 m deep (n = number of ponds).

Green-winged Teal

Density	n	Total % Marsh	% Forest	Tdisnitrogen	Turbidity
0	15	19 ± 5	30 ± 7	1.4 ± 0.4	2.6 ± 1.1
0.01–0.50	36	29 ± 5	24 ± 4	2.8 ± 0.5	5.2 ± 1.3
0.51–1.00	24	16 ± 4	18 ± 4	3.0 ± 0.6	8.4 ± 3.1
1.01–2.00	25	14 ± 3	22 ± 4	2.3 ± 0.3	7.2 ± 2.4
> 2.00	12	2 ± 1	22 ± 6	3.6 ± 0.6	8.6 ± 3.6

Mallard

Density	n	Depth (m)	% Marsh	Conductivity	Phosphorus	Turbidity
0.01–0.50	26	1.8 ± 0.2	31 ± 6	2373 ± 560	1.5 ± 1.8	4.7 ± 1.6
0.51–1.00	33	2.1 ± 0.2	15 ± 3	2457 ± 626	0.9 ± 0.5	7.6 ± 2.5
1.01–2.00	31	2.2 ± 0.2	16 ± 3	1984 ± 356	0.5 ± 0.1	5.3 ± 1.4
2.01–4.96	19	2.6 ± 0.3	7 ± 3	1687 ± 396	0.5 ± 0.1	9.1 ± 2.8

Northern Pintail

Density	n	Conductivity	% Marsh	% Forest	pH	Turbidity
0	49	1382 ± 196	26 ± 3	30 ± 4	8.94 ± 0.07	3.2 ± 0.6
0.01–0.05	34	2677 ± 564	19 ± 4	21 ± 4	9.05 ± 0.15	7.7 ± 2.3
0.51–1.50	17	1890 ± 387	10 ± 4	18 ± 4	9.23 ± 0.12	9.0 ± 3.7
1.51–3.50	12	3995 ± 1342	1 ± 0	5 ± 3	9.39 ± 0.10	11.8 ± 3.5

Blue-winged Teal

Density	n	Depth (m)	% Marsh	Nitrate Nitrogen	% Forest
0.00–1.00	23	2.1 ± 0.3	29 ± 6	0.023 ± 0.006	28 ± 5
1.01–2.00	25	1.6 ± 0.2	28 ± 5	0.016 ± 0.005	24 ± 5
2.01–4.00	22	1.9 ± 0.2	17 ± 4	0.015 ± 0.004	22 ± 5
4.01–8.00	26	2.2 ± 0.2	10 ± 2	0.022 ± 0.006	19 ± 4
8.01–31.00	16	2.9 ± 0.2	6 ± 2	0.032 ± 0.010	20 ± 4

Northern Shoveler

Density	n	% Marsh	% Forest	Conductivity	Tdisnitrogen
0	31	23 ± 4	35 ± 4	1017 ± 151	1.8 ± 0.3
0.01–0.25	14	33 ± 7	31 ± 8	1860 ± 713	2.1 ± 0.3
0.26–0.50	18	21 ± 6	20 ± 6	1788 ± 424	2.4 ± 0.4
0.51–1.00	16	16 ± 4	14 ± 4	3273 ± 893	3.0 ± 0.4
1.01–2.00	17	15 ± 6	17 ± 5	2679 ± 950	3.7 ± 1.2
> 2.01	16	2 ± 1	9 ± 3	3195 ± 691	3.5 ± 0.3

Northern Shoveler

Density	n	Phosphorus	Turbidity	Chloride	Calcium
0	31	0.2 ± 0.1	4.3 ± 1.3	11 ± 6	105 ± 13
0.01–0.25	14	0.2 ± 0.1	2.9 ± 1.0	4 ± 24	118 ± 13
0.26–0.50	18	1.4 ± 1.1	4.7 ± 2.0	24 ± 8	92 ± 16
0.51–1.00	16	1.0 ± 0.3	4.3 ± 1.0	97 ± 48	77 ± 16
1.01–2.00	17	0.6 ± 0.2	10.1 ± 4.4	34 ± 15	73 ± 22
> 2.01	16	2.0 ± 0.9	13.2 ± 3.7	108 ± 50	99 ± 55

Gadwall

Density	n	% Marsh	pH	Conductivity	Turbidity	Tdisnitrogen
0	48	30 ± 4	8.89 ± 0.11	1328 ± 262	2.5 ± 0.4	1.5 ± 0.2
0.02–0.20	20	16 ± 5	9.04 ± 0.14	3561 ± 1046	3.5 ± 1.2	2.9 ± 0.5
0.21–0.50	21	10 ± 3	9.21 ± 0.11	2455 ± 482	13.2 ± 3.8	3.8 ± 0.9
> 0.50	23	5 ± 2	9.33 ± 0.08	2274 ± 354	10.7 ± 2.8	3.7 ± 0.3

American Wigeon

Density	n	% Marsh	Chloride	Tdisnitrogen	pH	Turbidity
0	7	38 ± 14	4 ± 2	1.1 ± 0.5	8.6 ± 0.2	1.9 ± 0.9
0.01–0.50	25	33 ± 7	74 ± 30	1.9 ± 0.3	8.8 ± 0.2	3.6 ± 0.9
0.51–1.00	25	14 ± 3	54 ± 26	3.3 ± 0.8	9.2 ± 0.1	9.5 ± 3.5
1.01–2.00	19	18 ± 4	64 ± 37	2.0 ± 0.4	9.3 ± 0.1	3.5 ± 7.1
2.01–4.00	21	11 ± 3	23 ± 10	3.1 ± 0.5	9.0 ± 0.1	9.0 ± 2.5
> 4.00	15	4 ± 1	23 ± 7	3.4 ± 0.5	9.2 ± 0.1	7.5 ± 2.9

Table 7. Mean values (± SE) of selected physical and chemical pond variables in relation to densities of diving ducks expressed per area of water between 0 and 2 m deep (n = number of ponds).

Canvasback

Density	n	% Marsh	% Forest	Depth (m)	Tdisnitrogen	Phosphorus
0	69	19 ± 3	24 ± 3	1.9 ± 0.1	2.5 ± 0.3	0.6 ± 0.1
0.01–0.12	15	10 ± 5	32 ± 7	3.1 ± 0.4	2.3 ± 0.4	1.5 ± 1.3
0.13–0.40	14	21 ± 7	16 ± 6	2.1 ± 0.3	3.1 ± 0.3	1.8 ± 1.1
> 0.40	14	22 ± 6	16 ± 5	2.2 ± 0.3	3.1 ± 0.8	0.4 ± 0.2

Redhead

Density	n	Depth (m)	Conductivity	Calcium	% Marsh	Nitrate Nitrogen
0	66	1.8 ± 0.2	2004 ± 356	93 ± 12	19 ± 3	0.016 ± 0.003
0.01–0.20	16	2.4 ± 0.4	3484 ± 878	70 ± 18	14 ± 5	0.022 ± 0.006
0.20–1.00	21	2.5 ± 0.2	1665 ± 274	105 ± 15	21 ± 5	0.031 ± 0.008
> 1.00	9	2.4 ± 0.3	1761 ± 366	126 ± 30	19 ± 8	0.029 ± 0.011

Lesser Scaup

Density	n	Depth (m)	% Marsh	% Forest	Conductivity	Nitrate Nitrogen
0	23	1.4 ± 0.2	38 ± 5	23 ± 3	893 ± 158	0.017 ± 0.010
0.01–0.50	25	2.2 ± 0.3	18 ± 5	33 ± 5	2046 ± 413	0.017 ± 0.003
0.51–1.00	19	2.0 ± 0.3	16 ± 5	33 ± 6	2544 ± 589	0.022 ± 0.006
1.00–2.00	21	2.1 ± 0.3	12 ± 3	7 ± 2	3417 ± 928	1.20 ± 0.007
> 2.00	24	2.7 ± 0.3	9 ± 3	17 ± 3	1959 ± 498	0.027 ± 0.008

Barrow's Goldeneye

Density	n	Depth (m)	% Marsh	pH	Tdisnitrogen	Conductivity
0	5	0.8 ± 0.1	55 ± 11	7.60 ± 0.16	0.5 ± 0.3	263 ± 105
0.01–0.50	21	1.6 ± 0.2	34 ± 6	8.73 ± 0.17	1.9 ± 0.3	1899 ± 487
0.51–1.00	18	1.8 ± 0.3	20 ± 5	9.27 ± 0.11	2.8 ± 0.6	1845 ± 651
1.01–2.00	28	1.9 ± 0.2	17 ± 3	9.27 ± 0.09	2.6 ± 0.7	1750 ± 369
2.01–4.00	23	2.3 ± 0.3	8 ± 3	9.18 ± 0.09	3.6 ± 0.4	2601 ± 780
4.01–10.00	11	3.4 ± 0.3	5 ± 2	9.17 ± 0.11	2.3 ± 0.5	3582 ± 856
> 10.00	6	3.4 ± 0.3	2 ± 1	9.23 ± 0.22	3.6 ± 0.6	2700 ± 1018

Bufflehead

Density	n	Depth (m)	% Marsh	Turbidity	Magnesium	Chloride
0	7	1.1 ± 0.3	45 ± 0	2.9 ± 2.2	175 ± 150	104 ± 98
0.01–0.50	31	1.5 ± 0.1	25 ± 5	9.5 ± 2.7	100 ± 37	20 ± 5
0.51–1.00	24	2.1 ± 0.3	18 ± 4	7.2 ± 2.7	112 ± 36	41 ± 17
1.01–2.00	27	1.9 ± 0.2	17 ± 3	5.2 ± 1.0	83 ± 16	32 ± 21
> 2.00	23	3.3 ± 0.3	5 ± 1	3.7 ± 1.4	60 ± 13	91 ± 32

Ruddy Duck

Density	n	% Marsh	% Forest	Conductivity	Tdisnitrogen
0	56	19 ± 3	28 ± 3	1412 ± 227	2.3 ± 0.4
0.01–0.25	24	13 ± 4	24 ± 5	4110 ± 896	2.8 ± 0.2
0.26–1.00	18	21 ± 5	17 ± 5	2053 ± 455	3.3 ± 0.6
> 1.00	14	24 ± 7	6 ± 2	1724 ± 297	3.0 ± 0.5

Ruddy Duck

Density	n	Magnesium	Chloride	Sulphur	Nitrate Nitrogen
0	56	71 ± 17	19 ± 5	437 ± 168	0.014 ± 0.003
0.01–0.25	24	139 ± 48	119 ± 38	1767 ± 797	0.024 ± 0.006
0.26–1.00	18	125 ± 57	60 ± 38	656 ± 386	0.029 ± 0.008
> 1.00	14	78 ± 16	17 ± 4	281 ± 114	0.032 ± 0.010

Table 8. Mean values (±SE) of selected physical and chemical pond variables in relation to densities of coots and grebes expressed per area of water between 0 and 2 m deep (n = number of ponds).

Pied-billed Grebe Density	n	% Marsh	pH	Conductivity	Chloride
0	87	14 ± 2	9.1 ± 0.1	2313 ± 316	57 ± 14
0.01–0.10	16	29 ± 6	9.1 ± 0.1	1700 ± 427	17 ± 7
> 0.10	9	42 ± 9	8.7 ± 0.2	1156 ± 176	7 ± 3

Pied-billed Grebe Density	n	Sulphur	Phosphorus
0	87	862 ± 255	1.0 ± 0.3
0.01–0.10	16	449 ± 320	0.2 ± 0.1
> 0.10	9	53 ± 25	0.1 ± 0.0

Horned Grebe Density	n	Depth	% Marsh	pH	Conductivity
0	74	1.8 ± 0.1	22 ± 3	9.0 ± 0.1	1647 ± 261
0.01–0.14	12	2.6 ± 0.4	7 ± 2	9.4 ± 0.1	4496 ± 1027
0.15–0.30	15	3.0 ± 0.4	9 ± 2	9.3 ± 0.2	2180 ± 757
> 0.30	11	2.3 ± 0.4	24 ± 7	8.8 ± 0.3	2754 ± 898

Horned Grebe Density	n	Phosphorus	Tdisnitrogen
0	74	0.9 ± 0.3	2.4 ± 0.2
0.01–0.14	12	1.2 ± 0.5	4.1 ± 1.3
0.15–0.30	15	0.6 ± 0.2	3.5 ± 0.8
0.30	11	0.2 ± 0.1	1.6 ± 0.4

Eared Grebe Density	n	Depth	% Marsh	% Forest	pH
0	78	2.0 ± 0.1	22 ± 3	29 ± 3	8.9 ± 0.1
0.01–0.20	11	2.3 ± 0.3	12 ± 6	13 ± 5	9.2 ± 0.1
0.21–0.40	10	2.3 ± 0.3	15 ± 4	10 ± 7	9.4 ± 0.1
> 0.40	13	2.6 ± 0.4	7 ± 2	5 ± 3	9.5 ± 0.1

Eared Grebe Density	n	Conductivity	Phosphorus
0	78	1395 ± 179	0.5 ± 0.2
0.21–0.20	11	5468 ± 1677	0.9 ± 0.3
0.21–0.40	10	2381 ± 372	0.4 ± 0.1
> 0.40	13	3542 ± 802	2.8 ± 1.4

American Coot Density	n	% Marsh	% Close	Conductivity	Calcium	Nitrate Nitrogen
0	49	12 ± 3	23 ± 3	2061 ± 448	83 ± 14	0.017 ± 0.004
0.01–0.20	21	6 ± 2	23 ± 5	3654 ± 732	93 ± 25	0.022 ± 0.007
0.20–1.00	17	31 ± 7	35 ± 7	1548 ± 289	98 ± 19	0.015 ± 0.003
1.01–2.00	13	37 ± 8	15 ± 3	1510 ± 304	125 ± 20	0.017 ± 0.008
> 2.00	12	28 ± 5	15 ± 6	1262 ± 172	111 ± 18	0.046 ± 0.013

ferences are greater for the species whose numbers are most correlated with pond size. However, similar variables are often identified by several of the techniques although the proportion of variance explained and their position in the multiple regression differs. Those comparisons reinforce the fact that correlation and multiple regression only reveal the mathematical relationships present in the data set and those may not always be biologically relevant, *i.e.* they may not represent a cause and effect. The variable which is sorted first will influence which one will be selected next and so on.

Important chemical and physical parameters

Total dissolved nitrogen levels were usually associated positively with density of most bird species except the Horned Grebe. Conductivity also tended to be positively associated with bird density except for species associated with marshes (*i.e.* Redhead, Canvasback, Ruddy Duck, Coot). Both total dissolved nitrogen and conductivity reflect pond productivity (Wetzel, 1975). Phosphorus levels were positively associated with Northern Shoveler and Eared Grebe abundance.

The percent of the pond surrounded by forest represents some measure of the openness of the pond. Whether ponds surrounded by vegetation tended to be avoided by birds, or whether there was some other factor connected with this measure that affected birds, is unknown. The percent of forest was negatively correlated with total dissolved nitrogens and turbidity in our data set. Sulphur concentrations were highly variable and did not seem to influence many bird species except for a negative association with Green-winged Teal and Ruddy Duck numbers. Magnesium concentrations were also very variable between ponds. Magnesium concentrations were always negatively associated with bird density for the few species where there were some relationships. Similarly, chloride was usually negatively associated with bird density, except for the Horned Grebe where there may have been a positive association. Calcium levels tended to be associated positively with most diving ducks. Hardness was only highlighted for one species, the Bufflehead, and in a negative fashion. Within the range of pH present, pH did not appear as a major factor in explaining most waterfowl abundance. Mallard, Green-winged Teal, Pied-billed Grebe, Horned Grebe and perhaps Bufflehead tended to be negatively associated with pH, whereas Canvasback and Coot had a positive association.

Physical and chemical pond characteristics associated with bird abundance

Dabbling ducks

We summarize here the apparent associations between bird density and pond features observed with the ranking and regression procedures.

Green-winged Teal (Anas crecca). Green-winged Teal densities were much lower than Blue-winged Teal densities and the species was not as widespread. Ponds avoided by Green-winged Teals (13%) were often surrounded by trees, had low concentrations of total dissolved nitrogen, and low turbidity (Table 6). Marsh area and percent of forest were negatively associated with Green-winged Teal densities. Multiple regressions revealed a negative association with marsh area, pH and depth and a positive association with phosphorus, total dissolved nitrogen and conductivity (Table 3).

Mallard (Anas platyrhynchos). Ponds with low Mallard densities tended to be shallower than ponds with higher density. Marsh area, conductivity and total phosphorus values were associated negatively with Mallard densities (Table 6). Multiple regression results highlighted a negative relationship with Phosphorus and pH and a positive one with turbidity (Table 3).

Northern Pintail (Anas acuta). Pintails were less ubiquitous than Mallards, being absent from 49 ponds. Ponds without Pintails had lower conductivity, pH and turbidity levels than ponds with Pintails (Table 6). On used ponds, Pintail density was associated positively with pH and turbidity and negatively with percent marsh and percent forest. Multiple regression indicated a positive association with turbidity and negative associations with marsh area, percent of forest and magnesium.

Blue-winged Teal (Anas discors). Blue-winged Teals, like Mallards, were widespread, occurring on nearly all ponds. Marsh area tended to be lower on ponds with high densities of Blue-winged

Teal (Table 6). Ponds with high Blue-winged Teal densities tended to be deeper and have higher amounts of nitrate nitrogen than ponds with medium Blue-winged Teal densities. Multiple regression indicated a negative association with chloride and % of forest, and a positive association with pond depth and total dissolved nitrates (Table 3).

Northern Shoveler (Anas clypeata). Northern Shovelers were slightly more numerous than Gadwalls and were absent from 31 of the 112 ponds. Ponds without Shovelers had a lower conductivity, chloride, phosphorus, and total dissolved nitrogen levels, than used ponds (Table 6). On used ponds, Shoveler density was positively associated with conductivity, total dissolved nitrogen, and turbidity levels, and negatively with marsh area and proportion of forest cover (Table 6). Multiple regressions revealed strong positive associations with phosphorus and total dissolved nitrogen, and a negative one with calcium, forest cover and water depth (Table 3).

Gadwall (Anas strepera). Gadwalls occurred in low densities, with 48 ponds (43%) not frequented by the species. Unused ponds tended to have lower conductivity, and total dissolved nitrogen, and turbidity levels and a higher proportion of shoreline surrounded by forest and larger marshes than used ponds. On used ponds, Gadwall density was negatively associated with marsh area and positively associated with pH, turbidity, and total dissolved nitrogen (Table 6). Multiple regression identified total dissolved nitrogen, nitrate nitrogen and hardness as positively associated with Gadwall numbers, and calcium levels and forest cover as negatively associated (Table 3).

American Wigeon (Anas americana). American Wigeons were abundant and widely distributed, being absent from only 7 ponds which had low chloride, total dissolved nitrogen and turbidity levels (Table 6). American Wigeon densities were associated negatively with marsh area and positively with chloride, pH and total dissolved nitrogen. Multiple regressions indicated a negative association with marsh area, chloride and calcium, and a positive association with total dissolved nitrogen (Table 3).

Total dabbling ducks. Ponds with low densities of dabbling ducks tended to be shallower, have more marsh, lower pH, total dissolved nitrogen and turbidity levels, and higher chloride concentrations than ponds with high densities (Table 9). Multiple regressions suggested a positive relationship between the number of dabbling ducks and the levels of turbidity and total dissolved nitrogen (Table 3). Chloride concentrations, % of forest and % of marsh were negatively associated with dabbling duck numbers. Relationships with depth depended on the density unit used being positive when density was expressed per area 0–1 m deep, and negative when total area was used, possibly just reflecting a positive association between pond area and depth.

Diving ducks

Canvasback (Aythya valisineria). Canvasbacks occurred on a similar number of ponds as Redhead but in lower densities. The 69 unused ponds tended to be shallower, and have low phosphorus levels. On used ponds, Canvasback density was associated positively with marsh area and negatively with forest cover and depth (Table 7). Multiple regressions revealed positive associations with marsh area, pH and depth, and negative associations with % forest and chloride levels (Table 4).

Redhead (Aythya americana). Redheads were found only on less than half of the ponds with no obvious relationships with any of the habitat features (Table 2). Unused ponds tended to be shallower, have higher conductivity and lower calcium and nitrate nitrogen values but variability was high. Multiple regressions explained only a small portion of the variability identifying possible positive associations with depth, calcium and area of marsh (Table 4).

Table 9. Mean values (±SE) of selected physical and chemical pond variables in relation to densities of dabbling ducks and diving ducks expressed per area of water between 0–1 m deep and 0–2 m deep, respectively (n = number of ponds).

Dabbling ducks Density	n	Depth (m)	% Marsh	pH	Chloride
0.10–4.00	30	1.9 ± 0.2	35 ± 5	8.9 ± 0.1	51 ± 22
4.01–8.00	33	2.0 ± 0.3	20 ± 4	9.1 ± 0.1	62 ± 22
8.01–16.00	31	2.1 ± 0.2	9 ± 2	9.2 ± 0.1	44 ± 23
> 16.00	18	2.7 ± 0.2	5 ± 2	9.2 ± 0.1	16 ± 5

Dabbling ducks Density	n	Tdisnitrogen	Turbidity
0.10–4.00	30	1.8 ± 0.3	2.8 ± 0.8
4.01–8.00	33	2.7 ± 0.6	6.2 ± 2.3
8.01–16.00	31	3.0 ± 0.4	7.9 ± 1.9
> 16.00	18	3.1 ± 0.5	10.0 ± 3.1

Diving ducks Density	n	Depth (m)	% Marsh	pH	Conductivity	Nitrogen Nitrates
0.01–2.00	24	1.4 ± 0.1	37 ± 6	8.7 ± 0.2	1250 ± 338	0.018 ± 0.004
2.01–4.00	29	1.9 ± 0.2	17 ± 4	9.1 ± 0.1	1742 ± 361	0.016 ± 0.004
4.01–8.00	32	2.0 ± 0.2	17 ± 4	9.2 ± 0.1	2797 ± 675	0.023 ± 0.006
> 8.00	27	3.2 ± 0.2	6 ± 1	9.2 ± 0.1	2547 ± 451	0.025 ± 0.007

Diving ducks Density	n	Tdisnitrogen	Phosphorus	Turbidity
0.01–2.00	24	1.6 ± 0.3	1.1 ± 0.8	3.1 ± 0.8
2.01–4.00	29	2.9 ± 0.7	1.1 ± 0.8	8.7 ± 3.0
4.01–8.00	32	2.9 ± 0.4	0.7 ± 0.2	7.0 ± 1.9
> 8.00	27	3.0 ± 0.3	0.5 ± 0.1	6.0 ± 1.5

Lesser scaup (Aythya affinis). Lesser scaups were absent from 23 ponds characterized by shallow depth, large marshes, low conductivity and low nitrate nitrogen levels. Ponds with the highest densities of scaups were deeper, had smaller marshes and moderate conductivity levels. Multiple regressions suggested a negative association with marsh area and with the percent of forested shoreline and a positive association with pond depth and calcium levels.

Barrow's Goldeneye (Bucephala islandica). Barrow's Goldeneye was the most numerous and widespread species on the ponds surveyed. It was absent from only five ponds, likely because of their shallow depth, low pH, total dissolved nitrogen, calcium and conductivity levels, and large marsh area (Table 7). On the other ponds, Barrow's Goldeneye density was positively associated with water depth, Ph, and total dissolved nitrogen, and negatively with marsh area. Multiple regressions revealed positive associations with pond depth, conductivity, and total dissolved nitrogen levels, and negative associations with marsh area and phosphorus levels (Table 4).

Bufflehead (Bucephala albeola). Buffleheads were as widespread as Barrow's Goldeneyes but slightly less abundant. The seven ponds unused by Buffleheads were small and shallow, with marshes accounting for a large portion of the pond (Table 7). They had low levels of total dissolved nitrogen and high and variable levels of chloride and magnesium. On used ponds, Bufflehead density was positively associated with water depth and negatively with marsh area, turbidity, calcium and magnesium levels. Multiple regressions revealed a strong positive association only with pond depth and a negative association with turbidity and hardness (Table 4).

Ruddy Duck (Oxyura jamaicensis). Ruddy Ducks were just slightly more numerous than Redheads. Only half of the ponds were used by Ruddy Ducks. Unused ponds were shallower, had a smaller marsh area, and lower conductivity, total dissolved nitrogen and nitrate nitrogen levels (Table 7). Ruddy Duck density on used ponds was positively associated with marsh area and negatively with conductivity, magnesium, chloride, sulphur levels and % forest cover. Multiple regressions indicated a positive association with marsh area, depth and total dissolved nitrate levels, and a negative association with % forest and turbidity (Table 4).

Total diving ducks. Ponds with low densities of diving ducks tended to be shallower, have more marsh, lower pH, conductivity, nitrate nitrogen, total dissolved nitrogen and turbidity levels, and higher phosphorus levels than ponds with high densities (Table 9). Multiple regressions suggested positive relationships with depth, conductivity and total dissolved nitrogen and a negative association with phosphorus levels after the effect of total dissolved nitrogen had been removed (Table 4).

Coots and Grebes

Pied-billed Grebe (Podilymbus podiceps). Pied-billed Grebes were found on only 25 (22%) ponds. Ponds without Pied-billed Grebes tended to have smaller marshes, higher conductivity, chloride, sulphur and phosphorus levels than ponds with grebes (Table 8). High Pied-billed Grebe densities were associated with greater marsh area and lower pH, conductivity, chloride, sulphur and phosphorus levels (Table 8). Multiple regression identified marsh area, conductivity and calcium levels as positively associated with Pied-billed Grebe abundance (Table 5).

Horned Grebe (Podiceps auritus). Horned Grebes occurred only on 38 (34%) of the ponds surveyed. Ponds without Horned Grebes were shallower and had lower conductivity levels than ponds with grebes. Ponds with low densities of Horned Grebes had less marsh area, higher pH, higher conductivity, phosphorus and total dissolved nitrogen levels than ponds with higher densities of grebes (Table 8). Multiple regressions suggested positive associations with depth, chloride and sulphur levels, but negative associations with calcium and phosphorus levels (Table 5).

Eared Grebe (Podiceps nigricollis). Eared Grebes occurred on slightly fewer ponds than Horned Grebes (30%) but reached higher densities. Ponds without Eared Grebes tended to be shallower, had greater marsh area and % forest, and lower pH and conductivity levels than ponds with Eared Grebes (Table 8). Ponds with high densities of Eared Grebes tended to have less marsh area, not to be surrounded by forest, and have a higher pH and higher phosphorus levels than ponds with low densities. Multiple regressions suggested a positive association with phosphorus levels and possibly conductivity and magnesium, and a negative association with calcium and turbidity levels (Table 5).

American Coot (Fulica americana). Ponds without coots were characterized by low nitrate nitrogen and calcium levels, small marsh area, and moderate conductivity levels (Table 8). Ponds with low coot densities had less marsh, lower calcium and nitrate nitrogen levels, higher conductivity levels and a greater percent of forest than ponds with high coot densities. Multiple regressions suggested positive relationships with marsh area, concentrations of nitrate nitrogen, calcium and magnesium and a negative relationship with turbidity (Table 5).

Discussion

Density

As we have seen, bird density can be expressed in a variety of ways and the unit used can influence the type of relationships (positive and negative) with various physical and chemical parameters. Our analyses have emphasized the arbitrary nature of density measures. Density measures are an attempt to standardize abundance values by unit area by dividing. Regression is another way of removing area effect; it does so by subtracting. For species strongly associated with area such as the Barrow's Goldeneye, the different methods result in different variables being identified as the best predictor of Goldeneye density in the multiple regression (Table 4).

It must be emphasized that significance in a regression (or correlation) analysis does not indicate a causal relationship between the correlated variables; they may have no direct relationship. For example, a species may depend on water 0–1 m deep for food, thus resulting in a strong correlation between this area and species counts. The topography of the ponds may dictate that areas of 3–5 m and areas of 0–1 m are strongly correlated.

Consider the following diagram:

$$\underset{\text{Species count}}{\text{[A]}} \quad \underset{\substack{\text{correlation}\\ \text{due to}\\ \text{feeding}}}{\longleftrightarrow} \quad \underset{\text{area 0–1 m}}{\text{[B]}} \quad \underset{\substack{\text{correlation}\\ \text{due to}\\ \text{pond topography}}}{\longleftrightarrow} \quad \underset{\text{area 3–5 m}}{\text{[C]}}$$

Species count [A] and area 0–1 m [B] are correlated by direct cause – feeding; area 0–1 m [B] and area 3–5 m [C] are correlated by the topography of the ponds – bigger ponds have more of both. This may lead to a correlation between [A] and [C], but one will not cause the other.

The abundance of most diving ducks was more related to area than that of dabbling ducks. In fact in our data set, pond size tended to be an overwhelming factor for most species. As expected, the most abundant species were more influenced by pond size than the less numerous ones. This probably reflects the saturation of the habitat by some species, whereas others may not have used all suitable habitats.

Relationships between bird abundance and pond features

Our data set, although large, had several weaknesses. (1) We used the average number of waterfowl using a given pond over 5 years, but only measured chemical concentrations during one summer. This may partially explain the large amount of unexplained variability in the data set. Values of conductivity, for example, can vary by as much as 50% throughout the season and between years on some ponds (Scudder, 1969), and the same is probably true for other variables. However, the relative ranking of the ponds for a given variable should change little. (2) Several relationships in the data set are not linear. Productivity has been shown to increase with conductivity level up to 3000 μmhos and then to decrease at higher conductivity levels (Cannings & Scudder, 1978; Reynolds, 1979). That limits the power of the linear stepwise regression. That is why we also used the simple ranking based on density to explore the data. (3) Finally, several of the variables, both bird numbers and physical and chemical features, were not normally distributed as expected in such a data set. All variables, pH and percent excluded, were transformed with the log function. The arcsine transformation was used for percent and pH values were not transformed. These transformations improved the normality of some variables but several still remained skewed. Thus the significance level given for the multiple regression is likely biased for some variables. However, we do not emphasize statistical significance in this paper since we consider our analyses to be mostly exploratory and descriptive.

Although we only considered 14 variables in this paper, we measured more variables which we excluded because they were strongly correlated with the ones we chose. Conductivity levels were highly correlated with levels of sodium, salinity and total alkalinity, maximum depth with mean depth, and area of water 0–2 m in depth with area of water 0–3 m in depth. Those associations should be kept in mind when interpreting the results.

We will not discuss in depth the birds/pond features associations present in our data set. Some confirm already well known associations, *i.e.* importance of marsh area for American Coot, Pied-billed Grebe, Ruddy Duck and Canvasback, five species breeding in emergent vegetation. Others are less obvious and their biological significance uncertain.

Breeding waterfowl have two major requirements: food and nesting site. Thus associations between waterfowl and the physical or chemical features of a pond are likely due to the influence of these features on plants, and invertebrate type and abundance. Mallards are feeding generalists, whereas Shovelers are specialists and should respond to different pond features. It is likely that the territorial behaviour of some species influenced pond selection. Barrow's Goldeneye and Bufflehead are especially aggressive and often exclude other species from their territory (Savard, 1988a; Savard & Smith, 1987b). Several dabbling ducks are also territorial and tend to space themselves during the early part of the breeding season. This behaviour will influence, to some degree, pond selection. Also, the close proximity of several of our ponds may have resulted in birds using some ponds as a complex rather than single units.

We looked at some pairing of ponds of similar size but with different densities of waterfowl, and failed to find uniform characteristics separating high and low density ponds. It became obvious in examining these pairs that some different combinations of factors influenced abundance. For example, shallow ponds were not used by diving ducks in spite of the fact that other characteristics were suitable. It indicated the need for more larger sample sizes than we had when using the correlative type approach. It also stressed the need to control pond size in the field. Finally, the inclusion of social interactions in future analysis may help explain some of the unexplained differences observed in bird abundance between ponds.

Conclusion

The effect of pond size on bird abundance can be reduced by several ways each influencing to various degree the relationships with other variables. It is not clear whether there is a best way, although the regression approach seems more gentle than the use of density measures. Selection of the area to use should be based on biological relevance and objective sought. Results highlight the problems associated with interpreting correlative type studies, especially the difficulties in assessing the biological significance of the observed correlations. It underscores the urgent need for a more experimental approach to bird-habitat relation studies before realistic habitat evaluate models can be developed.

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