The Condor 96:411–421

HABITAT USE BY MALLARDS AND AMERICAN BLACK DUCKS BREEDING IN CENTRAL ONTARIO[1]

M. TODD MERENDINO[2]
Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7 Canada

C. DAVISON ANKNEY
Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7 Canada

Abstract. Mallards (*Anas platyrhynchos*) were virtually absent from central Ontario as recently as 1948 but now exceed 60 pairs/100 km^2 in some areas. Black Duck (*A. rubripes*) numbers in central Ontario appear stable with breeding densities in some areas exceeding 40 pairs/100 km^2. Densities of breeding Mallards and Black Ducks exhibit spatial variability suggesting that habitat quality may influence distributions. We used data from Canadian Wildlife Service breeding pair surveys to classify wetlands as used only by breeding Mallards, used only by breeding Black Ducks, shared by Mallards and Black Ducks, or vacant (i.e., not used by either species). We evaluated wetland fertility by analyzing water chemistry (color, pH, conductivity, alkalinity [$CaCO_3$], calcium, magnesium, sodium, potassium, total phosphorus) and physical characteristics (shoreline irregularity index [SI], percent open water, wetland size) for 447 wetlands. Wetlands that Mallards shared with Black Ducks or solely occupied were the most fertile. Vacant wetlands were least fertile. Areas that supported few Mallards or Black Ducks had relatively infertile wetlands; Mallards predominated in areas with relatively fertile wetlands. We conclude that wetland fertility has influenced the distribution of Mallards and Black Ducks in central Ontario. Mallards and Black Ducks apparently prefer wetlands with similar characteristics (i.e., high fertility, moderate open water, high SI, and small size), so competition for breeding sites is likely. Historical data from Ontario lead us to suspect that this competition may have contributed to the decline in Black Duck numbers.

Key words: Alkalinity; Black Duck; calcium; fertility; Mallard; Ontario; sympatric; wetland.

INTRODUCTION

Numerous factors have been cited as contributing to the decline of American Black Ducks (*Anas rubripes*) (Rusch et al. 1989), hereafter called Black Ducks, but Mallards (*A. platyrhynchos*), through hybridization (Ankney et al. 1987, 1989; Seymour 1990) and competitive exclusion from fertile wetlands (Merendino et al. 1993), may be the most significant cause. In southern Ontario, where breeding Mallards rapidly replaced breeding Black Ducks (Collins 1974, Dennis et al. 1989), Mallards first invaded the most fertile wetlands and replaced Black Ducks on those wetlands (Merendino et al. 1993). Also, highly fertile wetlands support more breeding pairs of Mallards than do less fertile wetlands (Dennis et al. 1989, Merendino et al. 1992).

In central Ontario breeding Mallards were rare as recently as 1948 (Hanson et al. 1949), but now exceed 60 pairs/100 km^2 in some areas (Ross 1992, Can. Wildlife Ser., unpubl. report). Unlike in southern Ontario, where the breeding range and densities of Black Ducks declined markedly as Mallard populations increased (Merendino et al. 1993), Black Duck numbers in central Ontario have remained relatively stable. At present Mallards and Black Ducks are largely sympatric in central Ontario. Overall, breeding densities of Mallards and Black Ducks in central Ontario exhibit a wide range of spatial variability, suggesting that habitat quality may be influencing their distributions (McNicol et al. 1987, Ross and Fillman 1990).

Unlike in southern Ontario, where Merendino et al. (1993) examined historical changes in breeding Mallard and Black Duck numbers and distribution, in this study we documented habitat use by sympatric breeding Mallards and Black Ducks in central Ontario. Our objectives were to determine: (1) if wetlands occupied by Mallards were more fertile than those used by Black

[1] Received 21 June 1993. Accepted 16 December 1993.

[2] Present address: Texas Parks and Wildlife Department, Matagorda County Courthouse, Bay City, TX 77414.

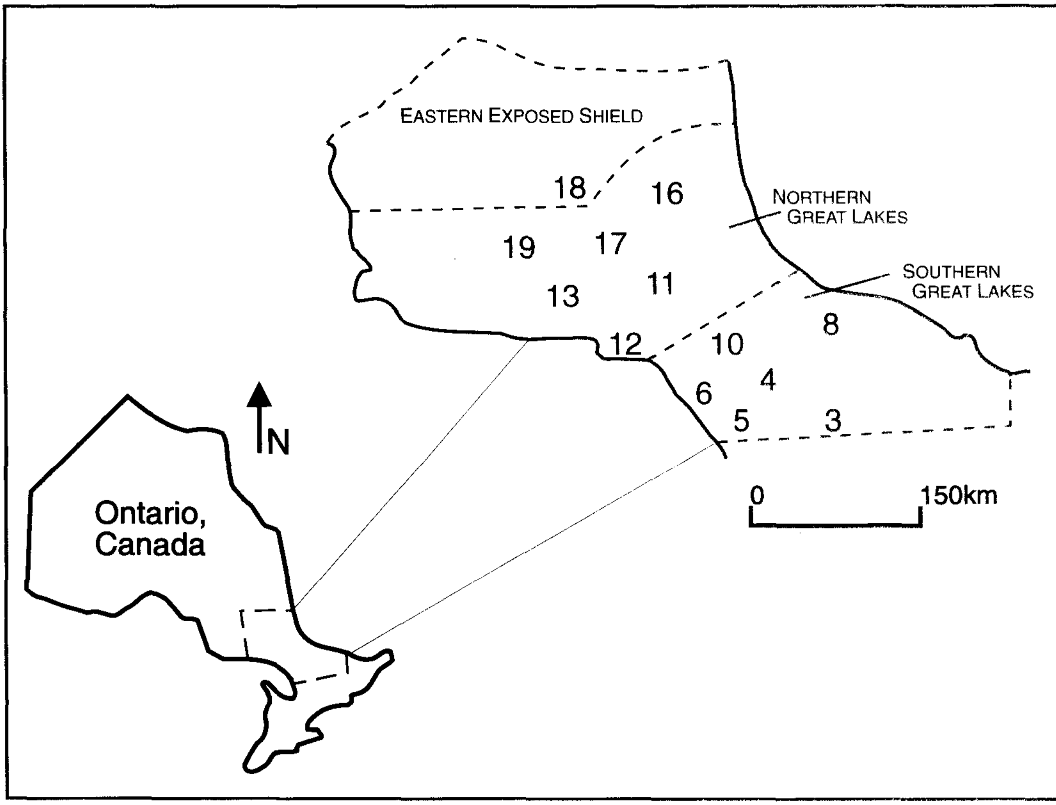

FIGURE 1. Approximate location of each 10 km × 10 km plot in central Ontario.

Ducks and those not used by either species, and (2) if geographical areas with the highest Mallard densities had the most fertile wetlands.

MATERIALS AND METHODS

STUDY AREA

The study area encompassed 60,000 km^2 of central Ontario (Fig. 1) and extended through three ecological zones, along a 400 km northwest to southeast gradient and a 170 km southwest to northeast gradient. Most of the area is underlain by pre-Cambrian bedrock (Ryder 1964, McNicol et al. 1987).

BREEDING PAIR LOCATIONS

Since 1990, the Canadian Wildlife Service (CWS) has conducted helicopter surveys of breeding waterfowl in 44 10 km × 10 km plots in northeastern Ontario. Plots were laid out systematically based on Universal Transverse Mercator blocks. Plots were located in the centers and southwest corners of all 100 km × 100 km UTM blocks. We chose 13 plots for study (Fig. 1), based on varying numbers of Mallards and Black Ducks (Table 1); plot numbers presented herein correspond to CWS long-term survey plot numbers. In 1990, we evaluated habitat in plots 11–13 and 16–19 that were located in the northern Great Lakes-St. Lawrence Lowlands Forest area; plot 18 was located in the eastern exposed shield (Fig. 1). Collectively, we hereafter refer to plots 11–13 and 16–19 as northern Great Lakes-St. Lawrence (NGLSL). In 1991 we evaluated habitat in plots 3–6, 8, and 10 that were located in the southern Great Lakes-St. Lawrence Lowlands Forest area (SGLSL) (Fig. 1).

Breeding pair surveys in our study plots were conducted during 1–14 May. During surveys, the location (i.e., wetland) of each indicated pair of ducks was noted on aerial photos. Data from 1990 and 1991 breeding pair surveys were used to select wetlands used by breeding pairs (i.e., Mallards or Black Ducks) and wetlands not used by either species in NGLSL and SGLSL, respectively. Wetlands were defined as follows: (1) Mallard—used only by Mallards. (2) Black Duck—used only by Black Ducks. (3) Shared—shared by Mallards and Black Ducks. (4) Vacant—wetlands on which no Mallards or Black Ducks were observed. Vacant wetlands were randomly selected from all vacant wetlands 0.41–20.0 ha in size, as such wetlands are most used by breeding waterfowl in central Ontario (McNicol et al. 1987).

HABITAT EVALUATION

Water chemistry. We collected water samples from 447 wetlands in central Ontario during summer 1990 and 1991; 240 wetlands (Mallard [n = 44], Black Duck [n = 47], shared [n = 24], vacant [n = 125]) in the NGLSL area were sampled from 31 July–3 August 1990 and 207 wetlands (Mallard [n = 61], Black Duck [n = 61], shared [n = 13], vacant [n = 72]) in the SGLSL area were sampled from 22 July–25 July 1991. A helicopter equipped with floats landed on open water in a wetland and two water samples (250 ml, 100 ml) were taken. Surface samples were taken from shallow wetlands (i.e., wetlands with emergents established toward the center or with floating leaved plants over most of the surface), whereas a 1 m tube was used to take a column sample from deeper wetlands (i.e., wetlands where emergents were established only around the edge) (McNicol et al. 1987, Brooksbank et al. 1989). In the field, samples were kept cool and later transferred to a refrigerator at 4°C. Conductivity and pH determinations were made at the end of the day samples were collected in 1990; in 1991, samples were shipped to the University of Western Ontario and kept in cold storage for five days before pH and conductivity determinations. The 250 ml samples were coarse filtered (Whatman #41 filter) before analysis (Great Lakes For. Cent., Sault Sainte Marie, Ontario) of alkalinity ($CaCO_3$) and cations (calcium, magnesium, sodium, potassium). The 100 ml samples were analyzed for apparent and true color as well as total phosphorus. Apparent color (before fine filtering; Whatman #42 filter) and true color (after fine filtering) were determined with an Hellige Aqua Tester. After true color determination, the 100 ml samples were stabilized with 1 ml of 30% H_2SO_4 before analysis of total phosphorus. Water chemistry data, except pH, conductivity

TABLE 1. Number of indicated pairs[a] of Mallards and Black Ducks on 13 10-km × 10-km plots in central Ontario, 1990–1991.

Plot	Mallard	Black Duck	Total	M:BD
3	10 (13)	45 (39)	55 (52)	1.0:4.5
4	8 (8)	26 (25)	34 (33)	1.0:3.3
5	14 (15)	6 (9)	20 (24)	2.3:1.0
6	51 (49)	7 (14)	58 (63)	7.3:1.0
8	2 (2)	21 (20)	23 (22)	1.0:10.5
10	58 (50)	32 (25)	90 (75)	1.8:1.0
11	52 (63)	6 (12)	58 (65)	8.7:1.0
12	46 (51)	9 (10)	55 (61)	5.1:1.0
13	19 (20)	12 (17)	31 (37)	1.6:1.0
16	1 (3)	12 (17)	13 (20)	1.0:12.0
17	3 (5)	5 (12)	8 (17)	1.0:1.6
18	9 (7)	16 (24)	25 (31)	1.0:1.7
19	7 (5)	27 (24)	34 (29)	1.0:3.9

[a] Number outside parentheses is number of indicated pairs present in year when habitat was evaluated. Plots 3–6, 8, and 10 were evaluated in 1991; plots 11–13 and 16–19 were evaluated in 1990. Numbers in parentheses are average number of indicated pairs based on survey data from 1990 and 1991. Ratios were computed from number of indicated pairs present in year in which the habitat was evaluated.

(μmhos/cm), and color (hazen units), are reported in mg/liter.

Physical characteristics. Physical characteristics evaluated were: shoreline irregularity index (SI), size (ha), and percent open water. Wetland size and perimeter (m) were determined from aerial photos by use of a computerized digitizing morphometry program. SI was computed using the equation: SI = $S/2\sqrt{a\pi}$, where S = meters of shoreline, a = wetland area in m^2 (Reid 1961: 34). An SI value of 1.0 indicated perfectly round wetlands, whereas values > 1.0 indicated increasingly irregular shorelines. Percent open water was estimated visually during sampling.

STATISTICAL ANALYSES

Habitat use by Mallards and Black Ducks. Our main objective was to evaluate habitat use by sympatric breeding Mallards and Black Ducks. Therefore, we conducted an overall analysis of 447 wetlands by combining waterfowl observations and habitat data from 1990 (NGLSL) [n = 240] with data from 1991 (SGLSL) [n = 207]. This was appropriate given that the two ecological areas where the plots are located are physiognomically similar and the data were collected in successive years. Thus, gross differences in water chemistry and physical wetland characteristics were unlikely (Merendino 1993) and significant annual differences between the two areas were also unlikely (Watt et al. 1979, Lewis 1982, Eilers et al. 1989). There were no obvious dif-

TABLE 2. Standardized canonical coefficients of the three canonical axes from the canonical variates analysis performed to separate the four wetland groups (Mallard only [n = 105], Black Duck only [n = 108], shared [n = 37], and vacant [n = 197]) in central Ontario.

Variable[b]	Standardized canonical coefficients[a]		
	CAN1	CAN2	CAN3
Water chemistry			
Alkalinity	0.8513	−0.4137	0.3745
Calcium	0.0914	0.1197	−0.9181
Color, apparent	0.4185	0.2832	−0.9015
Color, true	−0.3433	−0.5520	1.1573
Conductivity	−0.1052	0.4257	−0.1594
Magnesium	−0.1489	0.6682	0.7649
pH	0.1206	−0.1075	0.1352
Potassium	0.0799	0.0276	0.2149
Sodium	−0.0613	0.0344	0.5781
Total phosphorus	0.4086	0.0414	−0.0239
Physical			
% open water	−0.2105	−0.2692	−0.1924
SI	0.2457	−0.5691	0.0359
Size (ha)	0.0932	−0.0395	−0.4446
Eigenvalues	43.88	7.62	4.76
% variation explained	78.00	13.55	8.45
P-value	0.0001	0.0007	0.041

[a] Variables important in defining axes are underlined.
[b] Water chemistry variables, except pH, color (hazen units), and conductivity (μmhos/cm), measured in mg/liter; SI = shoreline irregularity index.

ferences in climatic conditions (temperatures, rainfall amounts, rainfall frequency, etc.) between survey years. Although water chemistry changes quite dramatically in early spring, primarily as a result of run-off from snowmelt (Ryder 1964, Patterson 1976, McNicol et al. 1987), water chemistry characteristics are quite similar during the period that wetlands are used by breeding waterfowl (e.g., May–September), especially in the relatively infertile wetlands of north-central Ontario (Ryder 1964, Patterson 1972, McNicol et al. 1987).

Multivariate Analysis of Variance (MANOVA; PROC MANOVA; SAS 1985) was used to determine if there was an overall difference in water chemistry and morphology among the four wetland groups (Mallard only, Black Duck only, shared, and vacant). One-way ANOVA output from the MANOVA was used to assess significance ($P \leq 0.05$) of each variable. To better explain among-group differences, mean separation tests (least significant difference tests [LSD]) were conducted on each physical variable and on alkalinity, calcium, pH, conductivity, and apparent color as they generally contributed most to separation of wetland groups and have been used by many researchers to assess waterbird abundance and distributions (Moyle 1956, Patterson 1976, Murphy et al. 1984, DesGranges and Darveau 1985, DesGranges and Hunter 1987, McNicol et al. 1987). Canonical variates analysis (CVA; PROC CANDISC; SAS 1985) was used to indicate which variables provided most separation among the treatment groups. Variances, covariances, and means generated from CVA analysis were used to construct 95% confidence ellipses around treatment means on the first two canonical axes.

Habitat quality in areas with varying densities of Mallards and Black Ducks. To determine if the most fertile area had the highest Mallard densities we combined wetland data into four "areas": (1) Mallard dominated, (2) Black Duck dominated, (3) shared, and (4) sparsely occupied (Table 1). Plots were primarily "assigned" a category (i.e., Mallard, Black Duck, shared, sparsely occupied) based on the number of indicated pairs present during the year in which habitat was

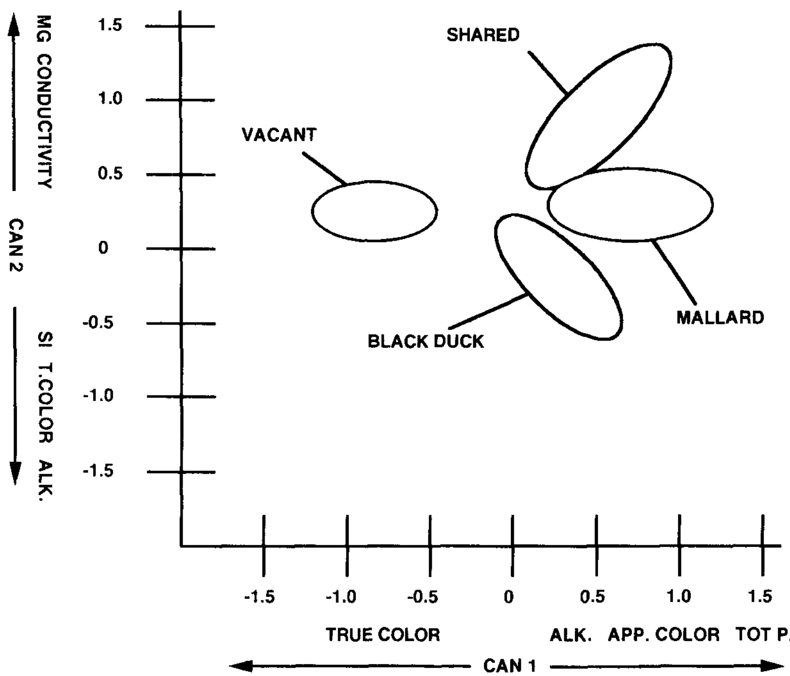

FIGURE 2. Ninety-five percent confidence ellipses on the first two canonical axes for each wetland group in central Ontario. Variables most important in defining axes are shown adjacent to arrows (see standardized canonical coefficients; Table 2). SI = shoreline irregularity, T. COLOR = true color, ALK. = alkalinity, MG = magnesium, APP. COLOR = apparent color, TOT. P = total phosphorus.

evaluated. The overall number of indicated pairs was also used in assigning plots to categories. Plots 6, 10, 11, and 12 were combined to form the Mallard dominated area, in which there were 207 Mallard pairs and 54 Black Duck pairs. Plots 3, 4, 8, and 19 were combined to form the Black Duck dominated area, in which there were 27 Mallard pairs and 120 Black Duck pairs. Plots 5, 13, and 18 were combined to form the shared area, in which there were 43 Mallard pairs and 34 Black Duck pairs. Plots 16 and 17 formed the sparsely occupied area, in which there were 5 Mallard pairs and 21 Black Duck pairs. MANOVA, CVA, and LSD tests were used to examine habitat differences among the four areas.

RESULTS

HABITAT USE BY MALLARDS AND BLACK DUCKS

There was an overall significant difference among wetland groups (Mallard only, Black Duck only, shared, and vacant) (Wilk's Lambda = 0.6165, $P < 0.0001$). The three canonical axes (CAN1, CAN2, CAN3) from the CVA described 78.0% ($P < 0.0001$), 13.6% ($P = 0.0007$), and 8.5% ($P = 0.041$) of the among-group variation, respectively (Table 2). Standardized canonical coefficients indicated that water chemistry characteristics were more important than physical characteristics in defining the axes (i.e., separating the wetland groups) (Table 2). CAN1, characterized by high values of alkalinity ($CaCO_3$), apparent color, and total phosphorus, relative to true color (Table 2), separated vacant wetlands from the three other groups (Fig. 2). CAN2, characterized by high values of magnesium and conductivity, relative to values for alkalinity, SI, and true color (Table 2), further separated Black Duck only wetlands from Mallard only and shared wetlands (Fig. 2). CAN3 was characterized by high values of true color, magnesium, and sodium relative to values of apparent color, calcium, and alkalinity (Table 2).

All water chemistry variables differed ($P < 0.0001$) among wetland groups (Table 3). Water chemistry constituents were, on average, highest in shared wetlands and Mallard wetlands and

TABLE 3. Averages of water chemical and physical variables for Mallard only, Black Duck only, shared (e.g., Mallards and Black Ducks), and vacant (e.g., no Mallards or Black Ducks) wetlands in central Ontario.

Variable[a]	Mallard only (n = 108)		Black Duck only (n = 105)		Shared (n = 37)		Vacant (n = 197)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water chemistry								
Alkalinity	11.51A[b]	1.15	7.17B	0.78	14.95A	2.69	4.21C	0.35
Calcium	5.58A	0.44	4.01B	0.27	6.57A	0.81	3.39C	0.17
Color, apparent	104.17A	4.45	95.33AB	6.13	83.11BC	7.99	76.29C	4.19
Color, true	86.48	3.74	80.48	5.02	67.43	6.65	63.81	3.63
Conductivity	50.34A	2.94	37.73B	1.77	57.58A	5.92	36.24B	1.24
Magnesium	1.76	0.16	0.98	0.05	1.86	0.29	1.03	0.06
pH	6.56A	0.04	6.45A	0.05	6.49A	0.09	6.20B	0.05
Potassium	0.53	0.03	0.43	0.03	0.51	0.05	0.38	0.02
Sodium	1.57	0.09	1.25	0.05	1.33	0.07	1.15	0.03
Total phosphorus	0.04	0.004	0.03	0.003	0.03	0.004	0.03	0.002
Physical								
% open water	68.24A	1.99	77.76B	1.75	74.19AB	3.77	85.91C	1.41
SI	1.74A	0.06	1.75A	0.06	1.63AB	0.08	1.49B	0.03
Size (ha)	5.08	0.50	5.45	0.47	6.90	1.00	4.85	0.35

[a] Water chemistry variables, except pH, color (hazen units), and conductivity (μmhos/cm), measured in mg/liter. SI = shoreline irregularity index.
[b] LSD tests were only conducted on alkalinity, calcium, apparent color, conductivity, pH, % open water, and shoreline irregularity (see methods section for rationale). Means in the same row followed by different letters are significantly ($P \leq 0.0001$) different; results from univariate output (3, 443 df) in MANOVA and LSD tests. All variables, except size ($P = 0.09$), were highly significantly different ($P \leq 0.0001$) among groups.

TABLE 4. Standardized canonical coefficients of the three canonical axes from a canonical variates analysis performed on data from four areas (see text) (e.g., Mallard dominated, Black Duck dominated, shared, and sparsely occupied) in central Ontario.

Variable[b]	Standardized canonical coefficients[a] CAN1	CAN2	CAN3
Water chemistry			
Alkalinity	0.9953	−0.0177	−0.3558
Calcium	−0.5424	1.2876	0.6419
Color, apparent	−0.3633	−1.1425	0.5009
Color, true	0.7141	0.9006	0.1811
Conductivity	−0.2538	−0.5957	−0.0665
Magnesium	0.2987	−0.7710	−0.0362
pH	0.5323	0.3707	−0.0388
Potassium	−0.1516	0.3322	0.3880
Sodium	−0.0781	−0.1005	−0.3803
Total phosphorus	0.2190	−0.0568	−0.7150
Physical			
% open water	−0.2828	0.3521	−0.1958
SI	−0.2680	0.1261	−0.1472
Size (ha)	−0.0134	−0.0921	0.2480
Eigenvalues	0.7991	0.1963	0.0493
% variation explained	76.50	18.79	4.71
P-value	0.0001	0.0001	0.033

[a] Variables important in defining axes are underlined.
[b] Water chemistry variables, except pH, color (hazen units), and conductivity (μmhos/cm), measured in mg/liter. SI = shoreline irregularity index.

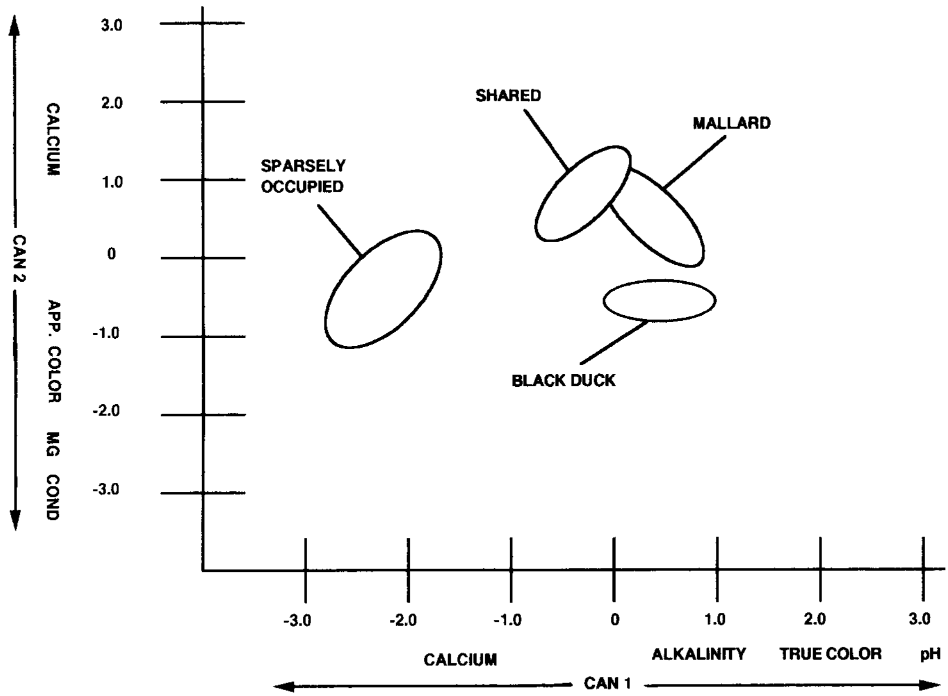

FIGURE 3. Ninety-five percent confidence ellipses on the first two canonical axes for Mallard dominated, Black Duck dominated, shared, and sparsely occupied areas in central Ontario. Variables most important in defining axes are shown adjacent to arrows (see standardized canonical coefficients; Table 4). APP. COLOR = apparent color; MG = magnesium; COND = conductivity.

lowest in vacant wetlands. Percent open water was lowest in Mallard wetlands and SI averaged lowest for vacant wetlands.

HABITAT QUALITY IN AREAS WITH VARYING DENSITIES OF MALLARDS AND BLACK DUCKS

There was significant variation among Mallard dominated, Black Duck dominated, shared, and sparsely occupied areas (Wilk's lambda = 0.4428, $P < 0.0001$). The three canonical axes (CAN1, CAN2, CAN3) from the CVA described 76.5% ($P \leq 0.0001$), 18.8% ($P \leq 0.001$), and 4.7% ($P = 0.33$) of the among-group variation, respectively (Table 4). Standardized canonical coefficients indicated that water chemistry contributed most to separation of the areas (Table 4). CAN1, characterized by high values of alkalinity, true color, and pH, relative to calcium (Table 4), clearly distinguished sparsely occupied areas from the other three areas (Fig. 3). CAN2, characterized by high values of calcium and true color (Table 4), separated shared and Mallard dominated areas from Black Duck dominated and sparsely occupied areas (Fig. 3).

Water chemistry constituents were lowest in wetlands in sparsely occupied areas (Table 5). On average, water chemistry constituents were highest in Mallard dominated areas; shared areas were similar to Black Duck dominated areas (Table 5).

DISCUSSION

Alkalinity ($CaCO_3$), calcium, conductivity, magnesium, pH, potassium, total phosphorus, and water color have been related to the fertility and productivity of wetlands in eastern North America, especially with regards to breeding waterfowl (Moyle 1956, Patterson 1976, DesGranges and Darveau 1985, Blancher and McAuley 1987, DesGranges and Hunter 1987, McNicol et al. 1987, McAuley and Longcore 1988). Wetlands with a higher nutrient content (eutrophic) are more productive (e.g., produce higher biomass) than those with a lower nutrient content (oligotrophic) (Cole 1983). Thus, we refer to wetlands with a higher nutrient content (i.e., high alkalinity, calcium, conductivity, etc.) as being more fertile and potentially more productive for breed-

TABLE 5. Averages of water chemical and physical variables for wetlands in Mallard dominated (plots 6, 10, 11, 12), Black Duck dominated (plots 3, 4, 8, 19), shared (e.g., similar numbers of Mallards and Black Ducks; plots 5, 13, 18), and sparsely occupied (e.g., few Mallards or Black Ducks; plots 16, 17) areas in central Ontario.

Variable[a]	Mallard areas (n = 172)		Black Duck areas (n = 129)		Shared areas (n = 90)		Sparsely occupied (n = 56)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water chemistry								
Alkalinity	9.21A[b]	0.82	7.66A	0.89	7.65A	0.92	2.09B	0.41
Calcium	4.58A	0.29	4.32A	0.30	4.82A	0.39	2.75B	0.22
Color, apparent	107.38A	3.92	79.80B	5.20	85.44B	6.25	51.96C	5.84
Color, true	88.54	3.28	68.41	4.53	72.39	5.21	40.80	4.66
Conductivity	45.39A	2.13	39.80AB	2.01	43.09A	2.63	33.00B	0.84
Magnesium	1.54	0.10	1.17	0.12	1.17	0.09	0.75	0.04
pH	6.46A	0.04	6.54A	0.04	6.39B	0.06	5.66C	0.09
Potassium	0.41	0.02	0.48	0.03	0.50	0.04	0.33	0.02
Sodium	1.35	0.04	1.31	0.06	1.30	0.08	1.05	0.04
Total phosphorus	0.04	0.002	0.04	0.003	0.03	0.003	0.02	0.002
Physical								
% open water	70.70A	1.80	81.55B	1.43	81.44B	2.10	92.77C	1.76
SI	1.58	0.03	1.66	0.05	1.66	0.07	1.61	0.04
Size (ha)	4.88	0.41	5.15	0.42	5.47	0.52	6.00	0.69

[a] Water chemistry variables, except pH, color (hazen units), and conductivity (μmhos/cm), measured in mg/liter. SI = shoreline irregularity index.
[b] LSD tests were only conducted on alkalinity, calcium, apparent color, conductivity, pH, % open water, and shoreline irregularity (see methods section for rationale). Means in the same row followed by different letters are significantly different; results from univariate output (3, 443 df) in MANOVA and LSD tests. All water chemistry variables, except conductivity (P = 0.024), potassium (P = 0.0029), and sodium (P = 0.0054) were highly significantly different ($P \leq 0.0001$) among areas. Of the physical variables, % open water was highly significantly different ($P \leq 0.0001$), and SI (P = 0.83) and size (P = 0.45) were not different among areas.

ing waterfowl than wetlands with a lower nutrient content. Based on higher mean alkalinity, cation concentrations, conductivity, total phosphorus, and water color, we conclude that Mallards and Black Ducks occupy wetlands that are more fertile than are unoccupied wetlands and that they also breed at higher densities in more fertile areas. On average, shared wetlands or Mallard only wetlands were more fertile than were Black Duck only wetlands. Vacant wetlands and areas with few breeding Mallards or Black Ducks were least fertile. Thus, as in southern Ontario (Merendino et al. 1992, 1993), wetland fertility apparently influences abundance and distribution of Mallards and Black Ducks in central Ontario. Our data support McNicol et al. (1987) who suggested that breeding waterfowl densities in central Ontario were highest in areas where the habitat appeared most fertile. Likewise, high breeding densities of Mallards in the Clay Belt area of northeastern Ontario (Ross and Fillman 1990) are likely due to abundance of productive wetlands there.

Although some temperate nesting ducks use nutrient stores obtained on wintering grounds to reproduce, migration costs result in supplemental nutrients being needed for successful reproduction (Owen and Reinecke 1977, Krapu 1981, Ankney et al. 1991). Generally, nutrients needed by Mallards and Black Ducks for reproduction, maintenance, and growth, especially sources of calcium, carbohydrate and protein rich plants, and invertebrates, are more available on more productive wetlands (Moyle 1956, Patterson 1972, Reinecke and Owen 1980, Ringelman et al. 1982a, DesGranges and Hunter 1987). The relatively small home range sizes of Mallards and Black Ducks that breed in forested habitats (Ringelman et al. 1982a, Dwyer 1992) may be the consequence of high energetic costs related to expanding territories in relatively infertile areas (Ringelman et al. 1982a), such as central Ontario. Therefore, selection of productive wetlands by nesting and brood rearing females is necessary to meet costs of reproduction, molt, and duckling growth (Ringelman et al. 1982b). For example, Patterson (1976) indicated that broods and fledged waterfowl generally concentrated on highly fertile wetlands in Ontario, and Ringelman et al. (1982a) indicated that breeding Black Ducks avoided wetland habitat types that supported low invertebrate densities. Wetland occupancy rates (e.g., percentage of wetlands used by breeding waterfowl) in central and southern

Ontario were approximately 45% (Ross 1987, McNicol et al. 1987) and 26% (Merendino 1993), respectively, so there is an abundance of wetlands available to breeding waterfowl. Our results indicate that Mallards and Black Ducks select the most fertile wetlands from those available. Habitat preferences (Ringelman et al. 1982a, Dwyer 1992) appear to be influenced by cover and invertebrate densities (Ringelman et al. 1982a).

Breeding Mallards were virtually absent from northern (Hanson et al. 1949) and central (Collins 1974) Ontario before 1950; thus, areas that are now dominated by Mallards were historically the exclusive domain of Black Ducks. Dwyer (1992) reported a similar scenario in the Adirondack Mountains of western New York. Preliminary examinations by Ross (1987) in northern Ontario indicated that breeding Black Ducks occupied a wider range of habitats than did Mallards. It is unclear if this indicates that Mallards are more habitat restricted than are Black Ducks (Ross 1987, Ross and Fillman 1990) or if Mallards first invaded the more productive areas (Merendino et al. 1993). Mallards and Black Ducks used similar habitat types in western New York (Dwyer 1992) and in areas of central and western Ontario (Dennis 1974, Dennis and North 1984). Our results further indicate that Mallards and Black Ducks select for similar wetland characteristics (i.e., high fertility, moderate open water, high SI, and small size) and that Mallards, on average, solely occupy or share with Black Ducks the most fertile wetlands.

Mallards and Black Ducks treat each other as conspecifics (Brodsky and Weatherhead 1984, Seymour 1990). Therefore, although some wetlands may have sufficient resources for several breeding pairs, inter- and intra-specific competition/aggression between Mallards and Black Ducks likely prevents overlap in use of many of them (Seymour 1990). Thus, we suggest that competitive exclusion likely explains why Mallards generally occupy the most fertile wetlands and dominate the most fertile areas in central Ontario. Studies of free ranging (Brodsky and Weatherhead 1984, Seymour 1990) and captive (Brodsky et al. 1988) Mallards and Black Ducks indicate that male Mallards are competitively superior to male Black Ducks when competing for a female. Therefore, Mallards may be superior to Black Ducks when acquiring and defending the best breeding sites (e.g., fertile wetlands).

Although anecdotal, evidence suggests that, on average, Black Ducks arrive on Ontario breeding areas 3–5 days before Mallards (Saunders and Dale 1933, Brooman 1954, Mills 1981). Thus, Black Ducks apparently have first opportunity to occupy productive wetlands. Pair : flock and male : female ratios (D'Eon 1992), however, indicate that, on average, Mallards begin nesting before Black Ducks do. Mallards initiate courtship activities earlier than do Black Ducks (Brodsky and Weatherhead 1984), perhaps because adult male Mallards have larger lipid reserves than do adult male Black Ducks in late autumn (Hanson et al. 1990). Moreover, because paired waterfowl are dominant to unpaired waterfowl (Hepp and Hair 1984), paired Mallards may exclude unpaired Black Ducks from productive winter feeding sites. Thus, female Mallards may store sufficient nutrients (Heitmeyer 1988) to begin nesting activities before female Black Ducks, and therefore, Mallard pairs may more aggressively occupy and defend productive wetlands. Similarly, if Black Duck females arrive on breeding areas with low energy reserves, they then must increase those reserves before nest initiation (Owen and Reinecke 1977). Given the relative scarcity of foods in early spring, Black Duck nest initiation would be delayed relative to that of Mallards.

Occupation of more fertile wetlands (i.e., better food supply) by Mallards might result in earlier nesting chronology (D'Eon 1992), larger clutch size (Laperle 1974), higher renesting frequency (Dwyer 1992), and increased duckling growth and survival (Desgranges and Hunter 1987); if so, further increases in Mallard and consequent decreases in Black Duck numbers may result (Ankney et al. 1987, Nichols et al. 1987). More research is needed to clarify the relation and interaction between wintering areas, food habits, nutrient reserves, nest initiation, and habitat use by Mallards and Black Ducks.

If central Ontario's Mallard population continues to increase, as at present (Ross, 1992, Can. Wildlife Ser., unpubl. report), there may be two negative consequences for Black Ducks. First, Mallards likely will displace Black Ducks from productive wetlands (Merendino et al. 1993). This may lower Black Duck reproductive rates, further exacerbating relative changes in Mallard and Black Duck numbers (Nichols et al. 1987). Second, it will lead to increased hybridization with Mallards (Ankney et al. 1987) and, ultimately, further the decline of Black Ducks (Ankney et al. 1987, D'Eon 1992). Results of future breeding pair surveys in central Ontario will shed further light on this scenario.

ACKNOWLEDGMENTS

M. E. Heitmeyer and an anonymous referee provided critical review of the manuscript. This research benefited greatly from comments by S. G. Curtis, D. G. Dennis, G. B. McCullough, D. K. McNicol, N. R. North, and R. K. Ross of CWS. R. K. Ross kindly provided access to unpublished CWS waterfowl survey data and maps of plot locations. Financial support was provided through the Black Duck Joint Venture via CWS and the Nature Conservancy of Canada, and by the Ontario Federation of Anglers and Hunters. Thanks to D. Kurylo and the Great Lakes Forestry Research Center, Sault Ste. Marie, Ontario, for water chemistry analyses. Field assistance was provided by J. Lozano, D. Hoysak, and S. Loughheed. We thank helicopter pilots L. McTaggert (Canadian Helicopters) and M. Fleming and M. Trottier (SkyTech Aviation) for their assistance in collecting water samples.

LITERATURE CITED

ANKNEY, C. D., D. G. DENNIS, AND R. C. BAILEY. 1987. Increasing Mallards, decreasing American Black Ducks: coincidence or cause and effect? J. Wildl. Manage. 51:523–529.

ANKNEY, C. D., D. G. DENNIS, AND R. C. BAILEY. 1989. Increasing Mallards, decreasing American Black Ducks—no evidence for cause and effect: a reply. J. Wildl. Manage. 53:1072–1075.

ANKNEY, C. D., A. D. AFTON, AND R. T. ALISAUSKAS. 1991. The role of nutrient reserves in limiting waterfowl reproduction. Condor 93:1029–1032.

BLANCHER, P. J., AND D. G. MCAULEY. 1987. Influence of wetland acidity on avian breeding success. Trans. N. Am. Wildl. Natur. Resour. Conf. 52: 628–635.

BRODSKY, L. M., AND P. J. WEATHERHEAD. 1984. Behavioral and ecological factors contributing to American Black Duck-Mallard hybridization. J. Wildl. Manage. 48:846–852.

BRODSKY, L. M., C. D. ANKNEY, AND D. G. DENNIS. 1988. The influence of male dominance on social interactions in Black Ducks and Mallards. Anim. Behav. 36:1371–1378.

BROOKSBANK, P., J. HAEMMERLI, G. HOWELL, AND L. JOHNSTON. 1989. Long range transport of airborne pollutants (LRTAP) aquatic effects monitoring. Environment Canada, Inland Waters Directorate, Ottawa. Tech. Bull. 156.

BROOMAN, R. C. 1954. History of the birds of Kingston, Ontario. Gilbert Press, St. Thomas, Ontario, Canada.

COLE, G. A. 1983. Textbook of limnology. 3rd ed. C. V. Mosby, St. Louis, MO.

COLLINS, J. M. 1974. The relative abundance of ducks breeding in southern Ontario in 1951 and 1971, p. 32–44. *In* H. Boyd [ed.], Canadian Wildlife Service waterfowl studies in eastern Canada, 1969–1973. Can. Wildl. Serv. Rep. Ser. No. 29.

DENNIS, D. G. 1974. Waterfowl observations during the nesting season in Precambrian and clay belt areas of north-central Ontario, p. 53–56. *In* H. Boyd [ed.], Canadian Wildlife Service Waterfowl Studies in eastern Canada, 1969–1973. Can. Wildl. Serv. Rep. Ser. No. 29.

DENNIS, D. G., AND N. R. NORTH. 1984. Waterfowl densities in northwestern Ontario during the 1979 breeding season, p. 6–9. *In* S. G. Curtis, D. G. Dennis, and H. Boyd [eds.], Waterfowl studies in Ontario, 1973–1981. Can. Wildl. Serv. Occas. Pap. No. 54.

DENNIS, D. G., G. B. MCCULLOUGH, N. R. NORTH, AND B. COLLINS. 1989. Surveys of breeding waterfowl in southern Ontario, 1971–1987. Can. Wildl. Serv. Prog. Note 180.

D'EON, R. G. 1992. Black Duck-Mallard behavioural interactions in relation to hybridization. M.Sc. thesis, University of New Brunswick, Canada.

DESGRANGES, J. L., AND M. DARVEAU. 1985. Effect of lake acidity and morphometry on the distribution of aquatic birds in southern Quebec. Holarct. Ecol. 8:181–190.

DESGRANGES, J. L., AND M. L. HUNTER. 1987. Duckling response to lake acidification. Trans. N. Am. Wildl. Natur. Conf. 52:636–644.

DWYER, C. P. 1992. The breeding ecology of sympatric Mallards and American Black Ducks in the western Adirondacks. M.Sc.thesis, State University of New York, Syracuse, NY.

EILERS, J. M., G. E. GLASS, A. K. POLLACK, AND J. A. SORENSEN. 1989. Changes in conductivity, alkalinity, calcium, and pH during a 50-year period in selected northern Wisconsin Lakes. Can. J. Fish. Aquat. Sci. 46:1929–1944.

HANSON, A. R., C. D. ANKNEY, AND D. G. DENNIS. 1990. Body weight and lipid reserves of American Black Ducks and Mallards during autumn. Can. J. Zool. 68:2098–2104.

HANSON, H. C., M. ROGERS, AND E. S. ROGERS. 1949. Waterfowl of the forested portions of the Canadian Pre-Cambrian Shield and the Palaeozoic Basin. Can. Field. Nat. 63:183–204.

HEITMEYER, M. E. 1988. Body composition of female Mallards in winter in relation to annual cycle events. Condor 90:669–680.

HEPP, G. A., AND J. D. HAIR. 1984. Dominance in wintering waterfowl (*Anitini*): effects of distribution of sexes. Condor 86:251–257.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

LAPERLE, M. 1974. Effects of water level fluctuation on duck breeding success, p. 18–30. *In* H. Boyd [ed.], Canadian Wildlife Service waterfowl studies in eastern Canada, 1969–1973. Can Wildl. Serv. Rep. Ser. No. 29.

LEWIS, W. J. 1982. Changes in pH and buffering capacity of lakes in the Colorado Rockies. Limnol. Oceanogr. 27:167–172.

MCAULEY, D. G., AND J. R. LONGCORE. 1988. Foods of juvenile Ring-necked Ducks: relationship to wetland pH. J. Wildl. Manage. 52:177–185.

MCNICOL, D. K., B. E. BENDELL, AND R. K. ROSS. 1987. Studies of the effects of acidification on aquatic wildlife in Ontario. Can. Wild. Serv. Occas. Pap. 62.

MERENDINO, M. T. 1993. The relationship between wetland productivity and the distribution of breeding Mallards, Black Ducks, and their broods. Ph.D.diss., University of Western Ontario, London, Canada.

MERENDINO, M. T., D. G. DENNIS, AND C. D. ANKNEY. 1992. Mallard harvest data: index of wetland quality for breeding waterfowl. Wildl. Soc. Bull. 20:171–175.

MERENDINO, M. T., C. D. ANKNEY, AND D. G. DENNIS. 1993. Increasing Mallards, decreasing American Black Ducks: more evidence for cause and effect. J. Wildl. Manage. 57:199–208.

MILLS, A. 1981. A cottager's guide to the birds of Muskoka and Parry Sound. Ampersand Printing, Guelph, Ontario, Canada.

MOYLE, J. B. 1956. Relationships between the chemistry of Minnesota surface waters and wildlife management. J. Wildl. Manage. 20:303–320.

MURPHY, S. M., B. KESSEL, AND L. J. VINING. 1984. Waterfowl populations and limnological characteristics of taiga ponds. J. Wildl. Manage. 48:1156–1163.

NICHOLS, J. D., H. H. OBRECHT, AND J. E. HINES. 1987. Survival and band recovery rates of sympatric American Black Ducks and Mallards. J. Wildl. Manage. 51:700–710.

OWEN, R. B., AND K. J. REINECKE. 1977. Bioenergetics of breeding dabbling ducks, p. 71–93. *In* T. A. Bookhout [ed.], Waterfowl and wetlands—an integrated review. The Wildlife Society, Madison, WI.

PATTERSON, J. H. 1972. The role of wetland heterogeneity in the regulation of duck populations in eastern Ontario. Ph.D.thesis, Carleton University, Ottawa, Canada.

PATTERSON, J. H. 1976. The role of environmental heterogeneity in the regulation of duck populations. J. Wildl. Manage. 40:22–32.

REID, G. K. 1961. Ecology of inland waters and estuaries. Van Nostrand Reinhold, New York.

REINECKE, K. J., AND R. B. OWEN. 1980. Food use and nutrition of Black Ducks nesting in Maine. J. Wildl. Manage. 44:549–558.

RINGELMAN, J. K., J. R. LONGCORE, AND R. B. OWEN. 1982a. Breeding habitat selection and home range of radio-marked Black Ducks (*Anas rubripes*) in Maine. Can. J. Zool. 60:241–248.

RINGELMAN, J. K., J. R. LONGCORE, AND R. B. OWEN. 1982b. Nest and brood attentiveness in female Black Ducks. Condor 84:110–116.

ROSS, R. K. 1987. Interim report on waterfowl breeding pair surveys in northern Ontario, 1980–1983. Can. Wildl. Serv. Prog. Note 168.

ROSS, R. K., AND D. FILLMAN. 1990. Distribution of American Black Duck and Mallard in northern Ontario. Can. Wildl. Serv. Prog. Note 189.

RUSCH, D. H., C. D. ANKNEY, H. BOYD, J. R. LONGCORE, F. MONTALBANO, J. K. RINGELMAN, AND V. D. STOTTS. 1989. Population ecology and harvest of the American Black Duck: a review. Wildl. Soc. Bull. 17:379–406.

RYDER, R. A. 1964. Chemical characteristics of Ontario lakes as related to glacial history. Trans. Am. Fish Soc. 93:260–268.

SAS INSTITUTE, INC. 1985. SAS user's guide: statistics. SAS Institute, Inc., Carey, NC.

SAUNDERS, W. E., AND E.M.S. DALE. 1933. History and list of birds of Middlesex County, Ontario. Trans. Roy. Can. Inst. 19:161–250.

SEYMOUR, N. R. 1990. Forced copulations in sympatric American Black Ducks and Mallards in Nova Scotia. Can. J. Zool. 68:1691–1696.

WATT, W. D., D. SCOTT, AND S. RAY. 1979. Acidification and other chemical changes in Halifax County lakes after 21 years. Limnol. Oceanogr. 24:1154–1161.