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The Relationship Between Wetland Productivity And The Distribution Of Breeding Mallards, Black Ducks, And Their Broods: Historical And Spatial Analysis

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THE RELATIONSHIP BETWEEN WETLAND PRODUCTIVITY AND THE DISTRIBUTION OF BREEDING MALLARDS, BLACK DUCKS, AND THEIR BROODS: HISTORICAL AND SPATIAL ANALYSIS

by

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ABSTRACT

During the last 50 years mallards have increased dramatically in southern Ontario and have completely replaced black ducks in many areas. In northern Ontario, black duck densities appear stable at present, however, mallard densities now exceed 60 pairs / 100 km^2 in many areas. I examined historical and spatial distributions of mallards and black ducks in Ontario in relation to water chemistry and physical habitat characteristics. My objectives were to determine 1) if mallards invaded the most fertile wetlands, and 2) if mallards replaced black ducks on the most productive wetlands.

I used Canadian Wildlife Service survey data (1971-87) to define 7 wetland categories regarding changes in mallard and black duck distributions in southern Ontario. In northern Ontario, I used 1990-1992 breeding pair survey data to define wetlands as used by mallards only, black ducks only, shared, or vacant. Habitat was evaluated based on water chemistry and physical characteristics.

In southern Ontario, wetlands where mallards first appeared were, on average, more fertile than those where mallards later appeared. Wetlands where mallards first replaced black ducks were more fertile than those where black ducks were replaced later. On Canadian Wildlife Service plots in southern Ontario, black ducks persist only on wetlands with extremely low fertility. Major conclusions

for southern Ontario:

1. Mallards did not invade southern Ontario randomly with respect to wetland fertility, but invaded the most fertile wetlands first.

2. Mallards replaced black ducks from fertile wetlands, and black ducks are now restricted to the least fertile area of southern Ontario.

In north-central Ontario, mallards occupy the most fertile wetlands, with areas dominated by mallards having the most fertile wetlands. Major conclusions for northern Ontario:

1. Wetland fertility has played a major role in the distribution and abundance of mallards in north-central Ontario.

2. Areas that support the most breeding mallards have the most productive wetlands.

3. Mallards and black ducks appear to select for similar wetland characteristics and likely compete for breeding sites.

Mallards and black ducks are ecological equivalents, therefore competition for breeding sites is likely. Of the many factors suggested as causing the decline of the black duck the mallard may be having the most significant impact.

It is not only an amusing, but also a highly instructive undertaking to investigate the deeper roots of the life-interest that moves a scientist, and particularly to find out what made him choose the object to which he devotes most of his work. I am able to, and I am going to give very sound rational reasons why I consider waterfowl are among the most rewarding subjects of ethological and other kinds of biological study. Yet I should be guilty of a lie if I pretended that these were my motives in turning to this order of birds in the first place.

Konrad Lorenz (International Zoology Yearbook, 1973)

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CHAPTER 1

GENERAL INTRODUCTION

1.1. REVIEW OF MALLARD AND BLACK DUCK RELATIONS

Throughout the world there are many "mallard-like" ducks (Delacour 1954) all of which are believed to have evolved from the common mallard (*Anas platyrhynchos*) (Johnsgard 1961a, Heusmann 1974). There were formerly 4 species and 2 subspecies in North America (Johnsgard 1961a). Most mallard-like species are reproductively isolated from one another by significant ecological barriers, mainly space. However, in North America such barriers (e.g., geography, habitat use, behavior) have either broken down or were never fully evolved, especially between mallards and American black ducks (*A. rupripes*); hereafter called black ducks (Johnsgard 1961a, Johnsgard 1967). Hybrid frequencies between mallards and black ducks average 5% across the black duck breeding range and approach 18% in some areas (Rusch et al. 1989). Year round contact between mallards and black ducks has resulted from an eastward range expansion by prairie nesting mallards into black duck breeding areas (Johnsgard 1961a, 1961b, 1967), the establishment of eastern mallard populations via game farm releases (Heusmann 1991), and utilization by mallards of forested breeding habitats (Dwyer 1992) and salt-marsh wintering habitats (Heusmann 1988) of the black duck.

Based upon genetic, morphologic, and behavior similarities, Johnsgard (1961a) concluded that the black duck was not a "good" species and should be considered a subspecies of the mallard. Ankney et al. (1986) concluded that genetic similarities and overlap of breeding range warranted the black duck being considered only a color morph of the mallard (Avise et al. 1989). Hepp et al. (1988) criticized Ankney et al's. (1986) taxonomic suggestion and stated that some reproductive isolating mechanisms still existed between "wild" mallards and black ducks. However, these mechanisms are not strong enough to prevent mixed pairs from forming where the two species overlap (Heusmann 1974, Brodsky and Weatherhead 1984, Brodsky et al. 1988, Brodsky et al. 1989). Consequently, along with the colonization of black duck breeding habitat by mallards there has been a decline in black duck numbers, an increase in hybrid numbers, and a dramatic increase in the number of mallards (Goodwin 1956, Johnsgard 1961a, 1961b, Ankney et al. 1987). The most dramatic changes have occurred in southern Ontario (Collins 1974, Ankney et al. 1987) where Dennis et al. (1989) estimated that the mallard population has a doubling time of 42 years, whereas, the black duck population has a half-life of 11 years. Similar changes have occurred in northwestern Ontario (Boyd 1984, Ankney et al. 1987). In north-central Ontario, mallards have increased from being virtually absent in the 1950's (Hanson et al. 1949) to breeding densities of over 60 pairs / 100km^2

in many areas (Ross 1992). Black duck populations in north-central Ontario appear stable at present (Ross 1992). The continental black duck population has been in a long-term decline since 1955, averaging 3-5% per year (Rusch et al. 1989).

1.2 AIM OF RESEARCH

From the previous discussion it is easy to see why studies of mallards and black ducks are so interesting and important with regard to taxonomy, ecology, and waterfowl management. Hunting, habitat loss / alteration, pesticides, acid rain and an increasing mallard population have been suggested as causing the decline of black ducks (Rusch et al. 1989). That mallards may be the most significant factor contributing to the decline of black ducks represents an "unmanageable" situation (Ankney et al. 1987).

My study was conducted to provide information concerning the role that mallards may have played in the decline of black ducks. The fact that mallards have expanded their breeding range into that of the black duck in conjunction with the black duck's apparent lack of competitive ability (see Kirby 1988, Brodsky et al. 1988, Seymour 1990) provided the major question that I asked in this study: Are the wetlands used by mallards during the breeding season more fertile (section 1.2.1, 2.3.1) than those used by black ducks? I used two approaches to answer this question: 1) an analysis of historical changes in mallard and black duck distributions in southern Ontario, and 2) an evaluation of the characteristics of wetlands currently used by sympatric breeding mallards and black ducks and their broods in north-central Ontario.

1.2.1. Wetland Fertility / Productivity

The productivity of wetland systems can be classified into 3 major groups (Cole 1983). Wetlands with a higher nutrient content (eutrophic) are more fertile and more productive (e.g., produce higher biomass) than those with a lower nutrient content (oligotrophic) (Cole 1983, Environment Canada 1984). In eastern regions of Canada and the United States, wetland systems lying above sedimentary bedrock having higher nutrient content than wetlands lying above metamorphic bedrock (Patterson 1972). Numerous water chemical constituents can be related to wetland fertility and productivity (Cole 1983, Environment Canada 1984). I chose pH, conductivity, alkalinity ($CaCO_3$), calcium, magnesium, potassium, color, and total phosphorus because those variables have been shown to be related to the fertility and productivity of wetlands in eastern North America (Moyle 1945, 1956, Bennett 1962, Cole 1983, Environnent Canada 1984), especially with regards to waterfowl (Moyle 1956, Patterson 1972, 1976, Murphy et al. 1984, Desgranges and Darveau 1985, Blancher and McCauley 1987, Desgranges and Hunter 1987, McNicol et al. 1987, Alvo et al. 1988, McCauley and Longcore 1988, Swanson and

Duebbert 1989, Sparling 1990, Parker et al. 1992) (see section 2.3.1). For purposes of my study, I will refer to wetlands with a high nutrient content as being more fertile and potentially more productive for breeding waterfowl than wetlands with a lower nutrient content.

1.3 SOUTHERN ONTARIO OBJECTIVES AND HYPOTHESES

As mallards moved east along the Great Lakes and north into the Pre-Cambrian shield (Dennis 1974a, Dennis and North 1984, Ross et al. 1984), the black duck breeding range has been restricted to areas farther east and north (Collins 1974, Ross et al. 1984, Kirby 1988). Across southern Ontario there is a gradient of wetland productivity from highly productive wetlands in the southwest to less productive wetlands in the east and north (Ryder 1964, Sparling and Nalewajko 1970, see Patterson 1972). This indicates that mallards may be occupying the "best" habitats and as a result black ducks may now occupy "poorer" habitats. The degree to which this is true and the consequence of such distribution is unknown. The major objectives in southern Ontario were to:

1. Document the historical pattern of mallard invasion into southern Ontario in relation to wetland fertility to determine if mallards first invaded fertile wetlands.
2. Determine if mallards had replaced black ducks on the most fertile wetlands.

I tested the null hypotheses that:

1. Wetlands that have had mallards since 1971 do not differ in fertility from either those more recently colonized by mallards or those used by black ducks since 1971.
2. Wetlands where breeding mallards have replaced breeding black ducks do not differ in fertility from wetlands where black ducks have not been replaced.

1.4 NORTH-CENTRAL ONTARIO OBJECTIVES AND HYPOTHESES

Although mallards were virtually absent from north-central Ontario as recently as 1950 (Hanson et al. 1949), mallards have increased dramatically and in some areas exceed 60 pairs / 100 km^2 (Ross 1992). Unlike southern Ontario where black ducks appeared to be quickly replaced by mallards, the black duck population in north-central Ontario is presently stable with breeding densities in some areas exceeding 40 pairs / 100 km^2 (Ross 1992). Overall, breeding densities of mallards and black ducks exhibit a wide range of spatial variability which suggests that habitat quality may be influencing their distributions. Given that breeding mallards and black ducks exhibit similar behaviours (Johnsgard 1961a, Brodsky and Weatherhead 1984, Seymour 1990), competition for resources such as mates, food, breeding sites, etc., likely occurs where they are sympatric.

The major objectives in north-central Ontario were to determine: 1) if mallards were occupying the most fertile wetlands relative to black ducks, 2) if mallard densities were highest in the most fertile area, and 3) compare habitat characteristics of wetlands used by mallard broods to those used by black duck broods.

I tested the null hypotheses that:

1. Characteristics of used wetlands (used by either breeding mallards, black ducks, or their broods) do not differ from a random sample of non-used wetlands.
2. Characteristics of wetlands used by breeding mallards do not differ from those used by breeding black ducks.
3. Characteristics of wetlands used by mallard broods do not differ from those used by black duck broods.

If competition and/or competitive exclusion was occurring in north-central Ontario then I predicted that:

1) mallards would occupy the most fertile wetlands and
2) areas with the highest mallard : black duck ratio would have the most fertile wetlands.

All predictions were based on the assumption that within and among plots mallards have invaded the most fertile wetlands.

1.5 THESIS FORMAT

This thesis is comprised of 5 chapters. The introductory (and present) chapter provides a general overview of mallard and black duck relations, trends in research, and study objectives. Chapter 2 provides brief life-history information on mallards and black ducks and describes the study areas and methodology. Chapter 3 is a study of historical changes in mallard and black duck distributions in southern Ontario in relation to wetland fertility and physical characteristics. Chapter 4 is a study of habitat use by sympatric breeding mallards and black ducks and their broods in north-central Ontario. Chapter 5, the concluding chapter, discusses the role that hunting, habitat loss, pesticides, etc., and the mallard have likely played in the decline of the black duck.

CHAPTER 2

STUDY ORGANISMS, STUDY AREAS, GENERAL METHODS

2.1 STUDY ORGANISMS

Mallards and black ducks are basically ecological equivalents (Bellrose 1980) being similar in morphology, behaviour, and genetics (see Chapter 1, Johnsgard 1961a, Ankney et al. 1986).

2.1.1 Breeding ranges and densities

The principal breeding range of the mallard is centered in the prairie pothole region of the United States and Canada which supports nearly 5 million breeding mallards and densities of up to 20 pairs per square mile (Bellrose 1980). Mallards have expanded their breeding range into eastern North America and have rapidly increased in many areas (Johnsgard 1961b, Johnsgard 1967, Collins 1974, Ross et al. 1984, Ankney et al. 1987, Dennis et al. 1989). Breeding mallards were extremely rare in Ontario prior to the 1950's (Saunders and Dale 1933, Hanson et al. 1949, Brooman 1954). Today, however, southwestern and south-central areas of southern Ontario support over 186 and 152 pairs / 100 km^2, respectively, with 75 pairs / 100 km^2 breeding in the Precambrian shield area (Gary McCullough, Can. Wildl. Serv. pers. commun. 1992). In northern and central Ontario, breeding mallard densities average 40 - 80 pairs / 100 km^2 in the Lake-of-the Woods area, at Cape Henrietta Maria, along the James Bay coast, and in the Sudbury - Lake Nipissing - Parry Sound area (Ross and Fillman 1990) and average nearly 19 pairs / 100 km^2 throughout northeastern Ontario (Ross 1992). Mallards now occur throughout most of the black duck breeding range in Ontario and elsewhere and also outnumber and have replaced black ducks in many areas.

The breeding range of the black duck is restricted to the northern tier of U.S. states east of the Mississippi River, north through the boreal forest of Canada to the James and Hudson's Bay coasts and east to Labrador and Newfoundland (Kortright 1942, Bellrose 1980). Breeding densities are highest in the forested regions of the Great Lakes and St. Lawrence River, St. John's River Valley in New Brunswick, and salt marshes of the Atlantic Coast (Bellrose 1980). In northern and central Ontario, highest black duck densities occur near Cape Henrietta Maria on the Hudson Bay coast (40 - 80 pairs / 100 km^2) and in the Sudbury - Lake Nipissing - Parry Sound - Algonquin Park area (20 - 40 pairs / 100km^2) (Ross and Fillman 1990) and average nearly 21 pairs / 100km^2 throughout northern and north-central Ontario (Ross 1992). In southern Ontario, highest breeding densities (26 pairs / 100 km^2) occur in the pre-Cambrian shield area (Gary McCullough, Can. Wildl. Serv. pers. commun. 1992). Historically, black ducks were common breeders throughout southern Ontario (Saunders and Dale 1933, Brooman 1954, Alison 1976). Today, however, they have been replaced by mallards in many areas (Collins 1974, Ankney et al. 1987, Dennis et al. 1989). In north-central Ontario, black duck densities appear stable at present (Ross 1992).

2.1.2 Wintering areas

Traditionally, mallards wintered further south and more inland than did black ducks which generally wintered in coastal salt-marshes along the Atlantic Coast (Bellrose 1980). However, increased agriculture at northern latitudes has resulted in an abundance of waste grain (see Dennis et al. 1984) that enables mallards to winter as far north as open water prevails. Mallards commonly overwinter in ice-free rivers throughout Ontario (pers. obsv., C. D. Ankney, pers. comm.). Mallards are also over-wintering in northern urban areas as a result of being fed by people (Goodwin et al. 1977, Heusmann and Burrell 1984, Heusmann 1988).

The largest concentrations of black ducks winter in salt-marshes along the Atlantic Coast, south from the Maritimes to Chesapeake Bay; lesser concentrations winter in the Lake Erie marshes, the Tennessee River Valley, and river valleys south from Ohio to Mississippi (Bellrose 1980).

2.1.3 Breeding ecology / food habits

Mallards and black ducks arrive on breeding areas as soon as ice-out occurs and begin arriving in southern Ontario by late March (Saunders and Dale 1933, Brooman 1954) and central Ontario in mid-April (Mills 1981). It should be noted, however, that mallards and black ducks commonly overwinter on ice-free rivers throughout southern Ontario (e.g., Thames River [pers. observ.] and Ottawa River [Brodsky and Weatherhead 1984]). Breeding mallards and black ducks use a variety of wetland, upland, and man-made nesting sites and overlap extensively in the types of habitats used (Stotts and Davis 1960, Laperle 1974, Dennis 1974a,b, Ringelman et al. 1982, Dwyer 1992). Both species exhibit territoriality and aggression during the breeding season (Brodsky et al. 1988, Seymour 1990). Mallards appear to begin nesting slightly earlier than do black ducks, based upon pair:flock ratios (Ross 1991) and male:female ratios (D'Eon 1992) and also on nests found (Laperle 1974). Incubation duration, clutch size, nesting success, hen survival, and growth and development of ducklings is similar between mallards and black ducks (Laperle 1974, Bellrose 1980, see also Dwyer 1992). Additionally, although both mallards and black ducks will renest, this behavior appears more prevalent in the mallard (see Bellrose 1980, Dwyer 1992) and this may give mallards a slight recruitment advantage over black ducks (see Laperle 1974).

Invertebrates are an important food resource to breeding females and ducklings of both species (Reinecke and Owen 1980, Swanson et al. 1985). Natural foods are supplemented with waste grain during winter (Bellrose 1980).

2.2 STUDY AREA

2.2.1 Southern Ontario.

The study area encompasses 51,000km^2 of Ontario, south of a line from the French River through Lake Nipissing to the Ottawa River (Fig. 2.1). The southern most portion of the study area, extending from Lake St. Clair to the Ontario/Quebec border, is underlain by calcareous bedrock, whereas the central portion of the study area is underlain by pre-Cambrian bedrock (see Ryder 1964, Sparling and Nalewajko 1970, Chapman and Putnam 1973, Scheider et al. 1979). Wetlands underlain by calcareous bedrock exhibit greater productivity than do wetlands within the pre-Cambrian shield area, due to higher pH, cation concentrations, and alkalinities (Ryder 1964, Sparling and Nalewajko 1970, Patterson 1972). Acid precipitation occurs throughout the study area (Dillon et al. 1978, Scheider et al. 1979, McNicol et al. 1987) further reducing the productivity (Scheider et al. 1979, McNicol et al. 1987) of many wetlands that were naturally relatively infertile due to the type of underlying bedrock (Moyle 1945, 1956, Ryder 1964, Sparling and Nalewajko 1970, Patterson 1972). Although the southwestern portion of the study area has undergone intense cultivation and urbanization since the early 1800's (Snell 1986), habitat within the central and eastern areas has remained relatively undisturbed (Dennis 1974, Dennis et al. 1989, Snell 1986) due to the topography

Figure 2.1. Delineation of southern Ontario study area.


ONTARIO
L. HURON
L. ONTARIO
NEW YORK, USA
L. ERIE

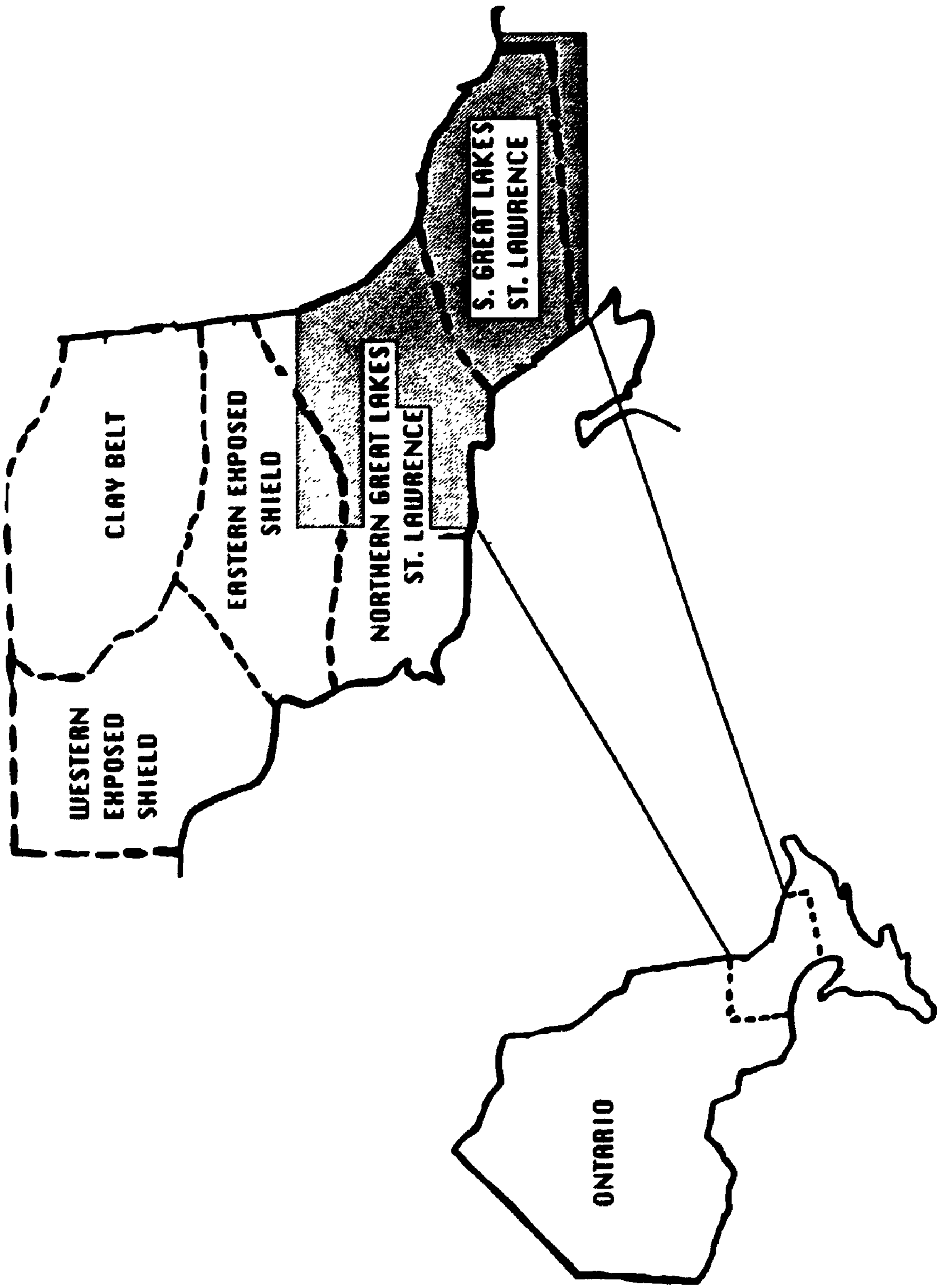
of the area which prevents agriculture.

There are a variety of wetland habitat types available for breeding waterfowl including deep and shallow emergent marshes, deciduous swamps, beaver floods, and man-made ponds and ditches (Appendix 1).

2.2.2 North-central Ontario

The study area encompasses 60,000 km^2 of north-central Ontario (Fig. 2.2). Most of the area is underlain by pre-Cambrian bedrock (Dennis 1974, Scheider et al. 1979, McNicol et al. 1987) and, thus, chemical concentrations and biological potential are much less than in most of southern Ontario (see section 2.2.1). Acid precipitation falls throughout the study area (Dillon et al. 1978, Pitblado et al. 1980, McNicol et al. 1987). The study area extends through 3 ecological zones (Fig. 2.2), these being southern and northern Great Lakes - St. Lawrence Forest area and eastern exposed shield (Ross 1992), along a 400 km northwest to southeast gradient and a 170 km southwest to northeast gradient. Wetland occupancy rates (percentage of wetlands used by breeding waterfowl) are approximately 45% (Ross 1987, McNicol et al. 1987), thus there are an abundance of wetlands available to breeding waterfowl. Habitat within the northern and western parts of the study area is dominated by coniferous forest, is quite hilly, and has an abundance of headwater wetlands (McNicol

Figure 2.2. Delineation of ecological zones (Ross 1992) and approximate limits of north-central Ontario study area (shaded).


S. GREAT LAKES
ST. LAWRENCE
NORTHERN GREAT LAKES
ST. LAWRENCE
EASTERN EXPOSED
SHIELD
CLAY BELT
WESTERN
EXPOSED
SHIELD
ONTARIO

et al. 1987). To the south and east, the habitat is more decidious and relatively flat (McNicol et al. 1987). Most habitat alteration within the study area is due to logging, cottage development (central Ontario), and agricultural practices (primarily southeast of Lake Nipissing and east of Sudbury) (see McNicol et al. 1987).

2.3 METHODS

In this section I present an overview of the water chemistry and physical characteristics that were used to evaluate wetlands. For more specific methodology see sections 3.2 and 4.3.3.

2.3.1 Water chemistry (Wetland Fertility)

Intensive sampling is generally required t- accurately quantify the abundance and diversity of invertebrate and plant species. Water chemistry variaLles, however, provide a relatively accurate index of overall wetland fertility and productivity (Moyle 1945, 1956, Northcote and Larkin 1956, Rawson 1960, Ryder 1964, Sparling and Nalewajko 1970, Patterson 1976, Desgranges and Darveau 1985, McNicol et al. 1987). The concentration of chemical constituents influences the types and abundance of vegetation, invertebrates, and fishes. Wetlands with high pH, cation, and alkalinity levels support a more abundant and diverse collection of plant and animal life than those with lower concentrations of those water chemistry constituents (see

Moyle 1945, 1956, Jahn and Hunt 1964, Crowder et al. 1976, Patterson 1976, Hellquist 1980, Murphy et al. 1984, Desgranges and Darveau 1985, McNicol et al. 1987, McCauley and Longcore 1988, Swanson and Duebbert 1989, Parker et al. 1992). Thus, it can be concluded that wetlands high in essential nutrients are more fertile and more productive than those wetlands with lower nutrient contents, especially for breeding waterfowl. Consequently, those more fertile wetlands are more attractive and productive for breeding and brood rearing waterfowl in that they provide the necessary nutrients for breeding, maintenance, growth, and survival (Patterson 1976, Desgranges and Darveau 1985, Desgranges and Hunter 1987, Blancher and McCauley 1987, McNicol et. al. 1987, McCauley and Longcore 1988, see also Sparling 1990).

Specifically, alkalinity [$CaCO_3$], calcium, pH, conductivity, phosphorus, and water color [indicator of organic content] are reflective of wetland fertility and productivity (Moyle 1945, 56, Bennett 1962, Patterson 1972, 76, Cole 1983), and are routinely evaluated in studies to assess waterbird abundance and distributions (Moyle 1956, Patterson 1972, 1976, Murphy et al. 1984, Desgranges and Darveau 1985, Longcore et al. 1987, Desgranges and Hunter 1987, McNicol et al. 1987, Alvo et al. 1988, Parker et al. 1992). I will refer to wetlands with a high pH, conductivity, alkalinity, color and cation concentration as being more fertile for breeding waterfowl than those wetlands with low pH, conductivity, alkalinity, color and cation concentrations.

Although a broad classification of fertility and productivity can be made based upon the glacial history of a lake, variation within glacial regions (Ryder 1964, see also McNicol et al. 1987) warrants the sampling of individual wetlands. Water samples were collected from 131 and 447 wetlands in southern and north-central Ontario, respectively. In southern Ontario water samples were collected from 14 May - 1 June 1990. In north-central Ontario 240 wetlands in the northern Great Lakes - St. Lawrence area were sampled, via helicopter, from 31 July - 3 August 1990 and 207 wetlands in the southern Great Lakes - St. Lawrence area were sampled from 22 July - 25 July 1991.

Two water samples (1 - 250ml sample [plastic bottle], 1 100-ml sample [glass bottle]) were taken from each wetland. In southern Ontario all samples were sub-surface grab samples; bottles were turned upside down and placed 10 - 15 cm below the water surface, turned right side-up and allowed to fill (Brooksbank et al. 1989). In north-central Ontario surface grab samples were taken from shallow wetlands (i.e., wetlands with emergents established toward the center of the wetland or with floating leaved plants over most of the wetland surface), whereas, a 1-m tube was used to take a column sample from deeper wetlands (i.e., wetlands where emergents were only established around the edge) (see McNicol et al. 1987). In the field, samples were kept in coolers and then transferred to a refrigerator and stored at 4°C.

The 250-ml samples [plastic bottles] were analyzed for pH, conductivity, alkalinity, calcium, magnesium, sodium, potassium. The 100-ml samples [glass bottles] were analyzed for total phosphorus, apparent color (north-central Ontario only), and true color (north-central Ontario only). In southern Ontario conductivity and pH were determined on site with portable meters, whereas, in north-central Ontario determinations were made at the end of each day (except for 1991 when samples were shipped to University of Western Ontario and kept in cold storage for 5 days prior to pH and conductivity determinations). Apparent color (before fine filtering; Whatman #41 filter [0.45 μm]) and true color (after filtering) were determined with an Hellige Aqua Tester. Alkalinity, cation, and total phosphorus analyses were conducted by personnel of the Great Lakes Forestry Research Center in Sault Ste. Marie, Ontario (see sections 3.2 and 4.3.3 for treatment of samples prior to being sent to the lab).

Although water chemistry varies seasonally and spatially within a wetland (Labaugh 1989, Swanson et al. 1988) water samples collected one time during the year are routinely used to characterize wetlands. Breeding waterfowl are using these wetlands only from late March - early April through late August, therefore, the water chemistry components that are influencing waterfowl use of a particular wetland are of most importance and interest during that time period. 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). However, water chemistry characteristics are quite similar during the period that wetlands are used by breeding waterfowl (e.g., April - September), especially in the relatively infertile wetlands of north-central Ontario (see Ryder 1964, Patterson 1972, McNicol et al. 1987). Thus, a single sample during this period should be an accurate representation of the wetlands water chemistry (Ryder 1964) and its influence on invertebrate and plant production and waterfowl use.

One-time sampling is commonly employed in waterbird studies (McNicol et al. 1987, Alvo et al. 1988, McCauley and Longcore 1988, Parker 1992). Furthermore, Ryder (1964) reported little within wetland variation at any one sampling period, and given the small size and shallowness of most wetlands in my study area, there was little need for multiple sampling within a wetland. Multiple samples taken within Plot 18 in 1990, whether surface grab, tube sample, or a combination of samples, indicated that there was little within wetland variation (Merendino unpubl.). Unlike wetlands of the prairie pothole region that undergo dramatic water level fluctuations and, therefore, dramatic changes in nutrient levels (Swanson and Duebbert 1989, Swanson et al. 1988, Labaugh 1989), water levels in most wetlands in north-central Ontario are relatively stable. Thus, short-term changes in water chemistry are probably slight (see data from Patterson 1972). Over the long-term water chemistry is remarkably stable, with changes being most significant within developed areas (e.g., as a result of agricultural or urban run-off) and areas impacted by acid precipitation (Watt et al. 1979, Lewis 1982, Eilers et al. 1989).

2.3.2 Physical characteristics

Physical characteristics (e.g., size, cover, edge, interspersion, etc.) of a wetland influence use by breeding and brood rearing waterfowl (Kaminski and Prince 1981, Swanson and Deubbert 1989). Breeding dabbling ducks generally prefer smaller wetlands with an abundance of cover and open water interspersion rather than larger, less vegetated wetlands (Weller and Spatcher 1965, Kaminski and Prince 1981, Ringelman and Longcore 1982, McNicol et al. 1987, Swanson and Duebbert 1989). Isolating mechanisms (e.g., cover, edge, shoreline irregularity, size) further influence wetland selection by breeding waterfowl (Dzubin 1969, Patterson 1976, Godin and Joyner 1981, Desgranges and Darveau 1985, McNicol et al. 1987). It has been suggested that breeding black ducks are less tolerant to disturbance (e.g., roadways, dwellings, forest clearing) than are mallards and that disturbance has played a role in the decline of black ducks in some areas (see Kirby 1988, Dieffenbach and Owen 1989). Other studies (Ringelman and Longcore 1982, Dwyer 1992) suggest that disturbance has little to influence on mallard distributions.

Physical characteristics that I evaluated were: shoreline irregularity index (SI), size, percent emergent cover (southern Ontario) or percent open water (northern Ontario), distance to disturbance (southern Ontario only), and growing degree days (southern Ontario only). An SI value of 1.0 indicated perfectly round wetlands, whereas values >1.0 indicated increasingly irregular shorelines. Percent open water and percent emergent cover were visually assessed during the period of water sampling described above. Size, SI, and distance to disturbance data were measured from aerial photos. Growing degree days were obtained from Environment Canada (1984). Although growing degree days are a measure of productivity (Environment Canada 1984), and possibly should be included with the water chemistry sections given their potential to be a productivity index, I have placed them in the physical characteristic section given their influence on the establishment of vegetation. See sections 3.2 and 4.3.3 for specific methodology regarding the evaluation of physical habitat characteristics.

CHAPTER 3

HISTORICAL CHANGES IN MALLARD AND BLACK DUCK DISTRIBUTIONS IN SOUTHERN ONTARIO IN RELATION TO WETLAND FERTILITY

3.1 INTRODUCTION

Historically, American black ducks (hereafter called black ducks) commonly bred in most of southern Ontario (Alison 1976), but the region is now dominated by breeding mallards (Dennis et al. 1989). Hanson et al. (1949) reported few mallards east of the Manitoba/Ontario border, but by 1959 mallards were common breeders in southern Ontario (see Collins 1974). In southern Ontario, mallards increased 600% between 1951-1971, whereas black ducks decreased 50% (Collins 1974); from 1971-1985, mallards increased another 51% while black ducks decreased 38% (Ankney et al. 1987). As their numbers increased, mallards moved east along the Great Lakes and north into the pre-Cambrian shield of Ontario (Dennis 1974, Ross et al. 1984, see also Heusmann 1991). Mallards now breed throughout southern Ontario (Dennis et al. 1989) and are also common breeders throughout most of northern Ontario (Ross and Fillman 1990). Additionally, mallards from game farm releases in the U.S. may have moved north into breeding black duck habitat (Heusmann 1991). Consequently, in Ontario, black ducks persist mainly in pre-Cambrian and northern boreal habitats.

Based on water chemistry data (e.g., higher alkalinity and cation concentrations), wetlands in southern Ontario are more fertile than are wetlands in the north, with a corresponding decrease in fertility in southern Ontario from southwest to northeast (Hanson et al. 1949, Ryder 1964, Sparling and Nalewajko 1970, Patterson 1976). Thus, mallards may have colonized, and replaced black ducks, on the "best" waterfowl habitats in Ontario and black ducks may now occupy "poorer" habitats.

Ankney et al. (1987) concluded that the rapid increase of mallards in southern Ontario had caused the decline of black duck populations there. They hypothesized that the mechanism whereby this occurred was introgressive hybridization and/or competitive exclusion. The latter possibility led to the major question asked in this study. Are wetlands used by mallards during the breeding season more fertile than those used by breeding black ducks? My objectives were to 1) determine if the invasion of mallards into southern Ontario was random with respect to habitat quality or if mallards first invaded the most productive wetlands, and 2) determine if mallards have replaced black ducks on the most productive wetlands.

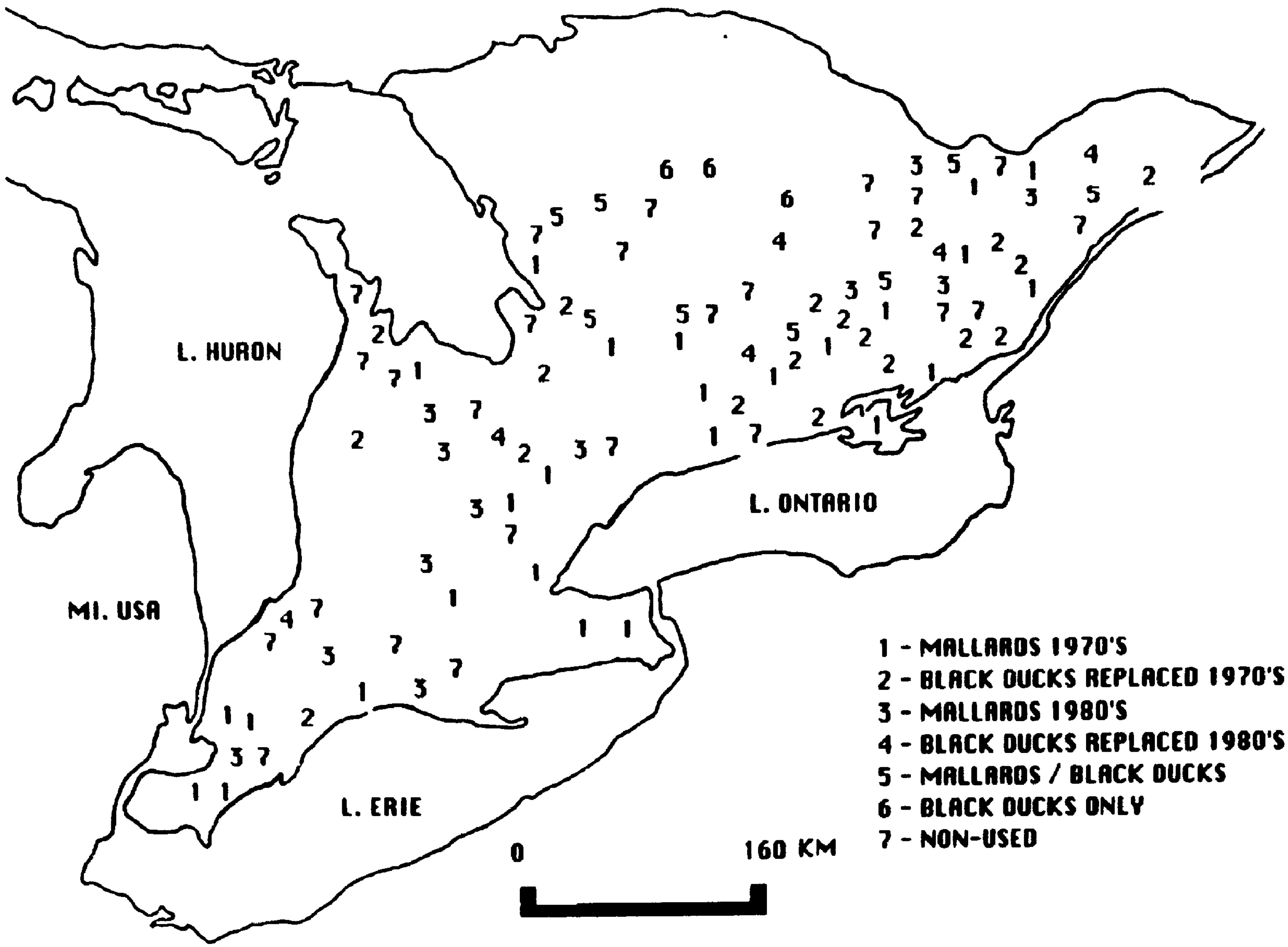
3.2 METHODS

In southern Ontario, 266 plots (0.8 km x 0.8 km) were surveyed for breeding waterfowl in 1971, 1976, 1981, 1985, and 1987 by CWS (Dennis 1974a, Dennis et al. 1989). Ground surveys were initiated in mid-April and concluded in mid-May

(Dennis 1974a). Dennis (1974a) provides complete information regarding survey methodology. Since 1981, the exact location (i.e., wetland) of breeding mallards and black ducks has been noted. Surveys before 1981 recorded only which plots were used, not which wetlands within a plot were used, but field notes were sufficiently detailed for me to determine specific wetlands used by mallards and/or black ducks during the 1971 and 1976 surveys. Thus, the CWS survey data enabled me to establish the historical pattern of mallard invasion into southern Ontario, and to define 7 wetland categories. One hundred and thirty-one wetlands, in 99 plots (Fig. 3.1), were categorized as follows:

1. MALLARDS 1970's (n=36) -- wetlands either continually used by breeding mallards since 1971 or wetlands colonized and continually used by mallards as of 1976 that have not been used by black ducks since before 1971;
2. MALLARDS 1980's (n=16) -- wetlands colonized and continually used by breeding mallards as of 1981, 1985, or 1987 that were not used by breeding mallards in the 1970's (i.e., vacant of mallards in the 1970's), and that have not been used by black ducks since before 1971;

Figure 3.1. Locations of the 99 survey plots where habitat evaluation was conducted in southern Ontario during summer 1990.


L. HURON
MI. USA
L. ONTARIO
L. ERIE
0
160 KM
1 - MALLARDS 1970'S
2 - BLACK DUCKS REPLACED 1970'S
3 - MALLARDS 1980'S
4 - BLACK DUCKS REPLACED 1980'S
5 - MALLARDS / BLACK DUCKS
6 - BLACK DUCKS ONLY
7 - NON-USED

3. BLACK DUCKS REPLACED 1970's (n=25) -- wetlands where breeding black ducks were replaced by breeding mallards in the 1970's (e.g., during the 1970's both mallards and black ducks were observed on these wetlands, but, at some time during the 1970's, black ducks were no longer observed, whereas, mallards have been continually observed since either 1971 or 1976;
4. BLACK DUCKS REPLACED 1980's (n=8) -- wetlands where breeding black ducks were replaced by breeding mallards in the 1980's (see also description for BLACK DUCKS REPLACED 1970'S);
5. MALLARDS / BLACK DUCKS (n=11) -- wetlands used by both mallards and black ducks as of 1987 (These wetlands were continuously used by black ducks since 1971, whereas, mallards began using these wetlands before 1985. In some years mallards and black ducks have co-occurred on these wetlands, but generally, the species have alternately used these wetlands).
6. BLACK DUCKS ONLY (n=5) -- wetlands that have been used only by breeding black ducks since the 1970's, and;

7. NON-USED (n=30) -- wetlands that have not been used by either breeding mallards or black ducks since surveys began in 1971. Non-used wetlands were randomly chosen from entire plots on which mallards or black ducks were never observed. By selecting non-used wetlands from plots where no mallards or black ducks had been observed, I conclude that I sampled wetlands that were avoided.

Wetlands were sampled only if I could specifically place them into one of 7 pre-defined categories. For example, wetlands colonized by mallards in the 1970's were those wetlands where mallards were seen in all survey years. So, in plot #1 there may have been 5 wetlands, but mallards were seen only on wetland #1 in all survey years, thus, for plot #1 only wetland #1 was sampled. The same is true for an entire plot. If a plot had 5 wetlands and mallards were seen sporadically throughout the plot (e.g., only on wetland #1 in 1971, only on wetland #3 in 1981, and only on wetland #4 in 1987) I could not place those wetlands into a category and thus, none were sampled and the plot was not represented in my analysis. My sampling of wetlands from 99 of 266 plots represented 37% of the survey plots. On the 266 plots there were 830 wetlands, thus, my sampling of 131 wetlands represented 16% of those available.

Water chemistry and physical characteristics were evaluated during 14 May - 1 June 1990. In the field, portable meters were used to determine conductivity (Hanna Instruments; HI 8033) and pH (Canlab Model H5503). Two surface water samples (a 250-ml and a 100-ml sample) were taken from each wetland. Samples were collected in a 250 ml plastic bottle and a 100 ml glass bottle which were rinsed with water from that site before sample collection. Bottles were then turned upside down and placed 10 - 15 cm below the water surface, turned right side-up and allowed to fill (Brooksbank et al. 1989). Samples were kept on ice in the field and later stored at 4 ^{o}C (D. Kurylo, Great Lakes Forestry Center, Sault Ste. Marie, Ont., pers. commun.). The 250-ml samples were coarse filtered through Whatman #41 filters before analysis (Great Lakes Forestry Center, Sault Ste. Marie, Ont.) for alkalinity ($CaCO_3$) and several cations (calcium, magnesium, sodium, potassium). The 100-ml samples were fine filtered (Whatman #41; 0.45 μm) and then stabilized with 1 ml of 30% H_2SO_4 before analysis of total phosphorus at the same laboratory. Additionally, to confirm field measurements, conductivity and pH were determined on a subset of samples sent to the lab. Lab measurements did not differ ($\underline{P}$ > 0.05, paired t-tests) from field measurements for either pH or conductivity, and therefore field measurements were used in all statistical analyses. Water chemistry values, except pH and conductivity, are reported in μg/L.

Physical variables measured for each wetland were:

wetland size, percent emergent cover, shoreline irregularity index (SI), distance from wetland to disturbance (occupied dwellings, agriculture, roads), and number of ponds per survey plot. A digitizer and planimeter were used to determine perimeter and area of wetlands from aerial photos (CWS unpublished data). 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 emergent cover was visually estimated, similar to that described by Environment Canada (1984). The CWS waterfowl survey was designed so that an edge of each plot was accessible from a road (Dennis 1974a). Therefore, the maximum distance from wetland to disturbance was approximately 1 km. Wetlands <1 km from seldom used roads (hunting camps, old logging roads), abandoned dwellings, or wetlands located in densely wooded areas were considered undisturbed and thus, 1 km was recorded as the distance to disturbance. Accumulated growing-degree-days above 5.5 ^{o}C for each wetland locale were obtained from Environment Canada (1984).

Multivariate Analysis of Variance (MANOVA) (PROC GLM; SAS Institute 1985) was used to determine if there was overall variation among the 7 wetland groups. Canonical Variates Analysis (CVA) (PROC CANDISC; SAS Institute 1985) was used to determine how the wetland groups differed with respect to the various habitat variables. Among-group differences were illustrated by constructing 95% confidence ellipses around group means on the first 2 canonical axes. Variances, covariances, and means generated from the CVA analysis were used to construct the confidence ellipses. To clarify among-group differences, least significant difference tests (LSD) were performed on the variables that contributed most to the canonical axes. Statistical analyses were performed on log(x+1) transformed data, except for pH, to correct for heterogeneity of variance and improve non-normality (Ott 1988).

3.3 RESULTS

MANOVA of all chemical and physical variables showed that there was significant variation among the 7 treatment groups (Wilk's lambda = 0.2285, $P < 0.0001$). The first two canonical axes (CAN1, CAN2) from the CVA described 48.4% ($P < 0.0001$) and 27.0% ($P = 0.004$) of the among-group variation, respectively (Table 3.1); the 3rd axis explained only 12.2% of the among-group variation ($P = 0.37$). Total and standardized canonical coefficients indicated that water chemistry variables were more important than physical variables in separating wetland groups; alkalinity and calcium contributed most to the separation (Table 3.1, Table 3.2). Although there was considerable overlap among the wetland groups (Fig. 3.2), CAN1, of which alkalinity, calcium, conductivity, and growing degree days were major

Table 3.1. Total canonical coefficients of the first two canonical axes for the canonical variates analysis performed on southern Ontario data.

Variable	CAN1[a]	CAN2
Water chemistry variables[b]		
Alkalinity ($CaCO_3$)	<u>0.8253</u>	-0.2058
Calcium	<u>0.7472</u>	-<u>0.5503</u>
Conductivity	<u>0.6437</u>	-<u>0.6546</u>
Magnesium	<u>0.6220</u>	-<u>0.5691</u>
pH	0.4155	-<u>0.6430</u>
Sodium	0.2984	-0.2773
Potassium	0.3654	-0.2770
Total Phosphorus	0.2320	0.1743
Physical variables		
Growing Degree days	<u>0.6959</u>	-0.0566
Disturbance (m)[c]	0.0255	-0.0258
Interspersion[d]	0.2663	<u>0.5476</u>
Ponds[e]	-0.1375	0.2387
SI[f]	0.3763	0.0933
Eigenvalues	0.905	0.504
% variation explained	48.4	27.0

[a]Variables correlated (r>0.50) with the axes are underlined. Only the first 2 axes were significant (CAN1 P<0.0001, CAN2 P<0.004, CAN3 P<0.2433).

Table 3.1. continued.

[b]All water chemistry variables, except pH and conductivity, measured in mg/L.

[c]Distance to disturbance.

[d]Visual estimate of percentage of emergent cover.

[e]Mean number of ponds per plot.

[f]Shoreline irregularity index (Reid 1961).

Table 3.2. Standardized canonical coefficients of the first 2 canonical axes from a canonical variates analysis performed to separate the 7 wetland groups in southern Ontario.

Variable	CAN1	CAN2
Water chemistry variables[b]		
Alkalinity ($CaCO_3$)	0.5925	0.1201
Calcium	0.8321	0.6506
Conductivity	-0.4205	-1.2543
Magnesium	-0.1022	-0.1184
pH	-0.2182	-0.5541
Sodium	0.1511	0.2337
Potassium	0.0013	-0.0467
Total phosphorus	-0.0025	0.1484
Physical variables		
Distance to disturbance (m)	0.0954	-0.2832
Degree days	0.5476	0.3860
Interspersion[c]	0.3772	0.3443
Ponds[c]	-0.2139	0.1829
SI	0.3144	0.3312
Wetland size (ha)	0.2186	0.3669
Eigenvalues	0.905	0.504
% variation explained	48.4	27.0

Table 3.2. continued.

[a]Variables important in defining the axes are underlined. Both axes were significant ($\underline{P} < 0.001$; $\underline{P} = 0.004$, respectively).

[b]Water chemistry variables, except pH, measured in mg/L.

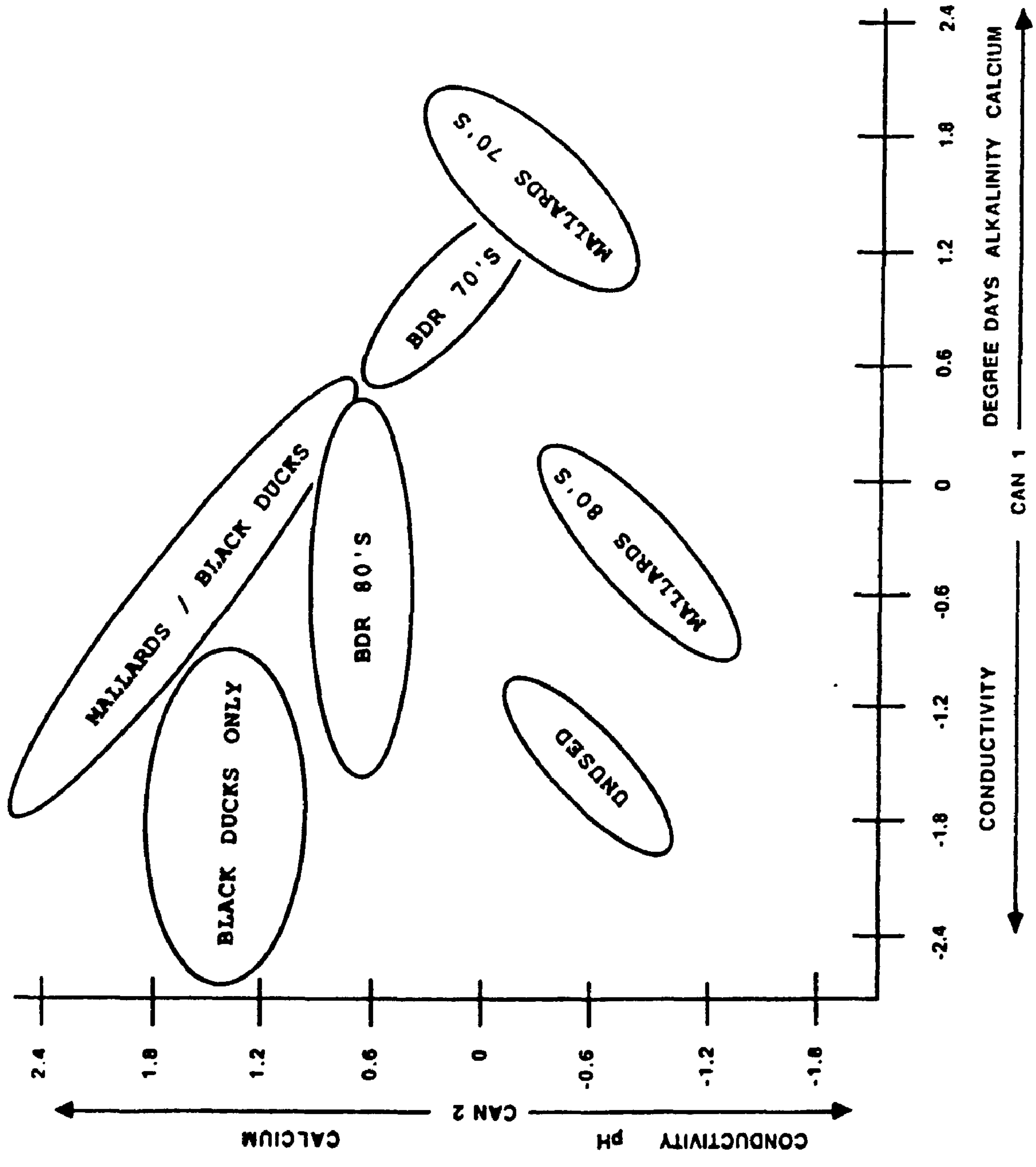
[c]Distance to disturbance

[d]Visual estimation of percentage of emergent cover.

[e]Mean number of ponds per plot

[f]Shoreline irregularity index (Reid 1961).

Figure 3.2. Ninety-five percent confidence ellipses on the first 2 canonical axes for each wetland group in southern Ontario. Variables important in defining the axes (see standardized canonical coefficients; Table 3.2) are shown adjacent to arrows. BDR 70's = black ducks replaced 1970's.


MALLARDS 70'S
BDR 70'S
MALLARDS / BLACK DUCKS
BDR 80'S
MALLARDS 80'S
BLACK DUCKS ONLY
UNUSED
-2.4
-1.8
-1.2
-0.6
0
0.6
1.2
1.8
2.4
CONDUCTIVITY
CAN 1
DEGREE DAYS ALKALINITY CALCIUM
CAN 2
CALCIUM
CONDUCTIVITY pH

components, distinguished 3 groups of wetlands: 1) MALLARDS 1970'S and BLACK DUCKS REPLACED 1970'S; 2) MALLARDS 1980'S and BLACK DUCKS REPLACED 1980'S; and 3) MALLARDS / BLACK DUCKS, BLACK DUCKS ONLY, and NON-USED wetlands (Fig. 3.2). CAN2, of which calcium, conductivity, and pH were major components, further distinguished MALLARDS / BLACK DUCK wetlands and BLACK DUCK ONLY wetlands from NON-USED wetlands (Fig. 3.2). CAN2 also separated BLACK DUCKS REPLACED 1980'S wetlands from MALLARDS 1980'S wetlands (Fig. 3.2).

Wetlands colonized by mallards in the 1970's (MALLARDS 1970'S) and 1980's (MALLARDS 1980'S), and wetlands where mallards replaced black ducks in the 1970's (BLACK DUCKS REPLACED 1970'S) had, on average, the highest alkalinity, calcium, pH, and conductivity (Table 3.3). Wetlands on which mallards replaced black ducks in the 1970's (BLACK DUCKS REPLACED 1970'S) had, on average, higher alkalinity, calcium, pH, and conductivity than did wetlands in which mallards replaced black ducks in the 1980's (BLACK DUCKS REPLACED 1980'S) (Table 3.3). BLACK DUCK ONLY wetlands had, on average, the lowest values for all water chemistry variables (Table 3.3). Magnesium and potassium (F = 7.54, P < 0.0001; F = 2.29, P = 0.0394, respectively, 6,124 df) were ordered similarly to other water chemistry variables (e.g., highest on MALLARDS 1970's wetlands and lowest on BLACK DUCK ONLY wetlands). Total phosphorus and sodium (F = 0.58, P = 0.7474; F = 1.77, P = 0.1110, respectively, 6,124 df) were

Table 3.3. Water chemistry variables that contributed the most[a] to separation of the 7 wetland categories and that were most useful in explaining the pattern of mallard colonization of southern Ontario.

		Water chemistry variables[b]							
		Alkalinity		Calcium		pH		Conductivity	
Wetland group[c]	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Mallards 1970's	36	177.5A[d]	9.7	71.6A	4.4	7.4A	0.1	493A	29.1
BD's replaced 1970's	25	139.8AB	18.0	54.8B	8.4	7.3A	0.1	411A	64.3
Mallards 1980's	16	142.6AB	21.7	58.3AB	5.9	7.5A	0.1	415A	37.1
BD's replaced 1980's	8	73.0BC	16.7	23.8CD	5.4	7.0AB	0.2	214B	45.6
Mallards / black ducks	11	72.1C	11.5	23.7DE	8.6	6.5BC	0.3	162BC	47.1
Black ducks only	5	19.0D	13.7	9.0E	4.6	6.0C	0.5	132C	39.0
Non-used	30	60.7C	10.3	31.9C	1.1	7.3A	0.2	307AB	37.8

[a] See canonical coefficients (Table 3.1).

[b] Alkalinity ($CaCO_3$) and calcium measured in mg/L; conductivity measured in μ mhos/cm.

Table 3.3. continuation of footnotes.

[c] BD's replaced 1970's = black ducks replaced 1970's; BD's replaced 1980's = black ducks replaced 1980's.

[d] Means in the same column followed by different letters are different (F = 10.61, 11.63, 5.92, and 10.21, for the 4 columns respectively; 6,124 df; $P < 0.001$). Results from univariate output in MANOVA and least significant difference (LSD) tests.

not different among wetland groups.

Growing degree days (Table 3.2) were the most important physical variable contributing to separation of wetland groups (F = 7.52, 6,124 df, P < 0.0001) and were ordered similarly to water chemistry variables (e.g., highest on MALLARDS 19[illegible]'s wetlands and lowest on BLACK DUCKS ONLY wetlands) (Table 3.4). Wetlands where mallards replaced black ducks in the 1980's (BLACK DUCKS REPLACED 1980'S) and wetlands where mallards and black ducks co-occurred (MALLARDS / BLACK DUCKS) had the highest values for percent emergent cover (F = 3.03, 6,124 df, P = 0.0085), and also were associated with the highest mean number of ponds per plot (F = 2.74, 6,124 df, P = 0.0156) (Table 3.4). Although mean water chemistry values were higher on NON-USED wetlands than on BLACK DUCK ONLY wetlands (Table 3.3), mean percent emergent cover and SI (F = 3.02, 6,124 df, P = 0.0086) were slightly higher on BLACK DUCK ONLY wetlands (Table 3.4). NON-USED wetlands (most typically small lakes or ponds) usually had rocky or sandy shores and lacked emergent vegetation. Distance from wetland to disturbance and wetland size did not differ (F = 0.70, P = 0.6502; F = 2.17, P = 0.0503, respectively, 6,124 df) among wetland groups.

Table 3.4. Physical variables that were important in explaining the pattern of mallard colonization of southern Ontario.

		Physical variables[a]							
		Ponds per plot		SI		% Emergent Cover		Degree days	
Wetland group	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Mallards 1970's	36	2.2C[b]	0.2	2.1A	0.2	15.4BC	1.7	3594A	46.1
BD's replaced 1970's	25	2.6BC	0.3	1.9AB	0.1	18.2AB	3.0	3544A	51.0
Mallards 1980's	16	2.1C	0.2	2.5A	0.4	13.4BC	3.7	3300B	75.0
BD's replaced 1980's	8	3.5AB	0.5	1.4B	0.1	21.3AB	5.5	3425AB	25.0
Mallards / black ducks	11	3.8A	0.7	2.0AB	0.3	24.1A	4.7	3236BC	75.4
Black ducks only	5	1.6C	0.4	1.7AB	0.1	14.0BC	4.0	3000C	126.5
Non-used	30	3.0AB	0.4	1.5AB	0.2	9.2C	1.9	3993B	64.1

[a] SI = shoreline irregularity index; % emergent cover = visual estimate of percent emergent cover; degree days = growing degree days.

Table 3.4. continuation of footnotes.

[b]Means in the same column followed by different letters are different ($F = 2.86$, $P = 0.013$; $F = 2.94$, $P = 0.018$; $F = 2.97$, $P = 0.008$; $F = 7.52$, $P < 0.0001$), for the 4 columns respectively, with 6,124 df). Results from univariate output in MANOVA and least significant difference (LSD) tests.

3.4 DISCUSSION

In my study area, breeding mallards first invaded and replaced breeding black ducks on wetlands with high values for alkalinity, calcium, pH, and conductivity. Hardwater wetlands (>40mg/L alkalinity as $CaCO_3$) generally receive greater use by breeding waterfowl (Moyle 1956, Jahn and Hunt 1964, Leitch 1964) and also support more fledged waterfowl than do softwater (<40mg/L alkalinity as $CaCO_3$) wetlands (Patterson 1976), due to greater abundance of vegetation and invertebrates (Leitch 1964, Krull 1970, Patterson 1976). Thus, in eastern North America, wetland alkalinity and calcium concentrations are good indicators of overall wetland productivity and quality for breeding waterfowl (Moyle 1945, Leitch 1964, Patterson 1976). Therefore, based on my data for alkalinity and calcium, as well as other water chemistry variables, I conclude that mallards first invaded the most productive and highest quality wetlands for waterfowl in southern Ontario.

Ringelman et al. (1982) suggested that because wetland habitats in Maine were relatively infertile and dispersed, the black duck breeding strategy must be one of careful selection of wetlands to form a small home range that minimizes flight costs while providing the diversity of wetland types necessary for successful breeding. Thus, I doubt that black ducks would select for infertile wetlands, especially in areas with low breeding densities and an abundance of high quality habitat, such as southern Ontario.

One explanation for the absence of black ducks from wetlands that they used previously (e.g., more productive wetlands) is that mallards and black ducks treat each other as conspecifics and that mallards have excluded (i.e., out-competed) black ducks from those wetlands. For example, in 1951, black ducks utilized only 13 of 27 sites in eastern Ontario, but, 7 of those were shared with mallards (Collins 1974). Additionally, between 1951-1971, mallards generally first appeared on sites used by black ducks, and subsequently replaced black ducks on some sites (Collins 1974) that were located in an area of highly fertile habitat (Merendino et al. 1992). From 1966-1970, in eastern Ontario, mallards and black ducks shared 8 of 21 wetlands (Patterson 1972). These data do not indicate that mallards filled a void left by a declining black duck population, but rather, indicate that mallards colonized wetlands used by black ducks, and ultimately, outcompeted black ducks for such sites. Although I cannot conclude with certainty that my observations reflect cause and effect, they are, in conjunction with the previously discussed data, consistent with the hypothesis that mallards have outcompeted black ducks for fertile wetlands.

The increase of mallards and decline of black ducks in my study area was most rapid in areas with highly fertile wetlands (Dennis et al. 1989, Merendino et al. 1992). The dramatic increase of mallards (Ankney et al. 1987, 1989, Dennis et al. 1989) may be related to successful reproduction (Dennis and North 1984), facilitated by their occupation of highly productive habitats (Krapu 1979). Consequently, if black duck recruitment suffered due to occupation of less fertile wetlands, especially those impacted by acid rain (see Blancher and McCauley 1987, Longcore et al. 1987, Sparling 1990), high rates of production by mallards would potentially exacerbate the effects of hybridization (Ankney et al. 1987, 1989) and changes in population levels (Nichols et al. 1987). In New Zealand, mallards are displacing grey ducks (Anas superciliosa), possibly due to their higher reproductive rates (see Caithness et al. 1991).

In Ontario, Brodsky and Weatherhead (1984) reported that mallard males outcompeted black duck males for mates. In Nova Scotia, Seymour (1990) provided evidence for greater aggression by mallards towards conspecifics (and black ducks) than was shown by black ducks. The results of those studies, and subsequent pen studies (Brodsky et al. 1988), suggest that mallards are, on average, dominate to black ducks, either in a pen or in the wild. Thus, I suggest that competitive exclusion played a major role in the shift of black duck breeding locations in Ontario.

In high population areas, breeding waterfowl appear to select wetlands based upon wetland morphometry (Evans and

Black 1956, Patterson 1976), but, in areas with low densities of breeding waterfowl (e.g., Wisconsin; Jahn and Hunt 1964), wetland fertility appears to be more important. Low breeding waterfowl densities in southern Ontario (Dennis 1974), in comparison to those for the prairies (see Bellrose 1980), may have allowed pioneering mallards to invade productive wetlands (Jahn and Hunt 1964), and subsequently, occupy less fertile wetlands as the population increased (Dzubin 1969). In my study, physical variables (e.g., percent emergent, SI) seemed most important when mallards and black ducks were selecting among relatively infertile wetlands (i.e., BLACK DUCKS ONLY, MALLARDS / BLACK DUCKS, and NON-USED) and when mallard and black ducks co-occurred (i.e., MALLARDS / BLACK DUCKS). Visual isolating mechanisms (percent emergent cover, mean number of ponds per plot) were most pronounced on wetlands where mallards and black ducks co-occurred (i.e., MALLARDS / BLACK DUCKS) and on wetlands where mallards most recently replaced black ducks (i.e., BLACK DUCKS REPLACED 1980's). Visual isolation is an important requirement in wetland selection by conspecific waterfowl (Dzubin 1969), and as mallards and black ducks generally treat each other as conspecifics (Brodsky and Weatherhead 1984, Seymour 1990), wetlands where they occur might be expected to have an abundance of cover.

Mallards may have replaced black ducks on the MALLARDS 1970'S wetland group before the initiation of breeding waterfowl surveys in 1971, but, this is unknown. However, because black ducks are purportedly less tolerant of disturbance (see Kirby 1988), especially visual (Diefenbach and Owen 1989), than are mallards, Conroy et al. (1989) argued that habitat alteration (primarily clearing of forests) was the cause of black duck disappearance from wetlands in southern Ontario (note that mean distance from disturbance was not different among my wetland categories; see also Ringelman and Longcore 1982). However, Snell (1986) reported that 86% of southern Ontario wetlands were forested in 1982. In Ontario, most habitat destruction occurred before 1967, and was most severe in the agricultural area of the southwest (Snell 1986). Alison (1976), citing from a historical reference (McNiff 1793), suggested that most habitat in extreme southwestern Ontario probably was never suitable for breeding black ducks, as expansive meadows and plains existed away from the forested valley of the Thames River. Additionally, Dennis et al. (1989) stated that most land cleared for agriculture in the 1970's was probably of low quality for breeding waterfowl. Black ducks reportedly were, however, common breeders around London (Middlesex County), as late as 1955. Wetlands in the eastern part of my study area have remained relatively undisturbed due to the topography of the area which prevents agriculture (Snell 1986, Dennis et al. 1989). Black ducks were common breeders in central and eastern Ontario in the late 1960's, but, have since been largely replaced by mallards in many areas in these regions. Beaver ponds are increasingly abundant and are heavily used by mallards in these regions (CWS unpubl. data). Mallards are quite numerous in forested areas in northern Ontario (Ross and Fillman 1990) and commonly breed in the (undisturbed) mixed and boreal forests of western Canada and Alaska (see Bellrose 1980) and New York (Dwyer 1992). Thus, I think that habitat "disturbance" had little, if anything, to do with the eastward expansion of mallards and their subsequent displacement of black ducks.

I am unaware of data suggesting that hunting played an important role in the decline of black ducks in Ontario (see Ankney et al. 1987, 1989). Restrictive regulations have been in place since the early 1980's in the United States and have resulted in a 40% decline in black duck harvest. No increase in mid-winter counts of black duck has been noted, however. If all of the 40% of the U.S. harvest that has been eliminated was previously additive, the historical decline in black ducks would have been much greater than 3% per year (Rusch et al. 1989); clearly it wasn't all additive. Even if part of the 40% was additive, however, its elimination should have resulted in increased mid-winter counts of black ducks. Mid-winter counts through 1992 clearly show that this has not occurred. This was predictable given that the analyses of Krementz et al.

(1987:689) suggested that "variations in hunting mortality are compensated for by other mortality sources in black ducks".

I find it highly unlikely that black ducks were "shot out" of southern Ontario in such a precise pattern as I report or that over-hunting could account for the dramatic increase of mallards and subsequent decline of black ducks in southern Ontario. The invasion by mallards into black duck habitat has occurred from west to east, thus, it may be argued that the pattern of mallard invasion into black duck habitat represents geographic progression. But, mallards appear to have invaded productive habitats associated with the Great Lakes and St. Lawrence River marshes (Fig.3.1), before invading portions of central and southwestern Ontario. If the pattern of mallard invasion was truly geographic progression, I believe that mallard invasion of black duck habitat would have appeared to me more of a direct front across the breadth of southern Ontario. More importantly, mallard densities in northern Ontario are highest in areas where the habitat is likely more productive (Ross 1987, McNicol et al. 1987, Ross and Fillman 1990). Mallards have apparently moved across infertile areas in western portions of northern Ontario, with few or no breeding pairs becoming established, only to predominate fertile areas that are further east (see Ross 1987, McNicol et al. 1987, Ross and Fillman 1990). This scenario will be examined in Chapter 4.

I suggest that mallards, through introgressive hybridization (Ankney et al. 1987, 1989, Seymour 1990) and competitive exclusion of black ducks from highly fertile wetlands, rather than human factors (e.g., hunting, habitat loss; Conroy et al. 1989), were the proximate cause of the decline of black ducks in southern Ontario. I predict that mallards will continue to increase their numbers and range in eastern Canada, regardless of changes in habitat or black duck numbers. Overall, the Ontario mallard/black duck situation is analogous to that of New Zealand where mallards are hybridizing with, and replacing grey ducks. Attempts to tie overhunting and habitat loss to that scenario (see Caithness et al. 1991) have been inconclusive at best.

3.5 MANAGEMENT IMPLICATIONS

In southern Ontario, the inverse relation between mallard and black duck numbers is obvious. Given the adaptability of mallards and their influence on black ducks, I am doubtful that any type of habitat management in southern Ontario could benefit black ducks specifically. I caution that attempts, such as impoundment construction (see Kirby 1988) or fertilization, to enhance breeding black duck habitat in areas that currently have stable black duck populations (e.g., the maritime provinces), may further stimulate invasion by mallards; the outcome of this would not be positive for black ducks. Perhaps low wetland fertility will slow the spread of mallards into wetlands currently used only by black ducks in southern and central Ontario, and subsequently slow the increase in mallards throughout eastern North America as fertile habitats become saturated. I believe, however, that mallards can and will use any habitats used by black ducks.

To better understand the effect of mallards on black duck populations, future studies should examine the reproductive ecology of "eastern" mallards and also the mechanisms, such as mallard dominance over black ducks (e.g., competitive exclusion; Brodsky et al. 1988) and earlier pairing by mallards (Brodsky and Weatherhead 1984), that may explain how mallards are able to replace black ducks on fertile wetlands. Additionally, studies to evaluate the role that habitat loss and alteration on the wintering grounds played in the decline of black ducks also may prove enlightening.

Given the increased evidence for the cause and effect relationship between increasing mallards and decreasing black ducks, I reiterate the suggestion of Ankney et al. (1987) that "it may be impossible to resolve the black duck problem by human intervention." Further, some management activities designed to benefit breeding black ducks (e.g., wetland fertilization, impoundment construction) may be of more benefit to breeding mallards.

CHAPTER 4

HABITAT USE BY SYMPATRIC MALLARDS AND AMERICAN BLACK DUCKS IN NORTH-CENTRAL ONTARIO

Numerous causes (e.g., hunting, habitat loss, mallards, etc.,) have been cited in the decline of black ducks (see Rusch et al. 1989 for review; see also Chapter 3). The mallard, through hybridization (Ankney et al. 1987, Seymour 1990) and competitive exclusion from fertile wetlands (Chapter 3), may be the most significant cause of declining black duck populations. In southern Ontario, mallards invaded the most fertile wetlands and displaced black ducks from such wetlands (Chapter 3). Highly fertile wetlands in southern Ontario support more breeding mallards than do low fertile wetlands and consequently, the decline of black ducks has been most rapid in the highly fertile wetlands (Dennis et al. 1989, Merendino et al. 1992).

Unlike southern Ontario where breeding mallards rapidly increased and became dominant (Dennis et al. 1989), breeding densities of black ducks are stable (Ross and Fillman 1990), with mallard populations increasing in some areas (Ross 1992). The distribution of mallards is more variable than that of black ducks (Ross and Fillman 1990), suggesting that habitat quality may be influencing breeding mallard distributions (Ross and Fillman 1990, McNicol et al. 1987). Dwyer (1992) provided valuable information on sympatric breeding mallards and black ducks in New York, but such data are lacking over most of eastern North America due to low breeding densities of either species where they are sympatric and/or inaccessibility of sympatric breeding areas. In north-central Ontario the overlap in mallard and black duck distributions (Ross and Fillman 1990) made possible a study of sympatric mallard/black duck habitat use.

In this study I document habitat use by sympatric breeding mallards and black ducks and their broods in north-central Ontario. My objectives were to determine: 1) if mallards were occupying the most fertile wetlands relative to black ducks, 2) if mallard densities were highest in the most fertile area, and 3) compare habitat characteristics of wetlands used by mallard broods to those used by black duck broods.

I also evaluated my predictions (section 1.2.2) that: 1) across north-central Ontario, mallards would occupy the most fertile wetlands and 2) areas with the highest mallard : black duck ratio would have the most fertile wetlands

4.2 STUDY AREA

The 13 study plots are located within the pre-Cambrian shield area of northeastern Ontario (Chapman and Putman 1973, see McNicol et al. 1987) and extend through 3 ecological zones: northern Great Lakes - St. Lawrence, southern Great Lakes - St. Lawrence, and eastern exposed shield (Ross 1992) (Fig.4.1). Each plot was 10km x 10km and, in total, the plots comprised an area 1300 km^2. The 13 plots are bounded in an area approximately 68,0000 km^2, along a 400 km northwest to southeast gradient and a 170 km southwest to northeast gradient (Fig. 4.1). In 1990, I evaluated habitat in plots 11-13 and 16-19 that were located in the northern Great Lakes - St. Lawrence Lowlands Forest area; plot 18 is located in the eastern exposed shield (Fig. 4.1). Collectively, I will hereafter refer to plots 11-13 and 16-19 as northern Great Lakes - St. Lawrence (NGLSL). In 1991 I evaluated habitat in plots 3-6, 8 and 10 that were located in the southern Great Lakes - St. Lawrence Lowlands Forest area (SGLSL) (Fig. 4.1).

4.3 METHODS

4.3.1 Breeding pair locations

Since 1990 the Canadian Wildlife Service (CWS) has conducted helicopter surveys of breeding waterfowl in 44 10km x 10km plots in northeastern Ontario. I chose 13 plots for my study, of which 6 are dominated by breeding black ducks, 5 are dominated by breeding mallards, and 2 have similar numbers of each species (Table 4.1). Surveys were initiated in the southernmost plots on or about 3 May and end in the northernmost plots on or about 22 May. During surveys the exact location (i.e., wetland) of each indicated pair of ducks is noted on aerial photos. Information

Figure 4.1. Approximate location of each 10km x 10km plot in north-central Ontario.

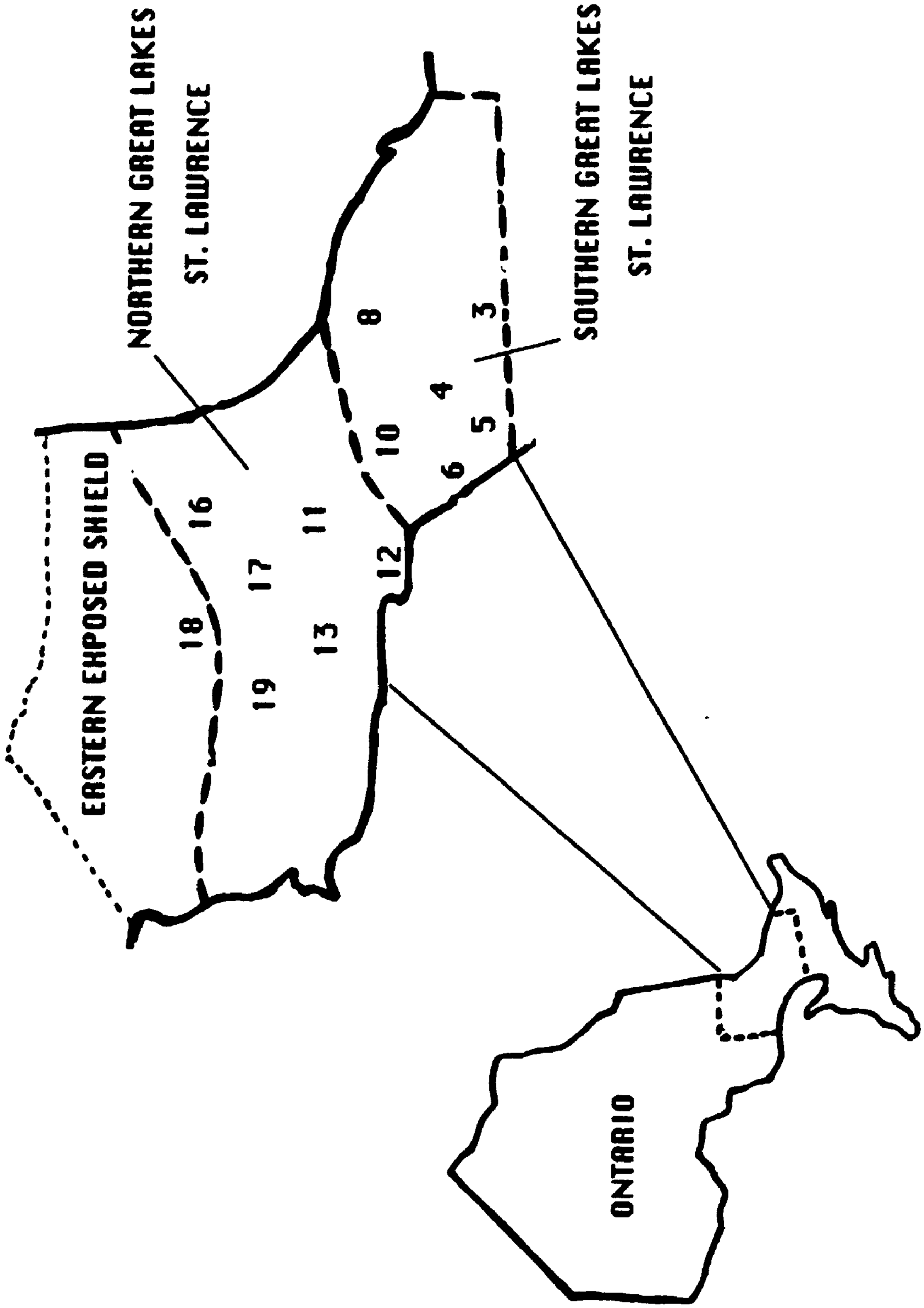

NORTHERN GREAT LAKES
ST. LAWRENCE
SOUTHERN GREAT LAKES
ST. LAWRENCE
EASTERN EXPOSED SHIELD
ONTARIO
3
4
5
6
8
10
11
12
13
16
17
18
19

Table 4.1. Average indicated pairs of mallards and black ducks on 13 10km x 10km plots in north-central Ontario, 1990-1992[1].

Plot	Mallard		Black duck		Total		M : BD
3	14	(10)[a]	38	(46)	52	(56)	1 : 5
4	9	(8)	24	(26)	33	(34)	1 : 3
5	22	(15)	9	(6)	31	(21)	3 : 1
6	55	(51)	19	(7)	74	(58)	7 : 1
8	1	(2)	23	(21)	24	(23)	1 : 11
10	59	(58)	23	(32)	82	(90)	2 : 1
11	62	(52)	14	(6)	76	(58)	9 : 1
12	61	(46)	12	(9)	73	(55)	5 : 1
13	23	(19)	19	(12)	42	(31)	2 : 1
16	3	(1)	16	(5)	19	(6)	1 : 5
17	5	(4)	25	(16)	30	(20)	1 : 4
18	11	(9)	25	(16)	36	(25)	1 : 2
19	5	(7)	28	(27)	33	(34)	1 : 4

[a]Numbers in parentheses are number of indicated pairs present in year when habitat was evaluated. Habitat was evaluated in 1991 for plots 3-6, 8, and 10, and in 1990 for plots 11-13 and 16-19.

obtained from 1990, 1991, and 1992 annual breeding pair surveys were used to determine which wetlands were used by breeding pairs (i.e., mallards or black ducks) and which wetlands were not used by either mallards or black ducks in NGLSL and SGLSL, respectively. Wetlands were defined as follows:

1) Mallard - used only by a mallard pair as denoted by the May breeding pair survey,

2) Black duck - used only by a black duck pair as denoted by the May breeding pair survey,

3) Shared - shared by mallards and black ducks as denoted by the May breeding pair survey,

4) Vacant - wetlands on which no mallards or black ducks were observed during May breeding pair surveys. Vacant wetlands were randomly selected from all vacant wetlands 0.41 - 20.0ha in size, as those wetlands are most used by breeding waterfowl (McNicol et al. 1987).

Radio telemetry is probably the preferred method for describing habitat use, but low breeding densities and inaccessibility of forested habitats result in low sample sizes (e.g., number of birds) for determining habitat use (see Ringelman et al. 1982, Dwyer 1992), and therefore provides "intensive" sampling within a localized area. I felt that pair locations, as determined from breeding pair surveys, would provide an "extensive" study of habitat use. In prairie habitats, one wetland does not meet all the requirements of breeding waterfowl (Dzubin 1969), thus, breeding waterfowl use many wetlands (Dzubin 1969, Dwyer et al. 1978). In eastern areas, the correlation between pair observations and use of a particular wetland is not perfect, but it is likely quite high (K. Ross, Can. Wildl. Serv. pers. commun. 1990). Dieffenbach and Owen (1989) classified wetlands as being used by black ducks if black ducks were observed for $\geq$ 1 of 4 visits and classified all other wetlands as unused. I believe that my classification of wetlands as used or unused based upon a single visit is acceptable given that: 1) during the breeding season males aggressively defend feeding and loafing areas from conspecifics (Dzubin 1969, Seymour and Titman 1978, Joyner 1980), 2) black ducks make considerable use of single wetlands (Seymour and Titman 1978, Ringelman et al. 1982), 3) many black ducks and mallards nest in or adjacent to wetlands (Ringelman and Longcore 1982, Dwyer 1992) that likely provide an important food resource (Ringelman and Longcore 1982), and 4) mallards and black ducks exhibit strong fidelity to breeding sites (Ringelman et al. 1982, Dwyer 1992).

4.3.2 Brood locations

Waterfowl brood surveys were conducted with a Bell 206B Jet Ranger helicopter, equipped with bubble windows or with doors removed to increase visibility, during summer 1990 in northern Ontario and during summer 1991 in central Ontario. Surveys were primarily conducted between 0700 hours and 1030 hours and between 1600 hours and 2000 hours, with low wind (<10km/hour) conditions. Two surveys were conducted in both years. In NGLSL, surveys were conducted from 11 July - 13 July 1990 and from 29 July - 3 August 1990. In SGLSL, surveys were conducted from 22 June - 25 June 1991 and from 21 July - 28 July 1991. During the second brood survey in each year, I evaluated water chemistry and physical characteristics (see section 4.3.4) of wetlands used by broods as follows:

1) Mallard brood (n=22 and n=19 in 1990 and 1991, respectively): wetlands where mallard broods were observed in either the first and/or second brood survey, and

2) Black duck brood (n=25 and n=20 in 1990 and 1991, respectively): wetlands where black duck broods were observed in either the first and/or second brood survey.

Although waterfowl broods often make considerable movements among wetlands, especially in prairie habitats, Ringelman et al. (1982) indicated that black ducks in Maine make few movements among wetlands and that the majority of broods are raised on 1-3 ponds. Therefore, brood observations are likely correlated with prolonged use of particular wetlands.

4.3.3 Habitat evaluation

Each wetland was evaluated based upon water chemistry and morphological variables. Habitat evaluation was conducted for 240 wetlands in NGLSL in 1990 (mallard [n=44], black duck [n=47], shared [n=24], vacant [n=125]) and for 207 wetlands in SGLSL in 1991 (mallard [n=61], black duck [n=61], shared [n=13], vacant [n=72]). Habitat evaluation was conducted via helicopter, during brood surveys (see 2.3) conducted from 31 July - 3 August in 1990 and from 22 July - 25 July 1991. The helicopter (equipped with floats) landed on open water in the wetlands. Two water samples (1 - 250ml and 1 - 100ml sample) were taken from each wetland. Surface water samples were taken in shallow wetlands (i.e., wetlands with emergents established toward the center of the wetland or with floating leaved plants over most of the wetland surface) (see McNicol et al. 1987). In deep wetlands (i.e., wetlands where emergents were only established around the edge) water samples were taken by lowering a 2 meter plastic tube through the water column (see McNicol et al. 1987). In the field, samples were kept on ice in styrofoam coolers. Samples were then transferred to a refrigerator and stored at 4°C. In 1990, portable, digital meters were used to determine pH and conductivity of all samples at the end of each day. In 1991, water samples were shipped to University of Western Ontario and subsequently stored at 4°C for 4 days before analysis of pH and conductivity. The 250ml samples were filtered through Whatman #41 filters to remove coarse particles and were then analyzed for alkalinity ($CaCO_3$) and cations (Ca, Mg, Na, and K). For the 100ml samples a Hellige Aqua Tester was used to determing apparent water color {before filtering} and true water color {after filtering through Whatman #42 filters}. Water color is reported in hazen units. After filtering and subsequent color analysis the 100ml samples were stabilized with 1ml of 30% H_2SO_4, and were then analyzed for total phosphorus. Samples were refrigerated at 4°C and were shipped to the lab within 2-4 days of collection. Alkalinity, cation, and total phosphorus analyses were conducted at the Great Lakes Forestry Center in Sault Ste. Marie, Ontar o. Conductivity and conductivity were determined on a subset of samples sent to the lab in 1990 and on all samples sent to the lab in 1991. All water chemistry values, except pH and color, are reported in mg/L.

Percent open water was visually estimated for each wetland. Wetland size (ha) and perimeter (m) were determined from aerial photos by use of a computerized digitizing morphometry program. Shoreline irregularity index (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.

4.4 STATISTICAL ANALYSES

4.4.1 Overall analysis of habitat use by breeding pairs

My main objective was to evaluate habitat use by sympatric breeding mallards and black ducks and to test the prediction (see prediction #1, page 8) that mallards would occupy the most fertile wetlands. Therefore, I conducted an overall analysis of all wetlands in which waterfowl observations and habitat data from 1990 (NGLSL) [n=240] were combined with data from 1991 (SGLSL) [n=207] to form the complete data set [n=447]. I believe that this was appropriate given that the two ecological areas where the plots are located are physiognomically similar, so, gross differences in water chemistry and physical wetland characteristics were not likely and significant differences between the two areas due to "year" effects were also unlikely (see section 2.3.1).

Multivariate Analysis of Variance (PROC MANOVA; SAS 1985), hereafter referred to as MANOVA, was used to determine if there was an overall difference in water chemistry and morphology among the 4 treatment groups (mallard [n=105], black duck [n=108], shared [n=37], and vacant [n=197]). Canonical variates analysis (PROC CANDISC; SAS 1985), hereafter referred to as CVA, was used to indicate which variables provided the 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 2 canonical axes. 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 the most to separation of wetland groups and have been used by many researchers to assess waterbird abundance and distributions (see section 2.3.1).

4.4.2 Was the pattern repeatable?

The same plots, and therefore areas, were not surveyed and evaluated in both years. Thus, it may be argued that there could be differences due to year and/or area effects (but see section 2.3.3, 4.4.1). Moreover, it could be argued that findings from one year of data represent only a "snap-shot" and that what is happening one year may not happen the next. I therefore repeated the previously discussed analyses (MANOVA, CVA, LSD tests), separately, for the 1990 (NGLSL) and 1991 (SGLSL) data sets, thus, providing analysis of 2 separate years and areas.

Further, to provide support for results from years when I had bird observation data and water chemistry data (e.g., bird observation data and habitat data from 1990 in NGLSL, and 1991 in SGLSL), I analyzed bird observation data from 1991 and 1992 in NGLSL with habitat data from 1990 in NGLSL and bird observation data from 1990 and 1992 in SGLSL with habitat data from 1991 in SGLSL. Again, I feel that the use of habitat data from one year to assess bird use in each of 3 years is appropriate given that short-term changes in water chemistry are probably not severe throughout the area (see section 2.3.1).

These analyses provide a separate comparison of habitat use patterns between years and areas and further test my prediction that mallards would occupy the most fertile wetlands.

4.4.2.1 Northern Great Lakes - St. Lawrence

Habitat was evaluated in 1990. Bird observation data were obtained from 1990, 1991, and 1992 breeding pair surveys. Group composition in 1990, 1991, and 1992, respectively, was as follows: mallard [n=44, 42, 52], black duck = [47, 42, 41], shared [n=24, 12, 24], and vacant [n=125, 144, 123]. Analyses were conducted separately for all years, thus, 3 analyses were conducted. Analyses consisted of MANOVA, CVA, and LSD tests as previously described (see section 4.4.1), except that LSD tests were only performed on 1990 data.

4.4.2.2 Southern Great Lakes - St. Lawrence

Habitat was evaluated in 1991. Bird observation data were obtained from 1990, 1991, and 1992 breeding pair surveys. Group composition in 1990, 1991, and 1992, respectively, was as follows: mallard [n=46, 61, 46], black duck = [57, 61, 57], shared [n=14, 13, 14], and vacant [n=90, 72, 90]. Analyses were conducted separately for all years, thus, 3 analyses were conducted. Analyses consisted of MANOVA, CVA, and LSD tests as previously described (see section 4.4.1), except that LSD tests were only performed on 1991 data.

4.4.3. Habitat quality in areas with varying densities of mallards and black ducks

To test my prediction (see prediction #2, page 8) that the area with the highest mallard : black duck ratio would have the most productive wetlands, I combined wetland data from plots dominated by mallards (plots 6, 10, 11, 12), from plots dominated by black ducks (plots 3, 4, 8, 19), from plots with similar numbers of mallards and black ducks (plots 5, 13, 18) and from plots with few mallards and black ducks (plots 16, 17) (see Table 4.1) into 4 areas (i.e., mallard dominated area, black duck dominated area, shared area, and sparsely occupied area). The number of wetlands in each area was: 172, 129, 90, and 56, respectively. MANOVA, CDA, and LSD tests were used to examine habitat differences among the 4 areas.

4.4.4 Habitat use by mallard and black duck broods

Brood observations were conducted in NGLSL in 1990 and in SGLSL in 1991 (see section 4.3.2). Brood wetlands were defined as those wetlands where broods were observed. A total of 41 mallard brood and 45 black duck brood wetlands were evaluated. Due to low number of brood wetlands in any one year or area, brood wetlands were combined between years and areas. Wetlands were not weighted by the number of broods (i.e., a wetland with more than one mallard brood or a wetland with a Class Ia-IIa and a Class IIb-III mallard brood was counted as one wetland), however, a wetland with a brood of each species was entered once for each species. A scarcity of wetlands used by both species prevented the formation of a separate category consisting of wetlands used by broods of both species. T-tests (PROC TTEST; SAS 1985) were used to determine if there were differences in habitat use between mallard and black duck broods.

4.5 RESULTS

4.5.1 Overall analysis of habitat use by breeding pairs

There was an overall difference among wetland groups (mallard, black duck, shared, and vacant wetlands) (Wilk's Lambda = 0.6165, $P < 0.0001$). The 3 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 4.2). Total canonical coefficients indicated that most water chemistry components were generally positively correlated with each axes, whereas, each of the physical variables was highly negatively correlated with one of the 3 axes (Table 4.2). 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 4.3). CAN1, which was characterized by high values of alkalinity ($CaCO_3$) (Table 4.3), separated vacant wetlands from the 3 other groups (Fig.4.2). CAN2, which was characterized by high values of magnesium and

Table 4.2. Total canonical coefficients of the 3 canonical axes from the canonical variates analysis performed to separate the 4 wetland groups[a] (mallard only [n=105], black duck only [n=108], shared [n=37], and vacant [n=197] in north-central Ontario.

	Total canonical coefficients[b]		
Variable[c]	CAN1	CAN2	CAN3
Water chemistry			
Alkalinity	0.8721	0.2123	-0.1109
Calcium	0.6288	0.4998	-0.1991
Color, apparent	0.4328	-0.0892	-0.3560
Color, true	0.4365	-0.1344	0.3913
Conductivity	0.4892	0.6324	-0.1770
Magnesium	0.5062	0.6663	0.[illegible]199
pH	0.4840	-0.0747	0.0478
Potassium	0.4090	0.2379	0.1825
Sodium	0.4737	0.2950	0.3942
Total phosphorus	0.5490	-0.0560	0.2158
Physical			
% open water	-0.4798	-0.2218	-0.2674
SI	0.3884	-0.3779	0.0140
Size (ha)	0.0914	-0.0840	-0.5027
Eigenvalues	43.88	7.62	4.76
% variation explained	78.00	13.55	8.45
P-value	0.0001	0.0007	0.0410

Table 4.2. continued

[a]Groups are defined in text.

[b]Variables highly correlated (r > 0.5) with each axes are underlined.

[c]Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L; SI = shoreline irregularity index.

Table 4.3. Standardized canonical coefficients of the 3 canonical axes from the canonical variates analysis performed to separate the 4 wetland groups[a] (mallard only [n=105], black duck only [n=108], shared [n=37], and vacant [n=197] in north-central Ontario.

	Standardized canonical coefficients[b]		
Variable[c]	CAN1	CAN2	CAN3
Water chemistry			
Alkalinity	0.8513	-0.4137	-0.3745
Calcium	0.0913	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	-0.0615	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	0.0410

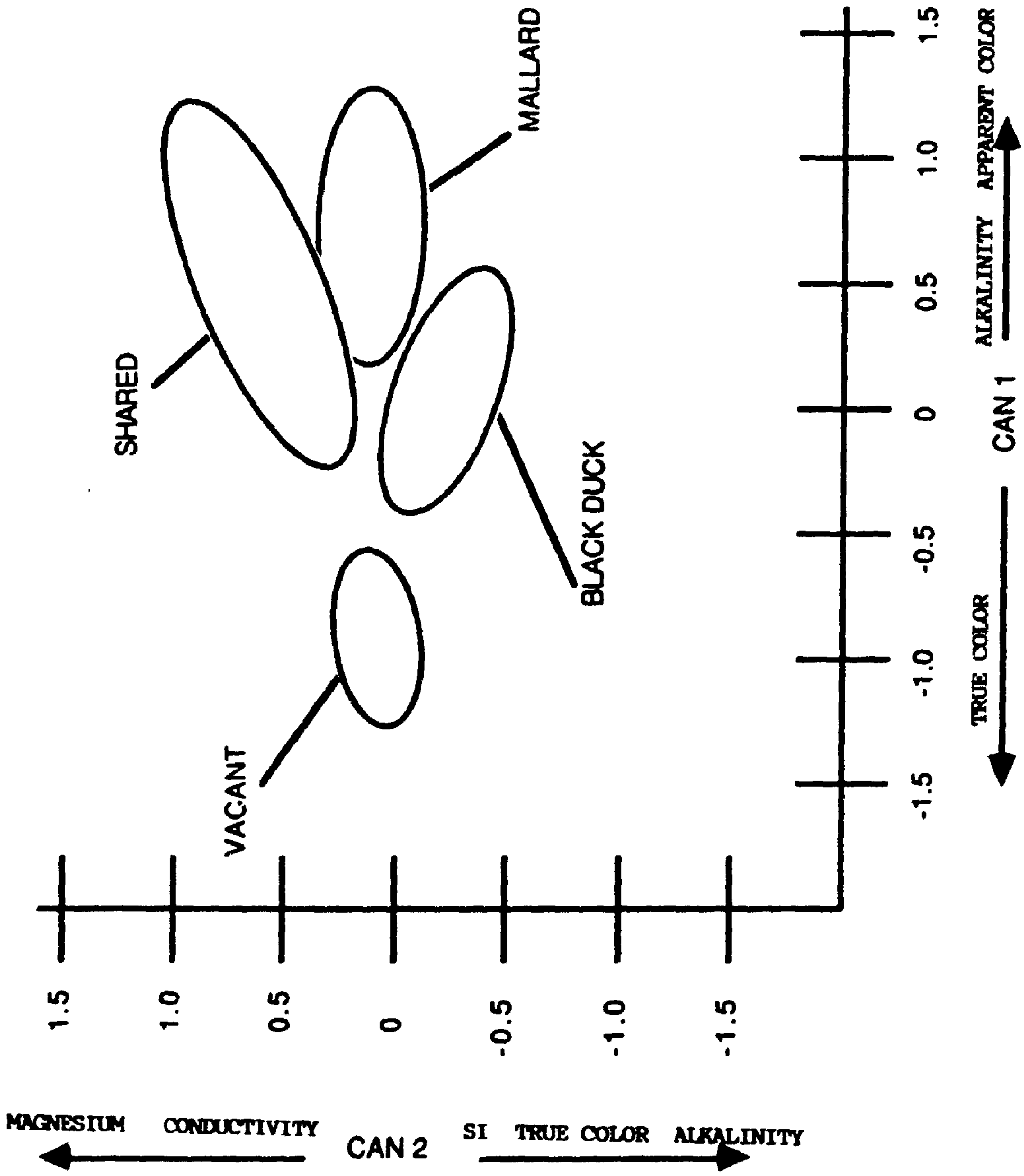
Table 4.3. continued.

[a]Groups are defined in text.

[b]Variables important in defining the axes are underlined.

[c]Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L; SI = shoreline irregularity index.

Figure 4.2. Ninety-five percent confidence ellipses on the first 2 canonical axes for each wetland group in north-central Ontario. Variables most important in defining the axes are shown adjacent to arrows (see standardized canonical coefficients; Table 4.3).


MALLARD
SHARED
BLACK DUCK
VACANT
1.5
1.0
0.5
0
-0.5
-1.0
-1.5
TRUE COLOR
CAN 1
ALKALINITY APPARENT COLOR
MAGNESIUM CONDUCTIVITY
CAN 2
SI TRUE COLOR ALKALINITY

relative to values of SI and true color (Table 4.3), further separated black duck only wetlands from mallard only wetlands and shared wetlands (Fig.4.2). CAN3 was characterized by high values of true color, magnesium, and sodium relative to values of apparent color and calcium (Table 4.3).

All water chemistry variables differed ($P < 0.0001$) among wetland groups. Shared wetlands and mallard wetlands were the most fertile, and vacant wetlands were the least fertile (Table 4.4). Percent open water was lowest in mallard wetlands (Table 4.4). SI was, on average, lowest for vacant wetlands (Table 4.4). Size was not different among groups, but, on average, shared wetlands were largest, whereas, vacant wetlands were smallest (Table 4.4).

These results support my prediction that mallards would occupy the most fertile areas.

4.5.2 Was the pattern repeatable?

These analyses were conducted to provide support for results of analyses conducted in sections 4.4.1 and 4.5.1 and to provide a further test of the preaiction that mallards would occupy the most fertile wetlands. Note that habitat data from NGLSL in 1990 was used to examine waterfowl distributions in that area in 1990, 1991, and 1992; habitat data from SGLSL in 1991 was used to examine waterfowl distributions in that area in 1990, 1991, and 1992.

Table 4.4. 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 north-central Ontario.

	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	P
Water chemistry[a]									
Alkalinity	11.51A[b]	1.15	7.17B	0.78	14.95A	2.69	4.21C	0.35	<0.0001
Calcium	5.58A	0.44	4.01B	0.27	6.57A	0.81	3.39C	0.17	<0.0001
Color, apparent	104.17A	4.45	95.33AB	6.13	83.11BC	7.99	76.29C	4.19	<0.0001
Color, true	86.48	3.74	80.48	5.02	67.43	6.65	63.81	3.63	<0.0001
Conductivity	50.34A	2.94	37.73B	1.77	57.58A	5.92	36.24B	1.24	<0.0001
Magnesium	1.76	0.16	0.98	0.05	1.86	0.29	1.03	0.06	<0.0001
pH	6.56A	0.04	6.45A	0.05	6.49A	0.09	6.20B	0.05	<0.0001
Potassium	0.53	0.03	0.43	0.03	0.51	0.05	0.38	0.02	<0.0001
Sodium	1.57	0.09	1.25	0.05	1.33	0.07	1.15	0.03	<0.0001
Total phosphorus	0.04	0.004	0.03	0.003	0.03	0.004	0.03	0.002	<0.0001

Table 4.4. continued.

Physical									
% open water	68.24C	1.99	77.76B	1.75	74.19BC	3.77	85.91A	1.41	<0.0001
SI	1.74A	0.06	1.75A	0.06	1.63AB	0.08	1.49B	0.03	<0.0001
Size (ha)	5.08	0.50	5.45	0.47	6.90	1.00	4.85	0.35	0.09

[a] Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SI = shoreline irregularity index.

[b] Means in the same row followed by different letters are different; results of univariate output (3,443 df.) in MANOVA and LSD tests.

4.5.2.1 Northern Great Lakes - St. Lawrence

In 1990, 1991 and 1992 there was an overall significant difference among wetland groups (mallard, black duck, shared, and vacant wetlands) (Wilk's Lambda = 0.5840, 0.6692, and 0.6170, respectively; $P < 0.0001$). The first canonical axes (CAN1) from each CVA described 72.4% ($P < 0.0001$), 75.1% ($P < 0.0001$) and 81.8% ($P < 0.0001$) of the among-group variation in 1990, 1991 and 1992, respectively (Table 4.5). CAN2 described 22.4% ($P = 0.0368$), 19.7% ($P = 0.4026$), and 15.3% ($P = 0.5155$) of the among-group variation in 1990, 1991, and 1992, respectively, but was only significant in 1990. CAN3 was not significant ($P = 0.761$, $P = 0.9108$, $P = 0.9764$) in 1990, 1991 or 1992, respectively.

In all years, total canonical coefficients indicated that most water chemistry components were generally positively correlated with each axes, whereas, of the physical variables, percent open water was negatively correlated with both axes and SI was negatively correlated with CAN2 (Table 4.5). In all years, standardized canonical coefficients indicated that water chemistry characteristics were more important than physical characteristics in defining the axes (i.e., separating the wetland groups). In 1990, CAN1, which was characterized by high values of alkalinity ($CaCO_3$) and apparent color relative to values of true color (Table 4.6), separated vacant wetlands from black duck wetlands; CAN1 also separated those 2 groups from

Table 4.5. Total canonical coefficients[a] of the significant canonical axes for each of 3 canonical variates analyses performed to separate the 4 wetland groups[b] (e.g., mallard only, black duck only, shared, and vacant) in each of 3 years with waterfowl observations in Northern Great Lakes - St. Lawrence area (e.g., plots 11-13, and 16-19) in north-central Ontario.

	1990[c]		1991	1992
Variable[d]	CAN1	CAN2	CAN1	CAN1
Water chemistry				
Alkalinity	0.8722	0.1387	0.9315	0.8187
Calcium	0.6479	0.4106	0.8148	0.6374
Color, apparent	0.4546	0.1061	0.5214	0.3879
Color, true	0.4262	0.0853	0.5104	0.3992
Conductivity	0.6613	0.4882	0.8244	0.7137
Magnesium	0.6947	0.5954	0.8380	0.6964
pH	0.6070	-0.0587	0.5333	0.4200
Potassium	0.2796	0.3206	0.3391	0.3879
Sodium	0.4309	0.4030	0.5663	0.4834
Total phosphorus	0.5177	0.0115	0.3922	0.4404
Physical				
% open water	-0.4604	-0.2754	-0.4130	-0.5314
SI	0.3606	-0.2799	0.3271	0.3865
Size	0.1278	0.0333	0.1130	0.3384
Eigenvalues	0.4536	0.1405	0.3403	0.4663
% variation explained	72.35	22.41	75.11	81.78
P-values	0.0001	0.0368	0.0001	0.0001

Table 4.5. continued.

[a]Variables highly correlated ($\underline{r} > 0.5$) with each axes are underlined.

[b]Groups are defined in text.

[c]Only year in which habitat was evaluated.

[d]Water chemistry variables, except pH and conductivity (μ mhos/cm), measured in mg/L; SI = shoreline irregularity index.

Table 4.6. Standardized canonical coefficients[a] of the significant axes for each of 3 canonical variates analyses performed to separate the 4 wetland groups[b] (e.g., mallard only, black duck only, shared, and vacant) in each of 3 years with waterfowl observations in Northern Great Lakes - St. Lawrence area (e.g., plots 11-13, and 16-19) in north-central Ontario.

	1990[c]		1991	1992
Variable[d]	CAN1	CAN2	CAN1	CAN1
Water chemistry				
Alkalinity	0.9085	-0.7507	0.7905	0.7654
Calcium	-0.0858	0.1893	0.0424	-0.1079
Color, apparent	0.7206	-0.0121	0.1561	-0.2091
Color, true	-0.7590	-0.2508	-0.1501	0.1167
Conductivity	0.2840	-0.0463	0.3691	0.4446
Magnesium	-0.2490	1.3285	-0.0950	-0.2422
pH	0.2301	-0.3851	-0.0499	-0.0987
Potassium	-0.0567	0.0706	-0.0698	0.0593
Sodium	-0.1504	0.2379	0.0553	-0.0479
Total phosphorus	0.3888	-0.1865	0.1408	0.1990
Physical				
% open water	-0.1964	-0.2535	-0.0771	-0.3341
SI	0.2222	-0.4650	0.1340	0.2456
Size	0.0893	0.0879	0.0927	0.3383
Eigenvalues	0.4536	0.1405	0.3403	0.4663
% variation explained	72.35	22.41	75.11	81.78
P-values	0.0001	0.0368	0.0001	0.0001

[a]Variables important in defining the axes are underlined.

Table 4.6. continued.

[a]Variables important in defining the axes are underlined.

[b]Groups are defined in text.

[c]Only year in which habitat was evaluated.

[d]Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L; SI = shoreline irregularity index.

shared and mallard wetlands (Fig.4.3). In 1990, CAN2, which was characterized by high values of magnesium relative to values of alkalinity and SI (Table 4.6), separated black duck wetlands from the 3 other groups (Fig. 4.3). In 1991 and 1992, CAN1 was characterized by high values of alkalinity (Table 4.6).

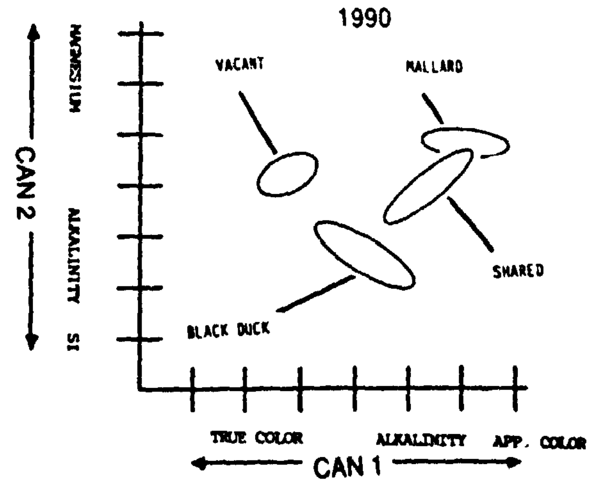
In all years, means for water chemistry variables were generally highest in mallard and shared wetland, and lowest in vacant wetlands (Tables 4.7, 4.8, 4.9). Black duck wetlands had higher water chemistry values than did vacant wetlands (Tables 4.7, 4.8, 4.9). Vacant wetlands had the greatest percentage of open water and lowest SI in all years (Tables 4.7, 4.8, 4.9). Among used wetlands, shared wetlands were generally the largest (Tables 4.7, 4.8, 4.9).

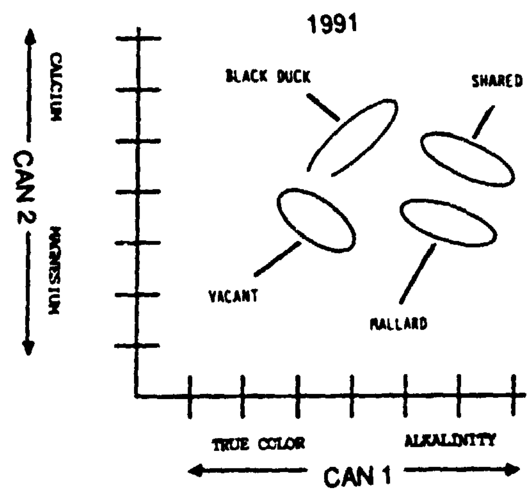
Results from all years in NGLSL are remarkably similar and further support results from section 4.5.1 and my prediction that mallards would occupy the most fertile wetlands.

4.5.2.2 Southern Great Lakes - St. Lawrence

In 1990, 1991, and 1992, there was an overall significant difference among wetland groups (mallard, black duck, shared, and vacant wetlands) (Wilk's Lambda = 0.5166, 0.4973, 0.4756; $P < 0.0001$) in 1991, 1990, and 1992, respectively. The first canonical axes (CAN1) from the CVA described 83.3% ($P < 0.0001$), 75.8% ($P < 0.0001$), and 78.7% ($P < 0.0001$) of the among-group variation in 1990, 1991, and

Figure 4.3. Ninety-five percent confidence ellipses on the first 2 canonical axes for each wetland group in Northern Great Lakes - St. Lawrence area (e.g., plots 11-13 and 16-19) in 1990, 1991, and 1992. Variables most important in defining the axes are shown adjacent to arrows (see standardized canonical coefficients; Table 4.6). Note that habitat was evaluated in 1990.


1990
VACANT
MALLARD
SHARED
BLACK DUCK
MAGNESIUM
ALKALINITY
SI
CAN 2
TRUE COLOR
ALKALINITY
APP. COLOR
CAN 1


1991
BLACK DUCK
SHARED
VACANT
MALLARD
CALCIUM
MAGNESIUM
CAN 2
TRUE COLOR
ALKALINITY
CAN 1

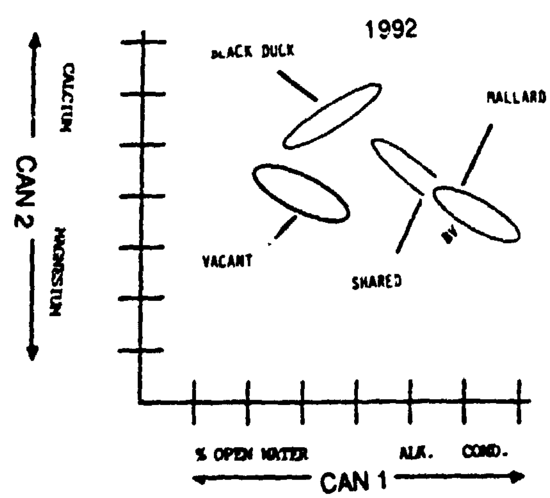

1992
BLACK DUCK
MALLARD
VACANT
SHARED
CALCIUM
MAGNESIUM
CAN 2
% OPEN WATER
ALK.
COND.
CAN 1

Table 4.7. Averages of water chemical and physical variables ' mallard only, black duck only, shared (e.g., mallard and black duck) and vacant (e.g., no mallards or black ducks) wetlands i summer 1990[a] in plots 11-13 and 16-19 in north-central Ontario.

	Mallard only (n=47)		Black duck only (n=44)		Shared (n=24)		Vacant (n=125)		
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P
Water chemistry[b]									
Alkalinity	15.95A[c]	2.29	6.39B	0.93	13.65A	3.18	4.54C	0.51	<0.0001
Calcium	7.09A	0.80	3.90B	0.39	6.51A	1.08	3.82B	0.25	<0.0001
Color, apparent	109.57A	7.01	90.34AB	10.54	84.58B	10.35	77.68B	5.80	0.0006
Color, true	84.26	5.13	72.39	7.94	65.83	8.00	63.80	4.97	0.0015
Conductivity	63.96A	5.20	38.89B	2.29	57.30A	7.10	39.73B	1.78	0.0001
Magnesium	2.37	0.24	1.05	0.08	1.84	0.31	1.21	0.09	0.0001
pH	6.50A	0.07	6.27A	0.08	6.52A	0.12	6.01B	0.06	0.0001
Potassium	0.50	0.05	0.39	0.05	0.41	0.05	0.37	0.02	0.0289
Sodium	1.62	0.09	1.26	0.10	1.36	0.10	1.21	0.04	0.0001
Total phosphorus	0.04	0.003	0.03	0.003	0.03	0.004	0.02	0.002	0.0001

Table 4.7. continued.

Physical									
% open water	64.89B	3.20	81.14A	2.77	73.75AB	5.10	86.04A	2.05	0.0003
SI	1.73A	0.09	1.75A	0.10	1.73A	0.11	1.50B	0.03	0.0068
Size	5.72	0.77	5.18	0.65	6.58	1.14	5.51	0.51	0.3471

[a] Bird observations and habitat data are from 1990.

[b] All water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SDI = shoreline development index.

[c] Means in the same row followed by different letters are different; results of univariate output (3, 236 df.) in MANOVA and LSD tests.

Table 4.8. 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 summer 1991[a] in plots 11-13 and 16-19 in north-central Ontario.

	Mallard only (n=42)		Black duck only (n=42)		Shared (n=12)		Vacant (n=144)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water chemistry[b]								
Alkalinity	16.32	2.55	7.67	1.04	20.28	4.86	4.69	0.52
Calcium	6.99	0.84	4.55	0.37	9.19	1.64	3.77	0.26
Color, apparent	103.93	7.69	97.74	10.94	112.50	15.25	76.70	5.19
Color, true	86.62	5.97	77.26	8.49	89.58	7.82	62.56	4.36
Conductivity	63.29	5.35	43.15	2.53	72.03	11.93	39.60	1.78
Magnesium	2.38	0.28	1.22	0.10	2.57	0.45	1.18	0.08
pH	6.43	0.10	6.29	0.10	6.71	0.12	6.08	0.05
Potassium	0.50	0.06	0.40	0.05	0.46	0.05	0.37	0.02
Sodium	1.57	0.09	1.33	0.09	1.65	0.16	1.21	0.04
Total phosphorus	0.03	0.003	0.03	0.003	0.03	0.003	0.03	0.003

Table 4.8 . continued

Physical								
% open water	64.17	3.38	82.26	3.05	78.33	6.23	83.72	1.96
SI	1.73	0.08	1.76	0.12	1.76	0.23	1.53	0.03
Size (ha)	6.07	0.84	5.43	0.74	6.83	3.25	5.41	0.40

[a] Bird observations are from 1991: habitat data are from 1990.

[b] Water chemistry variables, except pH and conductivity(μmhos/.cm), measured in mg/L.

Table 4.9. 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 summer 1992[a] in plots 11-13 and 16-19 in north-central Ontario.

	Mallard only (n=52)		Black duck only (n=41)		Shared (n=24)		Vacant (n=123)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water chemistry[b]								
Alkalinity	14.89	2.18	7.05	1.08	12.77	2.90	4.58	0.54
Calcium	6.67	0.74	4.58	0.46	6.17	1.06	3.70	0.25
Color, apparent	103.75	8.01	90.12	10.59	89.17	10.68	78.33	5.72
Color, true	84.33	6.80	70.49	7.89	71.25	8.32	62.72	4.68
Conductivity	61.68	4.67	40.58	2.68	57.89	7.27	38.83	1.80
Magnesium	2.22	0.23	1.17	0.10	1.84	0.27	1.18	0.09
pH	6.42	0.08	6.24	0.09	6.40	0.10	6.07	0.06
Potassium	0.50	0.05	0.33	0.03	0.50	0.10	0.38	0.03
Sodium	1.55	0.09	1.23	0.09	1.50	0.10	1.20	0.04

Table 4.9. continued.

Total phosphorus	0.04	0.007	0.02	0.003	0.03	0.003	0.03	0.002
Physical								
% open water	65.67	3.31	85.37	2.70	70.63	5.21	85.65	1.97
SI	1.73	0.07	1.76	0.13	1.81	0.15	1.49	0.03
Size (ha)	6.08	0.67	5.88	0.81	8.67	1.92	4.71	0.39

[a] Bird observations are from 1992; habitat data are from 1990.

[b] Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L.

1992, respectively (Table 4.10). CAN2 described 10.8% (P = 0.3321), 18.0% (P = 0.0291), and 14.5% (P = 0.0397) of the among-group variation in 1990, 1991, and 1992, respectively. CAN3 was not significant (P = 0.5770, P = 0.5019, P = 0.3828) in 1990, 1991, or 1992, respectively.

In all years, total canonical coefficients indicated that most water chemistry components were generally positively correlated with CAN1, whereas, of the physical variables, percent open water was negatively correlated with CAN1 (Table 4.10). In all years, 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 4.11). CAN1, which was characterized by high values of alkalinity ($CaCO_3$), calcium, conductivity, magnesium, and sodium (Table 4.11) relative to percent open water, separated vacant wetlands from the other 3 groups (Fig.4.4).

Group means for all habitat variables showed that vacant wetlands were distinctly separated from wetlands used by either mallards and/or black ducks, which were quite similar (Tables 4.12, 4.13, 4.14).

Results from all years in SGLSL are remarkably similar and support results of section 4.5.1 and my prediction that mallards would occupy the most fertile wetlands.

Table 4.10. Total canonical coefficients[a] of the significant canonical axes from a canonical variates analysis for each of 3 canonical variates analyses performed to separate the 4 wetland groups[b] (e.g., mallard only, black duck only, shared, and vacant) in each of 3 years with waterfowl observations in Southern Great Lakes - St. Lawrence area (e.g., plots 3-6, 8, and 10) in north-central Ontario.

	1990	1991[c]		1992	
Variable[d]	CAN1	CAN1	CAN2	CAN1	CAN2
Water chemistry					
Alkalinity	0.8835	0.8479	-0.3381	0.8651	-0.1259
Calcium	0.7176	0.7395	-0.3446	0.7343	-0.1659
Color, apparent	0.3042	0.3139	0.3050	0.3134	0.0628
Color, true	0.3161	0.3252	0.3442	0.2908	0.1271
Conductivity	0.5144	0.5025	-0.4469	0.5259	-0.1550
Magnesium	0.5189	0.5137	-0.2001	0.4719	0.2303
pH	0.0786	0.0935	0.2527	0.1361	-0.0121
Potassium	0.3767	0.4779	-0.1461	0.4219	0.2283
Sodium	0.4725	0.5386	0.2145	0.5410	0.3333
Total phosphorus	0.2077	0.4139	0.2304	0.0366	-0.3043
Physical					
% open water	-0.5947	-0.5369	-0.2346	-0.5550	-0.2445
SI	0.3674	0.3271	0.4670	0.3625	-0.0517
Size	0.0881	0.1638	-0.3186	0.1387	-0.0078
Eigenvalues	0.6934	0.6527	0.1548	0.7396	0.1389
% var. explained	83.32	75.79	17.98	78.70	14.78
P-value	0.0001	0.0001	0.0291	0.0001	0.0397

Table 4.10. continued.

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[a]Variables highly correlated ($\underline{r} > 0.5$) with each axes are underlined.

[b]Groups are defined in text.

[c]Only year for which habitat data was obtained.

[d]Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L; SI = shoreline irregularity index.

Table 4.11. Standardized canonical coefficients[a] of the significant axes for each of 3 canonical variates analyses performed to separate the 4 wetland groups[b] (e.g., mallard only, black duck only, shared, and vacant) in each of 3 years with waterfowl observations in Southern Great Lakes - St. Lawrence area (e.g., plots 3-6, 8, and 10) in north-central Ontario.

	1990	1991[c]		1992	
Variable[d]	CAN1	CAN1	CAN2	CAN1	CAN2
Water chemistry					
Alkalinity	0.7927	0.7543	-0.5087	0.8398	0.045
Calcium	0.0539	0.3892	0.2344	0.5182	-1.092
Color, apparent	0.1739	0.0205	-0.9301	0.9495	-1.765
Color, true	-0.1773	0.2816	0.9948	-0.6443	1.676
Conductivity	0.4030	-0.3333	-0.5901	-0.3846	-0.3727
Magnesium	0.1105	0.0368	-0.0856	-0.0699	0.8061
pH	-0.0549	0.0996	0.3896	0.1602	0.1304
Potassium	-0.0748	0.0457	-0.2051	-0.1289	0.4844
Sodium	0.0497	0.1122	0.6919	0.2857	0.5696
Total phosphorus	0.1766	0.2563	0.0931	-0.0937	-0.4950
Physical					
% open water	-0.0781	-0.3436	-0.113	-0.3308	-0.3274
SI	0.1319	-0.0038	0.5605	0.0441	-0.1852
Size	0.0908	0.1130	-0.1564	0.0659	0.1285
Eigenvalues	0.6934	0.6527	0.1548	0.7396	0.1389
% var. explained	83.32	75.79	17.98	78.70	14.78
P-value	0.0001	0.0001	0.0291	0.0001	0.0397

Table 4.11. continued.

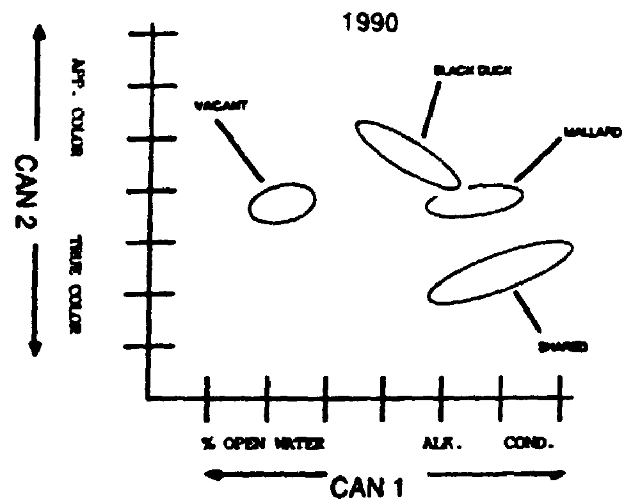
[a]Variables important in defining the axes are underlined.

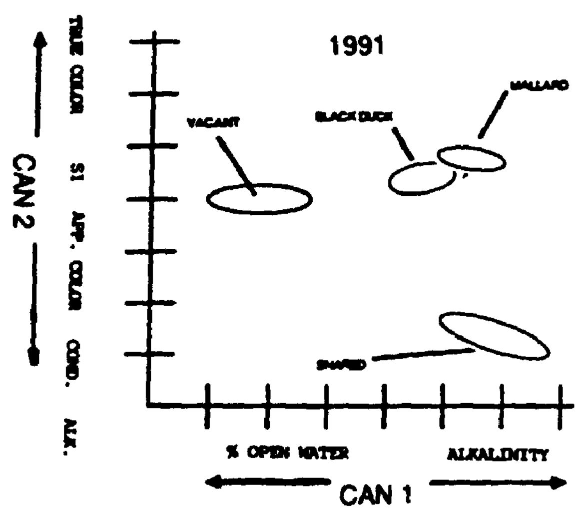
[b]Groups are defined in text.

[c]Only year in which habitat was evaluated.

[d]Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L; SI = shoreline irregularity index.

Figure 4.4. Ninety-five percent confidence ellipses on the first 2 canonical axes for each wetland group in Southern Great Lakes - St. Lawrence area (e.g., plots 3-6, 8, and 10) in 1990, 1991, and 1992. Variables most important in defining the axes are shown adjacent to arrows (see standardized canonical coefficients; Table 4.11). Note that habitat was evaluated in 1991.


1990
BLACK DUCK
VACANT
MALLARD
SHARED
APP. COLOR
TRUE COLOR
CAN 2
% OPEN WATER
ALK.
COND.
CAN 1


1991
TRUE COLOR
SI
APP. COLOR
COND.
ALK.
CAN 2
VACANT
BLACK DUCK
MALLARD
SHARED
% OPEN WATER
ALKALINITY
CAN 1

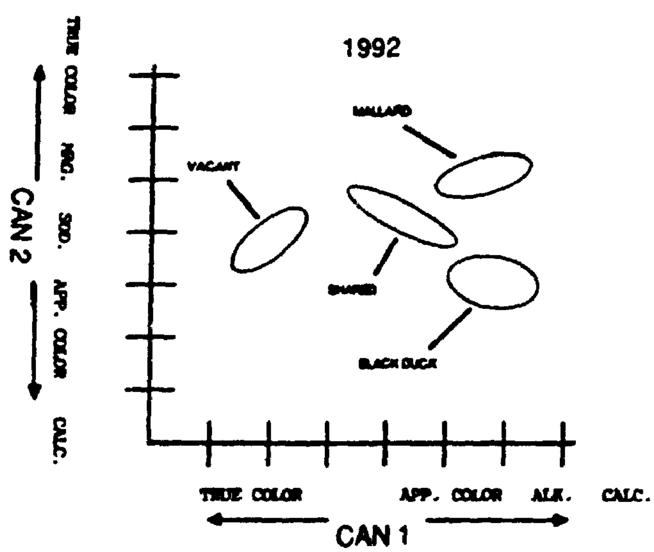

1992
TRUE COLOR
MAG.
SOD.
APP. COLOR
CALC.
CAN 2
MALLARD
VACANT
SHARED
BLACK DUCK
TRUE COLOR
APP. COLOR
ALK.
CALC.
CAN 1

Table 4.12. 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 summer 1990[a] in plots 3-6, 8, and 10 in north-central Ontario.

	Mallard only (n=46)		Black duck only (n=57)		Shared (n=14)		Vacant (n=90)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water chemistry[b]								
Alkalinity	10.34	1.70	9.34	1.27	9.21	1.84	3.50	0.24
Calcium	5.07	0.63	4.51	0.38	4.47	0.74	2.69	0.01
Color, apparent	87.28	6.67	95.70	5.82	115.75	12.34	82.33	5.97
Color, true	76.63	6.00	82.37	5.15	108.21	10.36	71.33	5.36
Conductivity	44.27	4.07	42.01	3.15	35.31	3.97	30.06	0.96
Magnesium	1.48	0.29	1.13	0.10	1.02	0.13	0.71	0.03
pH	6.60	0.05	6.61	0.05	6.41	0.15	6.53	0.06
Potassium	0.56	0.05	0.56	0.04	0.43	0.07	0.39	0.02
Sodium	1.45	0.14	1.42	0.11	1.21	0.10	1.09	0.03

Table 4.12. continued.

Total phosphorus	0.04	0.005	0.04	0.004	0.03	0.004	0.03	0.002
Physical								
% open water	71.30	2.68	72.54	2.29	70.36	5.31	85.56	1.45
SI	1.63	0.07	1.84	0.09	1.71	0.15	1.48	0.03
Size (ha)	5.49	0.82	4.93	0.72	4.64	1.03	4.32	0.40

[a] Bird observations are from 1990; habitat data are from 1991.

[b] Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SI= shoreline irregularity index.

Table 4.13. 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 summer 1991[a] in plots 3-6, 8, and 10 in north-central Ontario.

	Mallard only (n=61)		Black duck only (n=61)		Shared (n=13)		Vacant (n=72)		
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P
Water chemistry[b]									
Alkalinity	8.08B[c]	0.80	7.74B	1.16	17.35A	5.03	3.63C	0.34	<0.0001
Calcium	4.42B	0.42	4.08B	0.36	6.68A	1.24	2.63C	0.13	<0.0001
Color, apparent	100.00A	5.71	98.93A	7.37	80.38AB	12.81	73.89B	5.51	0.0131
Color, true	86.20	5.23	86.31	6.43	70.38	12.21	63.82	4.96	0.0015
Conductivity	39.85B	2.64	37.25B	2.57	58.10B	10.96	30.18C	1.11	<0.0001
Magnesium	1.29	0.20	0.93	0.06	1.90	0.61	0.71	0.03	<0.0001
pH	6.61A	0.05	6.59A	0.06	6.54A	0.10	6.21B	0.07	<0.0001
Potassium	0.55	0.04	0.47	0.03	0.68	0.11	0.38	0.03	<0.0001
Sodium	1.54	0.14	1.25	0.04	1.29	0.08	1.05	0.03	<0.0001
Total phosphorus	0.05	0.006	0.04	0.004	0.04	0.007	0.03	0.003	<0.0011

Table 4.13. continued.

Physical									
% open water	70.82B	2.48	75.33B	2.23	75.00B	5.39	85.69A	1 49	<0.0001
SI	1.74A	0.08	1.74A	0.07	1.45B	0.09	1.47B	0.04	0.0009
Size	4.59	0.65	5.65	0.66	7.48	1.96	3.70	0.33	0.0738

[a] Bird observations and habitat data are from 1991.

[b] All water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SDI = shoreline development index.

[c] Means in the same row followed by different letters are different; results of univariate output (3,203 df.) in MANOVA and LSD tests.

Table 4.14. 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 summer 1992[a] in plots 3-6, 8, and 10 in north-central Ontario.

	Mallard only (n=46)		Black duck only (n=57)		Shared (n=14)		Vacant (n=90)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water chemistry[b]								
Alkalinity	8.57	0.91	11.05	1.62	5.47	0.76	3.58	0.26
Calcium	4.60	0.52	5.05	0.46	3.15	0.30	2.68	0.11
Color, apparent	97.77	7.03	95.49	6.77	109.09	9.09	78.18	5.38
Color, true	86.21	6.52	81.07	5.84	96.82	9.10	68.35	4.85
Conductivity	41.12	3.12	44.35	3.57	31.05	2.69	30.13	0.97
Magnesium	1.36	0.25	1.21	0.15	0.79	0.06	0.73	0.03
pH	6.61	0.05	6.61	0.05	6.56	0.14	6.42	0.06
Potassium	0.61	0.06	0.52	0.04	0.38	0.05	0.39	0.02
Sodium	1.61	0.18	1.30	0.05	1.22	0.10	1.06	0.03

Table 4.14. continued.

Total phosphorus	0.04	0.005	0.04	0.004	0.03	0.003	0.03	0.002
Physical								
% open water	70.00	2.94	73.28	2.14	77.27	5.28	85.11	1.44
SI	1.72	0.10	1.74	0.08	1.73	0.08	1.49	0.04
Size (ha)	5.01	0.69	5.61	0.76	3.32	0.90	4.25	0.40

[a] Bird observations are from 1992; habitat data are from 1991.

[b] Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SI= shoreline irregularity index.

4.5.3. Influence of habitat quality on mallard and black duck distributions

There was significant variation among the 4 types of areas (e.g., mallard dominated, black duck dominated, shared, and sparsely occupied) (Wilk's lambda = 0.4428, $P < 0.0001$). Total canonical coefficients indicated that water chemistry variables, specifically, alkalinity, apparent and true color, and pH were positively correlated with CAN1 (Table 4.15). Standardized canonical coefficients indicated that water chemistry contributed most to the separation of wetland groups (Table 4.16). CAN1, which was characterized by high values of alkalinity, true color, and pH (Table 4.16), clearly distinguished sparsely occupied areas from the other 3 areas (Fig.4.5). CAN2, which was characterized by high values of calcium and true color (Table 4.16), separated shared and mallard dominated areas from black duck dominated and sparsely occupied areas (Fig. 4.5). Sparsely occupied areas were significantly less fertile than those areas dominated by either mallards or black ducks (Table 4.17). Mallard dominated areas were, on average, the most fertile (Table 4.17). Shared areas were similar to black duck dominated areas (Table 4.17).

These results support my prediction that the area with the highest mallard : black duck ratio would have the most fertile wetlands.

Table 4.15. Total canonical coefficients of the 3 canonical axes from a canonical variates analysis performed to separate the 4 areas[a] (e.g., mallard dominated, black duck dominated, shared, and sparsely occupied) in north-central Ontario.

	Total canonical coefficients[b]		
Variable[c]	CAN1	CAN2	CAN3
Water chemistry			
Alkalinity	0.7186	0.1618	0.1482
Calcium	0.3236	0.2445	0.3520
Color, apparent	0.5352	-0.2781	-0.4401
Color, true	0.5734	-0.1852	0.4217
Conductivity	0.1955	0.0753	0.2593
Magnesium	0.3630	-0.1992	0.2202
pH	0.6346	0.4520	-0.0450
Potassium	0.1503	0.3402	0.2104
Sodium	0.2508	0.0288	-0.0403
Total phosphorus	0.4203	-0.0710	-0.5583
Physical			
% open water	-0.4357	0.3837	-0.2080
SI	-0.0411	0.0742	-0.0738
Size (ha)	-0.1088	-0.0283	0.1068
Eigenvalues	0.7991	0.1963	0.0493
% variation explained	76.50	18.79	4.71
P-value	0.0001	0.0001	0.033

Table 4.15. continued.

[a]Areas are defined in text.

[b]Variables highly correlated (*r* > 0.5) with each axes are underlined.

[c]Water chemistry variables, except pH and conductivity (μ mhos/cm), measured in mg/L; SI = shoreline irregularity index.

Table 4.16. Standardized canonical coefficients of the 3 canonical axes from a canonical variates analysis performed to separate the 4 areas[a] (e.g., mallard dominated, black duck dominated, shared, and sparsely occupied) in north-central Ontario.

Variable[c]	Standardized canonical coefficients[b] 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

Table 4.16. continued

[a]Areas are defined in text.

[b]Variables important in defining the axes are underlined.

[c]Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L; SI = shoreline irregularity index.

Figure 4.5. Ninety-five percent confidence ellipses on the first 2 canonical axes for mallard dominated, black duck dominated, shared, and sparsely occupied areas in north-central Ontario. Variables most important in defining the axes are shown adjacent to arrows (see standardized canonical coefficients; Table 4.16).

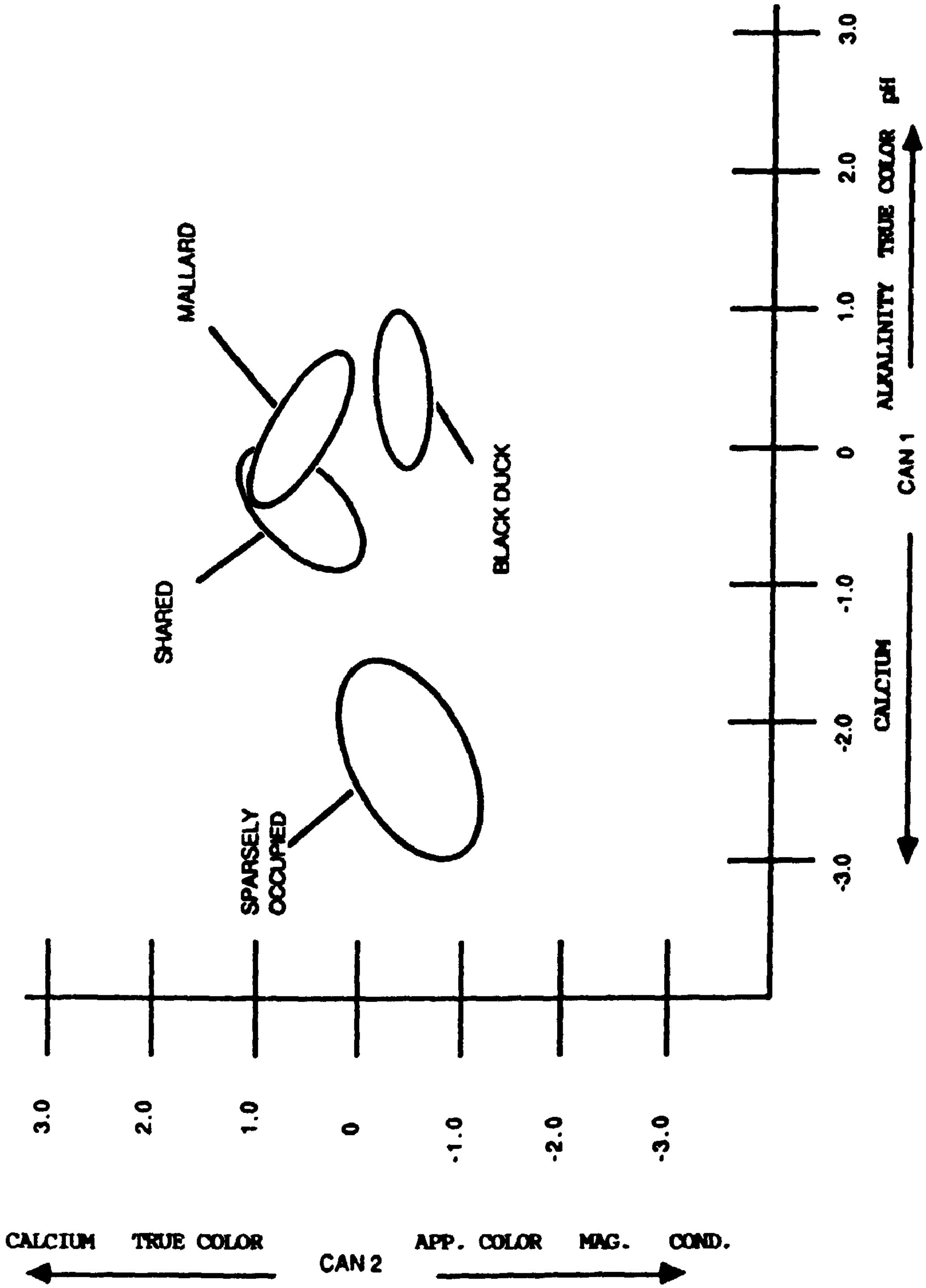

MALLARD
SHARED
BLACK DUCK
SPARSELY OCCUPIED
3.0
2.0
1.0
0
-1.0
-2.0
-3.0
CALCIUM
CAN 1
ALKALINITY TRUE COLOR pH
CALCIUM TRUE COLOR
CAN 2
APP. COLOR MAG. COND.

Table 4.17. 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[a] in north-central Ontario.

	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	P
Water chemistry[b]									
Alkalinity	9.21A[c]	0.82	7.66A	0.89	7.65A	0.92	2.09B	0.41	<0.0001
Calcium	4.58A	0.29	4.32A	0.30	4.82A	0.39	2.75B	0.22	<0.0001
Color, apparent	107.38A	3.92	79.80B	5.20	85.44B	6.25	51.96C	5.84	<0.0001
Color, true	88.54	3.28	68.41	4.53	72.39	5.21	40.80	4.66	<0.0001
Conductivity	45.39A	2.13	39.80AB	2.01	43.09A	2.63	33.00B	0.84	0.024
Magnesium	1.54	0.10	1.17	0.12	1.17	0.09	0.75	0.04	<0.0001
pH	6.46A	0.04	6.54A	0.04	6.39B	0.06	5.66C	0.09	<0.0001
Potassium	0.41	0.02	0.48	0.03	0.50	0.04	0.33	0.02	0.0029
Sodium	1.35	0.04	1.31	0.06	1.30	0.08	1.05	0.04	0.0054

Table 4.17. continued.

Total phosphorus	0.04	0.002	0.04	0.003	0.03	0.003	0.02	0.002	<0.0001
Physical									
% open water	70.70A	1.80	81.55B	1.43	81.44B	2.10	92.77C	1.76	<0.0001
SI	1.58	0.03	1.66	0.05	1.66	0.07	1.61	0.04	0.8382
Size (ha)	4.88	0.41	5.15	0.42	5.47	0.52	6.00	0.69	0.4514

[a] See table 4.1.

[b] Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SI = shoreline irregularity index.

[c] Means in the same row followed by different letters are different; results of univariate output (3, 443 df.) in MANOVA and LSD tests.

4.5.4 Brood habitat use

Alkalinity, pH, apparent color, and true color were higher (P = 0.0089, 0.0009, 0.0233, and 0.0341, respectively) on mallard brood wetlands than on black duck brood wetlands (Table 4.18). Other variables did not differ between brood wetlands. Although an analysis was not conducted, brood wetlands were, on average, more fertile, larger, and had more cover than did pair wetlands (Table 4.18). I did not analyze brood wetlands against vacant wetlands, but as wetlands used by breeding pairs of either mallards and/or black ducks were consistently more fertile wetlands (see sections 4.5.1, 4.5.2.1, 4.5.2.2, 4.5.3), then obviously, brood wetlands were more fertile than vacant wetlands.

Table 4.18. Averages of water chemical and physical variables for wetlands used by mallard or black duck broods in plots 3-6, 8, 10-13, and 16-19 in north-central Ontario during summer 1991 and 1990.[a]

	Brood wetlands[b]				Pair wetlands[c]	
	Mallard (n=41)		Black duck (n=45)		Mallard (108)	Black duck (105)
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	$\bar{x}$
Water chemistry[d]						
Alkalinity	13.51A[e]	2.18	7.54B	1.13	11.51	7.17
Calcium	5.67	0.70	4.32	0.46	5.58	4.01
Color, apparent	120.73A	9.58	95.56B	9.21	104.17	95.33
Color, true	95.26A	6.98	79.44B	7.66	86.48	80.48
Conductivity	51.72	4.97	40.42	3.49	50.34	37.73
Magnesium	1.81	0.23	1.21	0.15	1.76	0.98
pH	6.70A	0.08	6.58B	0.08	6.56	6.45
Potassium	0.53	0.06	0.40	0.04	0.53	0.43

Table 4.18. continued.

Sodium	1.61	0.18	1.26	0.07	1.57	1.25
Total phosphorus	0.04	0.003	0.03	0.003	0.04	0.03
Physical						
% open water	61.86	2.94	68.67	2.83	68.24	77.76
SI	2.51	0.94	1.68	0.07	1.74	1.75
Size (ha)	6.15	0.78	5.44	0.71	5.08	5.45

[a] Brood surveys were conducted in summer 1990 in plots 11-13 and 16-19 and in 1991 in plots 3-6, 8, and 10.

[b] Wetlands shared by mallard and black duck broods were counted as a separate wetland for each species.

[c] Pair data is from Table 4.4 and is only shown for comparison to brood wetlands

[d] Water chemistry variables, except pH and conductivity (μmhos/cm), measured in mg/L. SI= shoreline irregularity index.

[e] Brood means followed by different letters are different ($P < 0.05$).

4.6 DISCUSSION

My predictions that 1) across north-central Ontario, mallards would occupy the most fertile wetlands and 2) areas with the highest mallard : black duck ratio would have the most fertile wetlands were supported in all analyses. In all analyses, I found consistently that mallards shared or solely occupied wetlands that were considerably more fertile than vacant wetlands. On average, mallard only wetlands or shared wetlands were more fertile than black duck wetlands. The area dominated by mallards had the most fertile wetlands. Thus, as in southern Ontario, water chemistry has likely played a major role in the abundance and distributions of mallards and black ducks in north-central Ontario.

Most wetlands in north-central Ontario are underlain by pre-Cambrian bedrock (Ryder 1964, McNicol et al. 1987, see section 2.2.2) that results in low nutrient content of wetlands and, consequently, renders the wetlands relatively infertile especially to breeding waterfowl (Blancher and McCauley 1987, McNicol et al. 1987, see Chapter 3). Although temperate nesting ducks rely heavily upon nutrient stores obtained on the wintering grounds to reproduce (i.e., lay a clutch), the cost of migration results in supplemental nutrients being needed for successful reproduction after arrival on the breeding grounds (Krapu and Swanson 1975, Owen and Reinecke 1977, Afton 1979, 1980, Reinecke and Owen

1980, 1982, Ankney and Afton 1988, Ankney et al. 1991). Nutrients needed for reproduction, maintenance, and growth, especially calcium, carbohydrate, and protein rich plants and invertebrates, are more available on more productive wetlands (see Krapu and Swanson 1975, Blancher and McCauley 1987, Reinecke and Owen 1980). Thus, breeding waterfowl should attempt to occupy the most fertile habitats as possible, especially in areas such as north-central Ontario that have an abundance of relatively infertile wetlands and relatively low breeding waterfowl densities.

Small home range sizes of mallards and black ducks breeding in eastern forested habitats (Gilmer et al. 1975, Ringelman et al. 1982, Dwyer 1992) may be the consequence of it being too energetically costly (Wooley and Owen 1978) to expand territories in an otherwise infertile environment (Ringelman et al. 1978). This underscores the need for selecting wetlands that will meet the nutritional requirements of breeding. Wetland occupancy rates for all waterfowl species average 41% throughout north-central Ontario (Ross 1987, McNicol et al. 1987). Therefore, there are an abundance of wetlands from which breeding waterfowl, specifically, mallards and black ducks, can choose. I believe, as my data show, that at low densities (Jahn and Hunt 1964) or when pioneering, breeding waterfowl select the most fertile of wetlands, especially in a relatively infertile environment (Ringelman et al. 1982) with few conspecific waterfowl. Broods also utilize the most fertile habitats (this study, Patterson 1976), most likely due to their dependence on invertebrates which are more abundant on fertile wetlands (Krapu and Swanson 1975, Blancher and McCauley 1987, Reinecke and Owen 1980). Patterson (1976) and Godin and Joyner (1981) indicated that habitat use by breeding waterfowl (specifically dabbling ducks in Patterson 1976 and mallards in Godin and Joyner 1981) was influenced more by wetland morphology than water chemistry. However, I feel that their analyses were biased by waterfowl occupation of most, if not all, wetlands within relatively small study areas.

This study was not designed to assess competition and was of insufficient duration to document if mallards were replacing black ducks from fertile wetlands as I suggested had occurred in southern Ontario (see Chapter 3). Thus, I cannot say if mallards occupied wetlands more fertile than those used by black ducks due to competitive exclusion. My data indicate that mallards and black ducks select for similar wetland characteristics. Dennis (1974b), Dennis and North (1984), and Dwyer (1992) indicate considerable overlap in the types of habitat used by sympatric breeding mallards and black ducks (see also Appendix 1). Thus, competition for breeding sites is likely. Bellrose (1980) reported that the black duck is the mallard equivalent in eastern North America and, given the behavior and morphologic similarities between mallards and black ducks, we should expect them to have similar habitat requirements and therefore compete for breeding sites.

In north-central Ontario, areas dominated by mallards (e.g., combination of plots 5, 6, 10, 11, 12) were the most fertile followed by areas with similar numbers of both species (e.g., plots 13 and 18) which were similar to areas dominated by black ducks (e.g., plots 3, 4, 8, 16, 17, and 19). McNicol et al. (1987) reported that breeding waterfowl densities in north-central Ontario are highest in the Nipissing area due to superior habitat. Likewise, high breeding densities of mallards in the Clay Belt area of northern Ontario (Ross 1992) are likely due to the abundance of productive wetlands. Breeding mallards were virtually non-existent anywhere in northern Ontario before 1950 (Hanson et al. 1949). Thus, any area dominated by mallards today was probably historically dominated by black ducks. In the western Adirondacks in New York, Dwyer (1992) reports that black ducks make considerable use of wetlands with unconsolidated bottoms, whereas, in Maine, Ringelman et al. (1982) reports that black ducks generally avoid these areas. Unconsolidated bottom habitats are generally less fertile than other wetland types that may be available. It is interesting to note that in the area studied by Dwyer (1992) mallards are now relatively numerous, but in the area studied by Ringelman et al. (1982) mallards are considerably less common. The intrusion of mallards into forested black duck habitat in New York may have resulted in the black duck shifting to inferior habitats.

Among conspecific ducks, spacing and visual isolation are important requirements in wetland selection (Dzubin 1969, Seymour and Titman 1978). Wetlands shared by mallards and black ducks were on average larger than wetlands used solely by either species; this further indicates that mallards and black ducks treat each other as conspecifics (Brodsky and Weatherhead 1984, Seymour 1990) and, therefore, likely compete for breeding sites. Evidence from Brodsky and Weatherhead (1984), Brodsky et al. (1988), Seymour (1990), and Dwyer (1992) indicates that mallards are competitively superior to black ducks, especially during the breeding season. Thus, competitive exclusion likely explains why mallards generally occupy the most productive wetlands.

Black ducks traditionally wintered further north than did mallards and usually fed on protein-rich animal matter in coastal salt-marsh areas. Mallards wintered further south and inland and fed on a lipid / carbohydrate rich diet of natural and agricultural seeds. Increased agriculture in northern latitudes (Dennis et al. 1984), however, has provided an abundance of such food and enabled mallards to winter further north. Although black ducks utilize waste grain, it is believed that they do so to a lesser extent than do mallards, relying more instead on natural foods. Hanson et al. (1989) indicate that mallards generally stored more lipids than did black ducks during autumm. Lipid stores are important in survival (Nichols et al. 1987), pair formation (Brodsky et al. 1984), and reproductive success (Ankney and Afton 1988, Ankney and Alisauskas 1991, Ankney et al. 1991) and also may play an important role in mallard and black duck interactions.

Paired waterfowl are dominant to unpaired waterfowl (Hepp and Hair 1984), and individuals feeding on a highly nutritious diet, on average, pair earlier than do those on inferior diets (Brodsky and Weatherhead 1985, Hepp 1986). Mallards initiate courtship activities earlier than do black ducks (Brodsky and Weatherhead 1984), probably as a result of feeding on higher quality foods. Sex ratios for mallards and black ducks, as well as most waterfowl species, are male biased (Bellrose 1980) thus, unpaired male mallards would be able to court and pair with female black ducks before male black ducks initiated courtship (Brodsky and Weatherhead 1984). Moreover, paired mallards may exclude unpaired black ducks from productive wintering feeding sites. Mallards may therefore be able to store sufficient nutrients to begin nesting activities before black ducks do. In New Zealand, introduced mallards have an earlier breeding chronology than do native grey ducks, resulting in some male mallards pairing with grey ducks (Williams and Roderick 1973).

Although anecdotal, data for Ontario suggest that black ducks arrive on breeding areas 3-5 days before mallards (Saunders and Dale 1933, Brooman 1954, Mills 1981). Thus, black ducks would appear to have the first opportunity to occupy productive wetlands. Pair:flock (Ross 1991) and male:female ratios (D'Eon 1992), however, indicate that mallards begin nesting activities before black ducks. Perhaps higher lipid levels upon arrival (due to wintering ground affiliation and food habits) enable mallards to initiate nesting before black ducks do. Mallards may therefore be more aggressive in occupying and defending productive wetlands. Perhaps, black ducks arrive with insufficient lipid reserves as a consequence of wintering ground affiliation and must therefore increase lipid levels before nest initiation (Ringelman et al. 1982b (e.g., nutrient-reserve threshold for clutch initiation; see Ankney and Alisauskas 1991). Given the relatively scarcity of foods in early spring, black duck nest initiation would be delayed relative to that of mallards. Delayed nesting by black ducks might affect growth and survival of ducklings (Ringelman and Longcore 1982) and also potential to renest. Dwyer (1992) reported that mallards were more persistent renesters than were black ducks which (see also Appendix 2), again, may be due to occupation of more productive wetlands and or wintering ground affiliation. Occupation of the most fertile wetlands by mallards may result in differences in reproduction (i.e., earlier nesting chronology, larger clutch size, higher renesting frequency, or increased duckling growth and survival). Any (or all) of these could lead to further increases in mallard and consequent decreases in black duck numbers (Ankney et al. 1987, Nichols et al. 1987).

Although clutch size appears similar between sympatric breeding mallards and black ducks (Laperle 1974, Dwyer 1992, Appendix 3), mallards appear to renest more frequently than do black ducks and ultimately have a slightly higher reproductive output than do black ducks (Laperle 1974). This may be related to occupation of better habitats either on breeding or wintering grounds (Krapu 1981, Eldridge and Krapu 1988). Perhaps mallards are better at assimiliating nutrients stored from wintering grounds or nutrients acquired on breeding grounds than are black ducks. I believe that a bioenergetic study of sympatric wintering and breeding mallards and black ducks would contribute greatly to our further understanding of mallard and black duck interactions.

It is believed that the cutting of eastern forests and conversion to agriculture played a major role in the increase of mallards and subsequent decline of black ducks (Cringan 1960, Conroy et al. 1987). Although mallards commonly breed throughout the boreal forests of Canada and Alaska (Bellrose 1980), Conroy et al. (1987) argued that in southern Ontario the dramatic influx and subsequent increase of mallards and decline of black ducks was related to land-use changes and habitat loss (but see Chapter 3, Ankney et al. 1987, 1989). However, the same cannot be said for north-central Ontario. As a whole, the plots in north-central Ontario are relatively undisturbed. Disturbance is perhaps greatest in Plot 11, where cattle grazing and hay production is common, but, relative to southern Ontario, it is light. Logging is prevalent throughout northern Ontario and has occurred on many plots. Extensive cottage development has occurred in Plot 5 in the Muskoka Lakes area. Yet, black ducks are uniformly numerous in most areas. Although it is suggested that black ducks are less tolerant of disturbance than are mallards (see Kirby 1988, Dieffenbach and Owen 1988), there appears to be as much evidence against this argument as there is for it (Chapter 3, Ringelman and Longcore 1982, Dwyer 1992). Overall, the evidence that habitat loss/alteration and disturbance has played a role in the decline of black ducks and increase of mallards is inconclusive at best.

4.7 SUMMARY

In north-central Ontario, I believe that wetland fertility is an important component in wetland selection by breeding mallards and black ducks and has played a major role in mallard colonization. Nutrients needed for successful breeding, maintenance, and growth are more abundant in more fertile wetlands. Thus, breeding mallards and black ducks should attempt to occupy the most fertile wetlands as possible, especially in the relatively infertile environment of north-central Ontario. On average, mallards solely occupy or share with black ducks the most productive habitats. The consequences of this scenario on reproduction (e.g., clutch size, egg viability, survival and growth of ducklings) are not known. Mallards and black ducks treat each other as conspecifics and select for similar wetland characteristics (i.e., competition for breeding sites is likely). If the mallard population continues to increase, and there appears no reason that it will not, mallards will likely exclude black ducks from the most productive wetlands. This may have further effects on black ducks, as any differences in reproduction that favor mallards will exacerbate changes in population levels and hybridization. At present, mallards in northern Ontario continue to increase, primarily in the southern Great Lakes - St. Lawrence areas, whereas, black ducks are stable throughout northern Ontario (Ross 1992). D'Eon (1992) suggested that black ducks could "absorb" increases in mallard and hybrid numbers until a threshhold was reached after which black ducks would start to decline. The results of future breeding pair surveys in north-central will undoubtedly shed further light on this scenario.

Given the adaptability of the mallard to many areas and habitat types, as well as similarities in habitat use between mallards and black ducks, habitat management activities (e.g., wetland fertilization, impoundment construction) designed to solely enhance black duck production would be futile. However, given the relative infertility of north-central Ontario, such activities would be greatly beneficial to breeding waterfowl. To increase our understanding of the effect of breeding mallards on black ducks studies similar to mine should be conducted in other areas. I believe that a bioenergetics study of sympatric wintering and breeding mallards and black ducks would contribute greatly to our understanding of mallard and black duck interactions.

CHAPTER 5

CONCLUDING DISCUSSION

5.1 EFFECT OF MALLARDS ON BLACK DUCKS

Decreases of black ducks have been most rapid in areas where mallards have increased most dramatically (Rogers and Patterson 1984, Ankney et al. 1989, see Kirby 1988), suggesting that competition or hybridization (Kirby 1988, Ankney et al. 1987, Dennis et al. 1989) with mallards has played a major role in the decline of black ducks. My data are consistent with the thought that mallards have played a significant role in the decline of black ducks (Ankney et al. 1987, 1989), likely through competive exclusion of black ducks from fertile wetlands. In southern Ontario, I found that: 1) mallards first invaded into the most fertile wetlands, 2) of wetlands occupied by black ducks, they were first replaced by mallards on the most fertile ones, 3) as the mallard population increased, mallards sequentially moved into less fertile wetlands, 4) black ducks occur in the least fertile wetlands on CWS study plots, 5) mallards and black ducks appear able to share (at least for now) wetlands that have adequate cover, size, and SI, and 6) vacant wetlands are those wetlands that are relatively infertile and lack adequate cover. In north-central Ontario, I found that: 1) on average, mallards solely occupied or shared with black ducks the most fertile wetlands, 2) vacant wetlands were the least fertile, and 3) areas dominated by mallards had the most fertile wetlands.

My results suggest that mallards and black ducks select for similar wetland characteristics, but that mallards are perhaps capable of out-competing black ducks for choice sites. In southern Ontario, black ducks were apparently unable to compete with mallards for fertile wetlands and thus were relegated to use less fertile areas. Studies of free ranging (Brodsky and Weatherhead 1984) and captive (Brodsky et al. 1988) mallards and black ducks indicate that male mallards are competitively superior to male black ducks when competing for the same female. Therefore, mallards are probably superior at acquiring and defending the best breeding sites (e.g., fertile wetlands). Given the importance of nutrients to breeding and brood-rearing waterfowl (Krapu and Swanson 1975, Reinecke and Owen 1980, Ringelman et al. 1982) and the cost required (Wooley and Owen 1978) to expand the home range in relatively infertile environments, breeding mallards and black ducks should attempt to occupy the most fertile wetlands as possible (Ringelman et al. 1982). In north-central Ontario, an abundance of nutrient poor wetlands but relatively low breeding densities allow mallards and black ducks to occupy the more fertile of wetlands. In north-central Ontario, mallards and black ducks shared the most fertile wetlands, however, mallards dominated the most fertile areas. This suggests that water chemistry is important in wetland selection by mallards and black ducks and that mallards are capable of outcompeting black ducks for those wetlands.

Mallards and black ducks used similar habitat types in western New York (Dwyer 1992), the pre-Cambrian shield and clay belt areas of Ontario (Dennis 1974), and northwestern Ontario (Dennis and North 1984). Mallards and black ducks are basically ecological equivalents (Bellrose 1980), therefore we should expect them to have similar habitat requirements. In my study, wetlands used by both mallards and black ducks were generally larger, had considerable cover, and had high SI, further indicating that mallards and black ducks have similar habitat requirements and that they treat each other as conspecifics (Brodsky et al. 1988, Seymour 1990).

Mallards and black ducks are genetically similar (Ankney et al. 1986, Avise et al. 1989) and produce fertile hybrids (Phillips 1915). Phillips (1912) noted that many black ducks in Massachusetts exhibited >1 mallard characteristic and, subsequently, (Phillips 1915) indicated that mallard genes were dominant to those of black ducks (see Kirby 1988). Hybrid frequencies range from 0% in Newfoundland to 13% in Massachusetts and average 5% over the black duck breeding range (see Rusch et al. 1989). In Ontario, Ankney et al. (1987) indicated that the number of hybrids was highest in areas where mallards and black ducks had the greatest overlap and that the greatest decline of black ducks had occurred in areas with relatively the most hybrids. In Massachusetts, Heusmann (1988) reported that hybrid numbers increased from 8.1% in 1974 to 18.8% in 1987 in conjunction with a corresponding increase in the number of mallards and subsequent decline of black ducks. Hybridization between mallards and black ducks occurs via mixed pairs (Heusmann 1974, Brodsky et al. 1984) and/or forced copulations (Seymour 1990). It has been difficult to document exactly how much hybridization occurs (Rusch et al. 1989), but, hybridization appears to have played a major role in the decline of black ducks (Ankney et al. 1987, 1989). Mallards have been isolated from the New Zealand grey duck considerably longer than from the black duck, yet grey ducks are being genetically swamped by mallards that were introduced there (Gillespie 1985, Caithness et al. 1989).

It is suggested that the release of over 1.8 million pen-reared mallards in the Atlantic Flyway since 1940 has been a significant factor in the decline of black ducks (Heusmann 1991). However, due to low survival and reproductive potential of pen-reared mallards, Stanton et al. (1992) and Batt and Nelson (1990) concluded that such releases could not likely establish a self-sustaining breeding population. Given that mallards have increased dramatically in many eastern areas, especially southern Ontario (where game farm mallards were not released), in the last 40 years, releases most likely contributed very little to mallard population growth. It is believed that pioneering mallards in Ontario were derived from drought-displaced prairie nesting mallards (Ross and Fillman 1990, Heusmann 1991).

5.2 EFFECT OF HUNTING, HABITAT LOSS, PESTICIDES

Over-hunting (Grandy 1983), annual harvest (Krementz et 1987, 1988), and early harvest of local breeding populations (Reed and Boyd 1974, Parker 1991, Longcore et al. 1991), have been suggested as causing or contributing to the black duck decline. Since the early 1980's restrictive regulations have cut black duck harvest by 40% (see Rusch et al. 1989), yet black ducks continue to decline (Anon 1992: Atlantic Flyway Winter Survey). Boyd (1988) suggested that restrictive regulations had little effect on the total kill of black ducks. Analyses of band-recovery data suggest (or conclude) that hunting is compensatory in black ducks (Krementz et al. 1987, Nichols et al. 1987) and that rates of hunting mortality and survival of sympatric mallards and black ducks are similar (Nichols et al. 1987, see Rogers and Patterson 1984).

Ankney et al. (1987, 1989) argued that because mallards are pioneers to Ontario and other eastern areas, hunting should have caused them to decline or at least have inhibited population growth. There are no data to suggest that hunters select black ducks over mallards and quite likely the reverse is true (Ankney et al. 1987). Since 1961, mallard harvest in the Atlantic Flyway has increased from 138,700 (15.8% of total duck harvest) to 361,100 (25.4%), yet, mallards continue to increase; black duck harvest decreased from 217,300 (24.7%) to 140,500 (9.9%) (SEIS 1988).

In Quebec, Reed and Boyd (1974) argued that early and heavy harvest of black ducks could potentially deplete local breeding stocks. Reed and Boyd (1974), Parker (1991), and Longcore et al. (1991) suggested that delaying opening day might help to secure local breeding populations. However, black duck populations in New Brunswick appear to be maintaining themselves despite exhibiting a lower juvenile survival rate than in Ontario and Quebec (Rogers and Patterson 1984, see also D'Eon 1992). Additionally, those previous studies of hunting were conducted in managed wetland complexes where hunters were concentrated. Black ducks breed in uniformly low densities throughout their range. Thus, it is unlikely that high losses (perhaps artificially high; see Kirby 1988) of local populations are detrimental to the continental black duck population. Kirby (1988) suggested that such complexes resemble nothing more than "put and take" operations and Erskine (1987b) indicated that such complexes do little to increase local populations.

Habitat loss and change have been suggested as causing the decline of black ducks, indirectly by changing the landscape to that more suitable to breeding mallards and directly by loss of breeding and wintering habitat (Cringan 1960, Patterson and Rogers 1984, Conroy et al. 1987, Huesmann 1991). Changes in numbers and distributions of mallards and black ducks have been greatest in areas where breeding habitat has been altered by agriculture or urbanization (Rogers and Patterson 1984). Black ducks are purportedly less tolerant of disturbance, especially visual disturbance, than are mallards (see Kirby 1988, Dieffenbach and Owen 1989). However, distance from disturbance (e.g., farming, dwellings, roads) does not appear to influence wetland selection by breeding black ducks (Ringelman and Longcore 1982, Dwyer 1992, see Chapter 3). Given that the majority of the black duck breeding range is relatively isolated, I doubt if disturbance could account for the dramatic change in black duck numbers in Ontario. I believe that black ducks could adjust to such changes if mallards had not invaded altered areas. For example, black ducks were common breeders in the Toronto, Ontario area (Goodwin 1956) until replaced by mallards, yet black ducks still nest in urban areas of Ottawa, Ontario, and Halifax, Nova Scotia (C. D. Ankney, pers. commun. 1992).

Cringan (1960) suggested that land clearing and increased agriculture in southern Ontario allowed the mallard to expand its range from the prairie pothole region of Canada and the United States into areas traditionally occupied by breeding black ducks (Bellrose 1978). Mallards are, however, quite numerous in forested areas in northern Ontario (Ross and Fillman 1990) and commonly breed in the (undisturbed) mixed and boreal forests of western Canada and Alaska (Bellrose 1980). Mallards utilize a variety of forested habitat types throughout their eastern range (Cowardin 1969, Gilmer et al. 1975, Dwyer 1992). Mallards are the most widespread and perhaps the most adaptable of waterfowl species, thus, they can likely successfully occupy almost any habitat, epsecially those used by black ducks.

Habitat loss has also been speculated as causing the decline of black ducks, however, there appears to be a general concensus that breeding habitat for black ducks has improved during the period that black ducks have declined (Ankney et al. 1987, Kirby 1988, Rusch et al. 1989). Throughout the black duck breeding range there has been an increase in habitat created or modified by beaver (see Collins 1974, Ross et al. 1984, Dennis et al. 1989, Rusch et al. 1989, CWS unpubl. data), which is a preferred habitat of breeding black ducks (Kirby 1988, Appendix 1). Therefore, it does not appear that habitat loss on the breeding grounds would explain the decline of black ducks. Expanding beaver populations have, however, probably facilitated the spread of mallards into forested breeding areas of the black duck (Collins 1974, Ankney et al. 1989, G. B. McCullough, Can. Wildl. Serv., pers. commun.) by providing an abundance of highly productive wetland habitat (Renouf 1972, Ringelman and Longcore 1982, Kirby 1988). Loss of wintering habitat, specifically salt-marsh habitat along the Atlantic Coast (Tiner 1984, National Wetlands Inventory Group 1986), may explain some of the black duck decline. The greatest rate of decline of black ducks has, however, occurred in the Mississippi Flyway and not in the Atlantic Flyway. Coincidentally, mallards have increased most rapidly in the Mississippi Flyway.

Most of the black duck breeding range is subject to acid precipitation with 17% being highly sensitive (Longcore et al. 1987). Acid rain may have contributed to the decline of black ducks (see Kirby 1988) through reduced reproductive success via lack of mineral and/or food resources for either egg formation and/or growth and survival of ducklings (Longcore et al. 1987, McNicol et al. 1987, Blancher and McCauley 1987, Desgranges and Hunter 1988, McCauley and Longcore 1988, Sparling 1990). Pesticides may have also contributed to the black duck decline (Hunter et al. 1984). Mallards are vulnerable to the effects of acid rain and pesticides, however, they appear to be slightly less affected than are black ducks (Hunter et al. 1984, Sparling 1990).

5.3 CONCLUSION

The mallard / black duck situation represents a significant evolutionary event but, unfortunately, it has also turned into a political one (Grandy 1983, Feireband 1984). Based on my interpretation of studies to date (see Rusch et al. 1989 for review), I believe that hunting, habitat loss, pesticides, etc., can not account for the dramatic increase of mallards and subsequent decline of black ducks in Ontario, or elsewhere in eastern North America. Support for the role that an increasing mallard population has played in the decline of the black duck (competitive exclusion, hybridization) has been documented many times (Ankney et al. 1987, Brodsky et al. 1988, 1989, Ankney et al. 1989, Seymour 1990, D'Eon 1992, this study), thus suggesting that mallards have been the most significant factor in the decline of black ducks. As mallards continue to increase throughout the black ducks range, I predict that mallards will likely replace (displace) black ducks from wetlands and entire areas where they co-occur, via competitive exclusion and/or hybridization.

APPENDICES

APPENDIX 1

WETLAND AVAILABILITY AND USE BY BREEDING WATERFOWL IN SOUTHERN ONTARIO

Numerous studies have documented the types, availability, and waterfowl use of wetland habitats in the prairie pothole region of the United States and Canada (see Swanson and Duebbert 1989). Knowledge of habitat use by breeding waterfowl in eastern breeding areas is limited, however, due to low breeding densities (Bellrose 1978) and difficulty in surveying forested habitats (Rusch et al. 1989). Waterfowl habitat use studies in eastern breeding areas have been done on locally intensive scales (Patterson 1976, Courcelles and Bedard 1978) or worked with post-breeding waterfowl (Gilmer et al. 1977, Ringelman et al. 1982, Dennis and North 1984, Frazer 1990). Although these studies provide precise local information they do not provide long-term information on population trends, habitat availability, or habitat use over a large breeding area.

In northern Ontario, Ross and Fillman (1990) document distributions of American black ducks and mallards, and Dennis (1974a) documents waterfowl use in relation to vegetative cover and open water interspersion, but neither study examines use of specific habitat types. Dennis (1974b) examined waterfowl habitat use in southern Ontario in relation to the Canada Land Inventory (CLI) waterfowl habitat classification system, but concluded that the system did not perform well in southern Ontario.

Populations of most waterfowl species have been stable or have increased since 1971 in southern Ontario (Dennis et al. 1989) and suggest that wetland habitat in eastern North America is becoming increasingly important for breeding waterfowl. The lack of information regarding waterfowl habitat use in eastern North America and the importance of lower Great Lakes - St. Lawrence River Basin habitats to breeding waterfowl (Anon. 1986) prompted this study. Our objectives were: 1) to quantify and describe breeding waterfowl habitat; 2) to estimate the number of breeding waterfowl that utilize specific wetland habitat types; and 3) to investigate breeding pair use of various wetland habitat types in southern Ontario.

METHODS

To establish long-term population trends of waterfowl breeding in southern Ontario an extensive ground survey (132,000 km^2) was initiated in 1971 by the Canadian Wildlife Service (CWS). The survey was designed to cover plots of countryside (0.8 km x 0.8 km), rather than wetland units, due to the diversity of habitat types which could affect breeding pair densities and waterfowl distributions in southern Ontario (Dennis 1974b). Two hundred and sixty-six plots have been censused by ground crews in all survey years (1971, 72, 76, 81, 85, and 87) (Dennis 1974b, Dennis et al.

1989), whereas, 349 were surveyed in 1987. Data from 349 plots surveyed in 1987 (Fig.1) provide the data used to estimate wetland abundance and breeding waterfowl populations in southern Ontario. Data from 266 plots surveyed in 1981 were combined with data from 349 plots surveyed in 1987 to evaluate waterfowl use of specific habitat types.

From mid-April to early May, ground crews (2-3 observers and a Labrador retriever) search all habitats in each plot and record the number, species, and sex of encountered waterfowl. In 1981, wetlands on the study plots were categorized into 15 habitat types (Table 1) based upon a modification of the system described by Wheeler and March (1979). Since 1981, area of each habitat type were delimited on aerial photos and the number, sex, and species of waterfowl was recorded for each habitat type. A map digitizer was used to determine the area of each habitat type from aerial photos as delineated by survey personnel. Wetland numbers, hectares, and waterfowl occuring on study plots were expanded to provide estimates for the 132,000 km^2 southern Ontario study area.

To determine habitat preference, chi-square analysis and z-statistics were used to compute 95% confidence intervals for the proportion of waterfowl occurrence in each habitat type (Neu et al. 1974). Only mallards were observed in enough quantity to allow use of the chi-square test (Ott

1988) among all habitat types. Chi-square tests for black ducks, blue-winged teal, and wood ducks were calculated based on 6 habitats, due to low observations for those species. Confidence intervals were constructed on all habitat types for mallards and on the 6 habitats used in chi-square tests for black ducks, blue-winged teal, and wood ducks. Habitat availability values (proportion of available area) greater than the upper end of the confidence interval (proportion use) indicated avoidance, whereas, values less than the lower end indicated preference (Neu et al. 1974). For each species, observed habitat use was the number of birds observed in each habitat type. The number of waterfowl using a particular habitat type was averaged between the 1981 and 1987 surveys. Expected habitat use was calculated by multiplying the percent available area of each habitat type by the total number of birds observed in all habitat types. Habitat availability was similar between years (G. B. McCullough, Can. Wildl. Serv., pers. commun.), thus, habitat availabity was averaged between 1981 and 1987. Low breeding pair densities precluded analyses for, common goldeneye (*Bucephala clangula*), common merganser (*Mergus merganser*), green-winged teal (*Anas crecca*), and ring-necked ducks (*Aythya collaris*).

RESULTS

Habitat availability / Estimated breeding populations

Within the study area there were 836 wetlands comprising 2387 hectares of wetland habitat. Habitat types that accounted for the most area were open water lakes (1125 ha or 47%) and beaver ponds (597 ha or 25%) (Table 2). The remaining 28% of the wetland area was composed of 13 habitat types. Beaver floods (161 wetlands) were the most numerous habitat type, followed by open water ponds (138 wetlands), streams (98 wetlands), and shallow marshes (80 wetlands) (Table 2). Open water lakes average 17 ha in size, whereas, other habitats ranged between 0.2 - 6.0 ha. Waterfowl occupancy rates varied between 11% for bogs and seasonally flooded basins to 50% for deciduous swamps and 43% for beaver ponds. Average waterfowl occupancy rate for all habitats was 26% (Table 2).

Total wetland acreage in southern Ontario was estimated at 1.25 million hectares, based upon data from 349 survey plots (Table 3). Total waterfowl were estimated at 382,366 breeding pairs, with mallards (42%), wood ducks (13%), blue-winged teal (6%), black ducks (4%), and Canada geese (4%) comprising most of the total (Table 3). Estimated pair densities per hectare were: 3.2 mallards, 1.0 wood ducks, 0.46 blue-winged teal, 0.28 black ducks, and 0.27 Canada geese.

Habitat Use

Neither mallards (χ^2 = 1348, 14 df, $P<0.05$), black ducks (χ^2 = 65.8, 5 df, $P\leq 0.05$), blue-winged teal (χ^2 = 531, 14 df, $P\leq 0.05$), nor wood ducks (χ^2 = 639, 14 df, $P\leq 0.05$)

used habitats in proportion to their availability. Mallards preferred shallow marshes, open water ponds, streams, and ditches, and generally used other habitats in proportion to their availability (Table 4). Black ducks preferred beaver ponds, and few were observed on other habitat types. Blue-winged teal preferred open water ponds and shallow marshes, and, used shrub swamps, deciduous swamps, streams, and ditches quite heavily. Wood ducks preferred beaver ponds, deciduous swamps, and open water ponds, and used shallow marshes and streams quite heavily. Open water lakes, rivers, and coniferous swamps were avoided by all dabbling ducks (Table 4). Twenty-one of 62 Canada geese were observed on open water ponds. Common goldeneye (14 of 14 birds) and common mergansers (30 of 35 birds) were associated with open water lakes. Green-winged teal (21 birds) were not concentrating on any specific habitat type. Ring-necked ducks (13 of 16 birds) were associated with beaver ponds.

DISCUSSION

Dennis (1974b) initially reported on the significance of breeding waterfowl populations in southern Ontario, since which, mallards, wood ducks, and Canada geese have increased 2, 3, and 6 fold, respectively (Dennis et al. 1989). These species have also increased in other eastern breeding areas and reflect the increasing importance of eastern breeding habitats to the Mississippi and Atlantic Flyways, especially for mallards and wood ducks. Mallard and wood duck harvest is substantial in Ontario (Legris and Levesque 1991) and in the Mississippi and Atlantic Flyways (Anon. 1988), and signify the importance of waterfowl produced in eastern areas to that harvest.

Of 2.3 million hectares of wetlands present in southern Ontario in 1800, Snell (1987) estimated that only 933,000 hectares remain. We estimate that there are 1.25 million ha of wetland habitat, which may be due to increases in beaver flood habitat (Ross et al. 1984), activities of Ducks Unlimited, and decreased agricultural activity (Snell 1987). Although habitat loss has been quite extensive in extreme southwestern Ontario due to intense agricultural activities, wetland habitat in central and eastern Ontario has remained relatively unchanged due to a rolling topography and rock outcrops of the Pre-Cambrian shield (Snell 1987, see Dennis 1974b).

Due to low waterfowl densities (Bellrose 1978) and an abundance of wetlands, breeding waterfowl habitat in eastern areas is not generally considered to be limiting. However, unlike highly productive prairie wetlands, wetlands in eastern areas generally exhibit low fertility due to the type of underlying bedrock geology (Patterson 1976, Longcore et al. 1987). Low fertility may be in part responsible for the low densities of breeding waterfowl, especially dabbling ducks, when compared to those for prairie wetlands (Kantrud and Stewart 1977). Patterson (1976) reported that wetlands in eastern Ontario that exhibited high $CaCO_3$ concentrations could support more fledged waterfowl than wetlands in the infertile areas of the pre-cambrian shield, probably due to greater abundance of invertebrates and submerged vegetation (Moyle 1956, Krull 1970).

Nearly 50% of the available habitat in southern Ontario is open-water lakes that are avoided by most dabbling ducks, whereas, preferred habitats (e.g., beaver ponds, deciduous swamps, ponds) account for only 31% of the available habitat. Increasing waterfowl populations (mallards, wood ducks, and canada geese) in southern Ontario may be saturating preferred and/or fertile habitats, as reflected by decreasing population growth rates (Ross et al. 1984, Dennis et al. 1989). In southern Ontario, population increases of dabbling ducks (1971-1987) were highest in areas with highly fertile wetlands (Merendino et al. 1992).

In southern Ontario, beaver floods comprised 25% of the wetland area and were an important habitat component for most species, especially black ducks, wood ducks, and ring-necked ducks. Numerous authors have commented on the value of beaver ponds to breeding waterfowl, especially black ducks (see Kirby 1988). Beaver floods may be less affected by drought than isolated wetlands, thus, providing important habitat in dry years. Additionally, new beaver floods provide highly productive habitat to breeding waterfowl.

Beaver ponds have increased in southern Ontario and have contributed to the increase of mallards (Collins 1974) and wood ducks (Ross et al. 1984, Dennis et al. 1989) by providing an abundance of wetland habitat.

Except for beaver floods and open water lakes, other habitat types comprised between 0-6% of the available area and accounted for between 0-10% of the waterfowl use in southern Ontario. Seasonal and semi-permanent wetlands receive heavy use by dabbling ducks in the prairie pothole region (Kantrud and Stewart 1977), however, they represent <2% of the available habitat in southern Ontario, therefore, dabbling ducks must utilize other habitat types. High occupancy rates for open water lakes are due primarily to use by common goldeneye and common merganser.

MANAGEMENT IMPLICATIONS

This study provides information relating to the types and availability of various wetland habitats in southern Ontario and documents habitat use by breeding waterfowl in southern Ontario. Habitat management for breeding waterfowl in eastern areas should incorporate aspects of beaver management (e.g., proper harvest management) given the importance of beaver floods to breeding dabbling ducks. Additionally, the abundance of open water lakes, that are avoided by dabbling ducks, may limit waterfowl populations in eastern areas. Population increases of popular hunted species (mallards, wood ducks, Canada geese) underscore the need for studies throughout eastern breeding areas to further our knowledge of the importance of eastern breeding areas to North American waterfowl populations and of eastern waterfowl production to annual harvests.

Table A.1. Description of wetland habitats on 349 (0.8km x 0.8km) plots in the 132,000 km^2 southern Ontario study area.

Habitat type	Description
Seasonal	
Seasonal basin	soil waterlogged, but not usually wet into the growing season; wetland vegetation usually not present (sheet water).
Wet meadow	standing water during most of the growing season; vegetation is sedges (*Carex spp.*) and grasses.
Marsh	
Deep emergent marsh	water $\geq$1 m deep; vegetation consisting of cattail, bulrush, and pondweeds (*Potomogeton spp.*).
Shallow emergent marsh	water $\leq$1 m deep; vegetation consisting of cattail (*Typha spp.*), bulrush (*Scirpus spp.*), sedges, and arrowheads (*Sagittaria spp.*).
Open water	
Ditch	municipal or farm drainages generally wet year round; emergent vegetation may be present.
Lake	emergent vegetation present only along shoreline.

Table A.1. continued.

Pond	man-made or natural; emergent vegetation present only along shoreline.
River	permanent riverine habitats.
Stream	permanent or intermittent streams to 5m wide; may contain emergent and submergent vegetation.
Wooded	
Beaver flood	habitats created or modified by beaver.
Bog	soil waterlogged; vegetation consisting of black spruce (Picea mariana), tamarack (Larix laricina), and sphagnum moss (Sphagnum spp.).
Coniferous swamp	water to 30cm deep; vegetation consisting of cedars (Thuja spp.).
Conif / Decid swamp	coniferous and deciduous vegetation.
Deciduous swamp	water to 30cm deep; vegetation consisting of ash (Fraxinus spp.) and maple (Acer spp.).
Shrub swamp	soil usually waterlogged; vegetation consisting of alder (Alnus spp.), willow (Salix spp.), sedges, and grasses.

Table A.2. Habitat availability and waterfowl occupancy rates on 349 (0.8 km x 0.8 km) study plots in the 132,000 km^2 southern Ontario study area, 1987.

Type	Number	Area (ha)	% area	% Occupied
Seasonal				
Seas. flooded	55	12.26	0.5	11
Wet meadow	16	14.07	0.6	19
Marsh				
Shallow marsh	80	30.38	1.3	18
Deep marsh	12	46.02	1.9	25
Open water				
Ditch	61	14.46	0.6	26
Lake	61	1,125.52	47.2	44
Pond	138	56.26	2.4	26
River	36	153.35	6.4	39
Stream	98	35.82	1.5	27
Wooded				
Beaver flood	161	597.40	25.0	43
Bog	9	18.57	0.8	11
Coniferous swamp	7	55.75	2.3	14
Con/Dcd swamp	11	63.61	2.7	18
Deciduous swamp	42	81.32	3.4	50
Shrub swamp	49	82.37	3.5	24

Table A.3. Number and area of wetland habitat types in southern Ontario and breeding pairs of waterfowl utilizing those habitats as estimated from 349 (0.8km x 0.8km) study plots in 1987.

Type	Wetland habitat		Estimated breeding pairs				
	Number	Area	Mallard	Black duck	Wood duck	Blue-winged teal	Canada goose
Seasonal							
flooded basin	26,566	5,514	8,242	0	0	0	0
wet meadow	10,373	9,641	2,486	0	0	0	0
Marsh							
Deep	10,125	18,135	4,616	0	0	710	0
Shallow	31,925	11,350	5,326	0	1,775	1,065	710
Open Water							
Ditch	33,389	9,310	9,447	0	0	710	710
Lake	35,734	577,068	12,072	3,303	1,775	1,775	1,065
Pond	72,458	44,936	42,684	0	3,551	5,079	6,714
River	18,647	64,045	7,812	0	1,883	0	1,065

Table A.3. continued.

Stream	62,947	23,427	24,404	355	1,420	1,065	710
Wooded							
Peaver flood	92,354	358,160	24,360	10,481	28,557	3,906	1,420
Bog	5,541	11,156	0	0	355	0	0
Conif. swamp	4,831	22,692	355	0	355	0	0
Cnf/Dec swamp	3,906	22,586	1,775	0	0	355	0
Decid. swamp	24,296	43,536	11,330	0	9,910	5,294	710
Shrub swamp	20,197	31,354	5,681	0	0	1,775	355
Totals	453,292	1,252,910	160,590	14,139	49,581	22,779	13,459

Table A.4. Habitat availability and use[a] by waterfowl breeding in southern Ontario, 1981-1987.

Type	% avail.	% use[b]			
		Mallard	Black duck	Wood duck	Blue-winged teal
Seasonal					
Seasonal basin	0.8	2.7+	0.0	0.6	0.0
Wet meadow	0.6	0.9	0.0	0.0	2.4
Marsh					
Shallow Marsh	1.4	6.1+	<u>5.6</u>	<u>5.0</u>+	10.7
Deep Marsh	2.0	3.0	0.0	1.9	9.4
Open water					
Ditch	0.6	5.4+	0.0	0.6	4.8
Lake	47.8	7.9-	<u>16.7</u>-	<u>2.5</u>-	<u>4.8</u>-
Pond	2.3	30.2+	<u>5.6</u>	<u>8.1</u>+	<u>12.7</u>+
River	6.5	4.3	<u>2.8</u>	<u>2.5</u>-	<u>5.6</u>

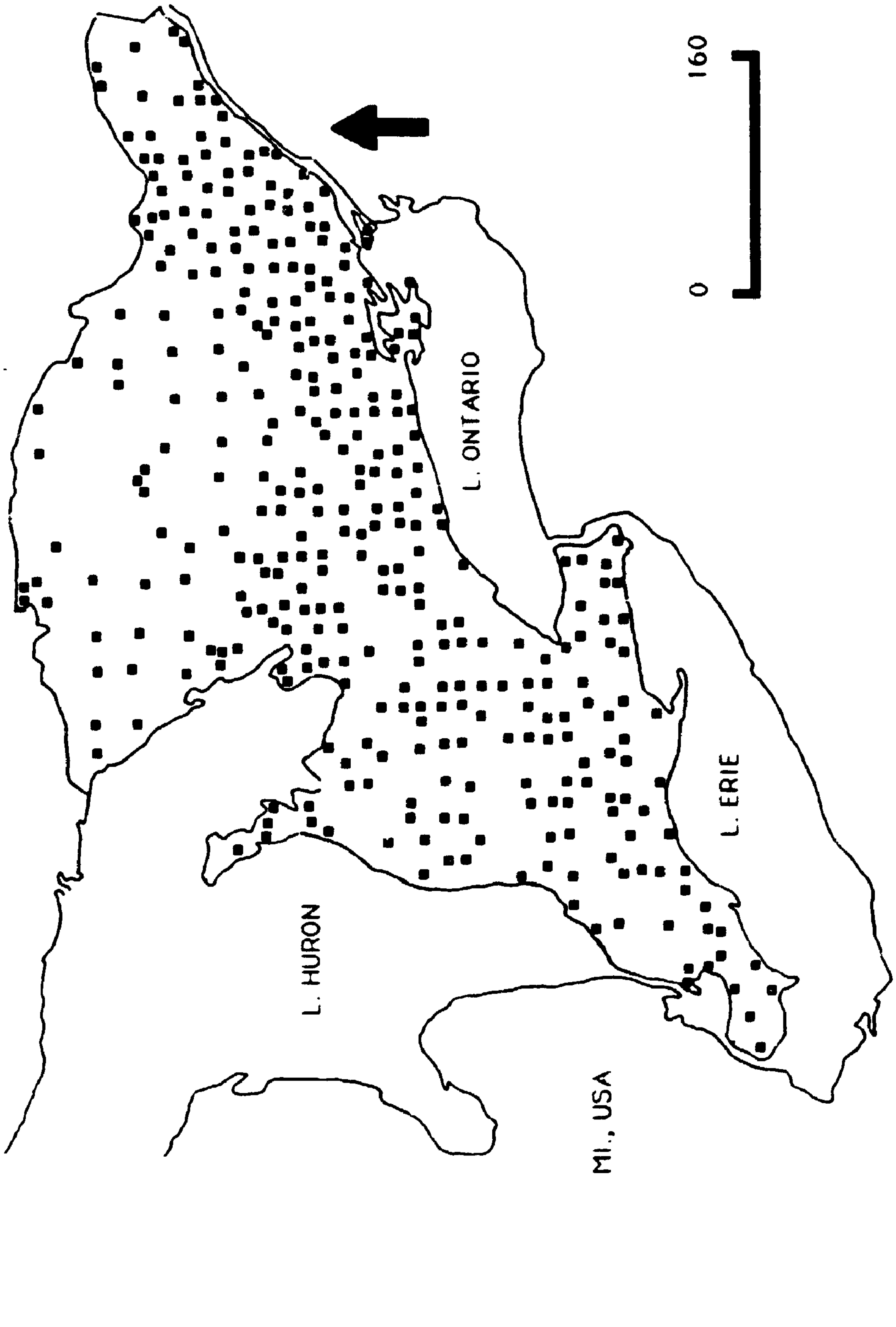
Table A.4. continued.

Stream	1.5	10.2+	2.8	6.9	6.3+
Wooded					
Shrub swamp	3.6	4.2	0.0	2.5	7.9+
Coniferous swamp	1.5	0.2	0.0	0.6	0.0
Cnf/Dcd swamp	2.7	1.3	0.0	0.0	0.8
Deciduous swamp	3.5	5.6	2.8	20.6+	8.7
Bog	0.8	0.0	0.0	0.6	0.0
Beaver flood	24.5	18.0	63.9+	47.5+	26.2+

[a]Percent availability and use were averaged between 266 plots surveyed in 1981 and 349 plots surveyed in 1987.

[b]+ and - indicate habitats used in proportions greater or less than availability, as determined by chi-square tests and subsequent 95% Bonferroni Z confidence intervals (Neu et al. 1975). All habitats were used in chi-square test and construction of confidence intervals for mallards. Underlined values represent habitats used in chi-square test and confidence interval construction for black ducks, wood ducks,

Figure A.1. Approximate location of each 0.8 km x 0.8 km survey plot in southern Ontario


L. ONTARIO
L. ERIE
L. HURON
MI., USA
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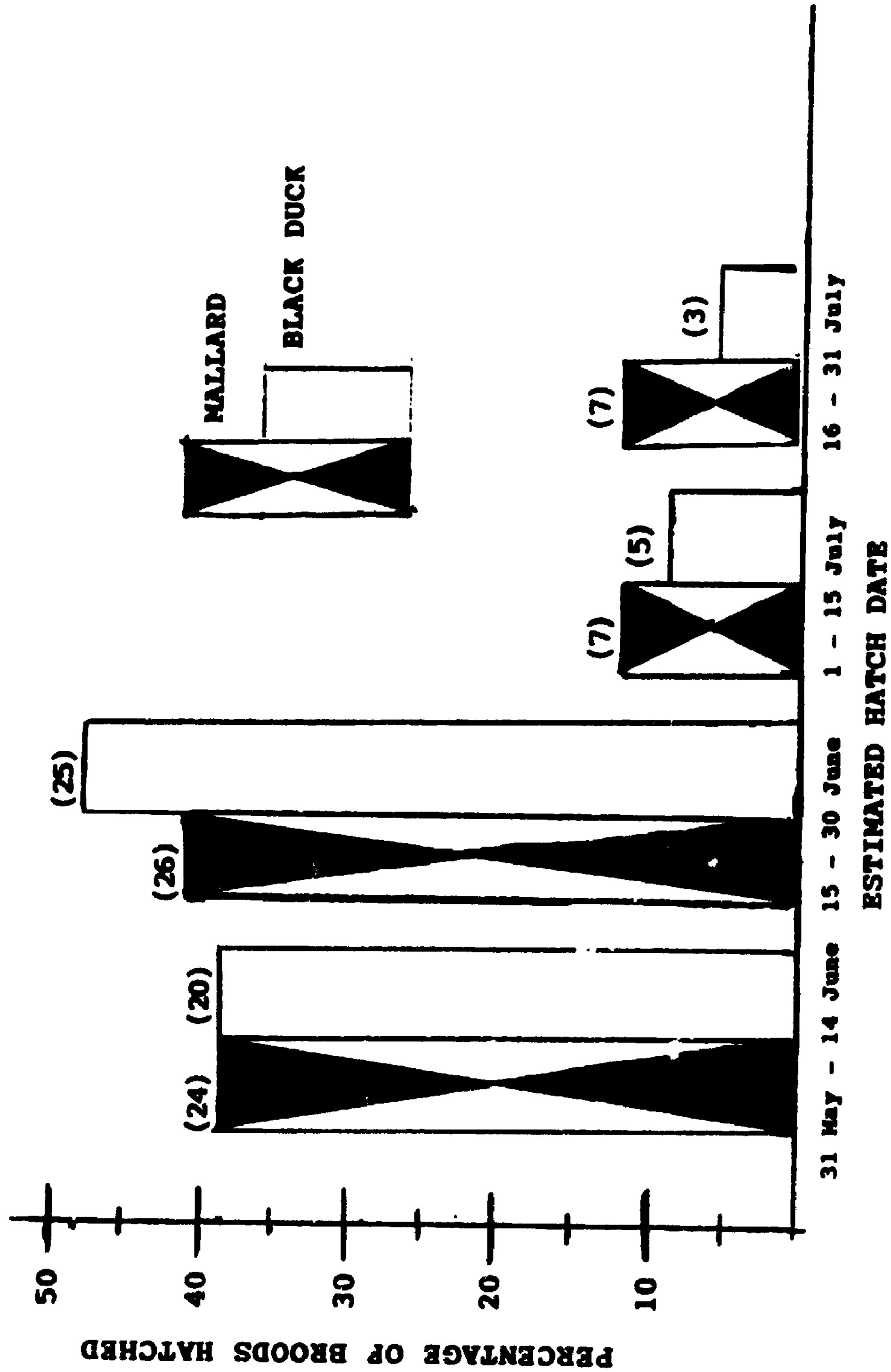
160

APPENDIX 2

Figure A2. Hatch chronology of mallard and black duck broods in north-central Ontario.


MALLARD
BLACK DUCK
PERCENTAGE OF BROODS HATCHED
50
40
30
20
10
(24)
(20)
(26)
(25)
(7)
(5)
(7)
(3)
31 May - 14 June
15 - 30 June
1 - 15 July
16 - 31 July
ESTIMATED HATCH DATE

Appendix 3. Mean brood size and number of broods of mallards and black ducks observed in north-central Ontario during summer, 1990[1] - 1991[2].

	Class Ia-IIa	Class IIb-III	overall
		Mallards	
1st survey	4.8 (11)[3]	3.5 (2)	4.6 (13)
2nd survey	4.2 (25)	4.6 (25)	4.4 (50)
overall	4.4 (36)	4.5 (27)	4.5 (63)
		Black ducks	
1st survey	4.1 (13)	none observed	4.1 (13)
2nd survey	5.0 (7)	3.6 (34)	3.6 (34)
overall	4.4 (20)	3.6 (34)	3.9 (54)

[1]Surveys were conducted in plots 11, 12, 13, 14, 16, 17, 18, and 19 (see Fig 4.1). The first survey was conducted 11 July - 13 July and the second survey was conducted 31 July - 3 August.

[2]Surveys were conducted in plots 3, 4, 5, 6, 8, and 10 (see Fig. 4.1). The first survey was conducted 24 - 25 June and the second survey was conducted 22 - 25 July.

[3]Number of broods observed.

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