

**INFLUENCE OF TUNDRA SWANS ON AQUATIC VEGETATION AND
STAGING WATERFOWL AT LONG POINT, ONTARIO**

by

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ABSTRACT

Over the past several decades, Tundra Swan (*Cygnus columbianus columbianus*) populations have increased considerably in North America causing concern that large numbers of swans may negatively affect aquatic plant and waterfowl communities at key staging areas. Thus, this study was done to determine if: 1) swans have a negative effect on seasonal abundance of aquatic plants, 2) abundance, proximity, and foraging activity of swans affect abundance, distribution, and diurnal activities of other staging waterfowl, 3) swan proximity and foraging activity affect foraging bout activities and feeding methods of American Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*) at Long Point, Lake Erie. Exclosure experiments done in aquatic habitats showed that swans (and geese) did not have a strong additive, negative effect on aquatic plants during fall. Observational evidence suggested that swans did not greatly reduce food availability because they spent less time feeding than did most other waterfowl. Overall, waterfowl densities were not negatively correlated with swan densities in large marsh complexes or in small wetlands. To the contrary, some ducks actually showed positive correlations with increasing swan densities. Pond-level waterfowl distributions showed that ducks did not avoid swans. Further, swans rarely attacked ducks and only did so when foraging, thus some slight avoidance was observed when ducks and swans were feeding together. Abundance, proximity, and foraging activities of swans did not have negative effects on time waterfowl spent feeding. In fact, some species increased their feeding activity in response to swan foraging activities. American Black Ducks and Mallards also increased their foraging intensity and decreased their vigilance when swans were feeding on ponds; each of these species also altered their feeding methods when foraging with active and

inactive swans. Given these results, I conclude that Tundra Swans generally did not greatly reduce abundance of *Vallisineria americana* and *Potamogeton pectinatus* during fall and did not have large negative effects on abundance, distribution, or activities of other staging waterfowl at Long Point, Ontario.

Key words: abundance, activity, aggression, American Black Duck, *Anas platyrhynchos*, *Anas rubripes*, association, aquatic, behaviour, community, competition, *Cygnus columbianus*, distribution, duck, exclosure, facilitation, feed, foraging, geese, heterospecific, interaction, interspecific, Lake Erie, Long Point, macrophytes, Mallard, Ontario, *Potamogeton pectinatus*, sago pondweed, time, Tundra Swan, *Vallisineria americana*, vegetation, vigilance, waterfowl, wild celery.

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CHAPTER 1. GENERAL INTRODUCTION

1.1. INTRODUCTION

Interspecific interactions among animals have long interested ecologists (Gause 1934, Elton 1946, Lack 1947, Hutchinson 1959, MacArthur and Levins 1967, Lack 1971, Cody and Diamond 1975, Connell 1983, Schoener 1983, Keddy 1989). This interest has resulted in much debate surrounding the relative importance of different types of major ecological interactions (e.g., competition, predation, commensalism, and mutualism) and what role these have in determining patterns of species abundance, diversity, distribution, and behaviour commonly observed in nature (Wiens 1977, Diamond 1978, Connor and Simberloff 1979, Strong et al. 1979, Connell 1980, Schoener 1982, Roughgarden 1983, Strong et al. 1984). Such interest and conflict resulted in major changes in how ecologists viewed interactions among animals and between animals and their environments and largely contributed to the development of the discipline of community ecology (Cody and Diamond 1975, Anderson and Kikkawa 1983, Diamond and Case 1986).

Interactions among community members most often have been studied in the context of competition over limited resources. Interspecific competition has received considerable attention because many ecologists believe it is one of the most important determinants of large and small-scale structure in at least some communities (Cody 1974, Diamond 1978, Connell 1975, Connell 1983, Schoener 1983, Roughgarden 1983). Interspecific competition can be defined as the direct or indirect struggle among species for use of resources, such as food and space, that are limited in supply (Keddy 1989).

Competitive interactions often are divided into two main mechanisms, interference and exploitative competition (Keddy 1989). Interference occurs when one species limits another species access to resources through some type of direct interaction, such as interspecific aggression or fighting. Exploitative competition, however, does not require physical contact between species or that competitors even show temporal overlap in their occupancy of critical habitats. Rather, under this type of competition, one species reduces the quantity or quality of resources, usually food, available to other species by consumption or degradation of the limiting resources. Regardless of what mechanism is employed, strong interspecific competition should lead to resource partitioning when food availability is low, whereas species should show niche expansion when resources are more abundant (MacArthur and Levins 1967, Diamond 1978, Schoener 1974, but see Wiens 1977).

Providing strong, definite proof for competition under natural conditions is extremely difficult (Connell 1980, Connell 1983, Schoener 1983, Diamond 1983). Experimental manipulation of putative competitors or their resources provides the best test of interspecific competition, but such manipulations often are extremely difficult or impossible to do in some communities and over relatively large scales of investigation (Keddy 1989). Observation of interspecific niche shifts and changes in species abundances or distributions offer more equivocal and relatively weak evidence to support competition. However, this kind of observational evidence can be collected in a way that uses natural environmental variation to approximate an experimental approach and can encompass larger spatial and temporal scales than do human-induced experiments (Diamond 1983). Documentation of patterns consistent with competition, such as an

increase in abundance when putative competitors are absent versus present, is a less desirable approach to unequivocally demonstrate interspecific competition, but it can be extremely useful in generating hypotheses and determining or refining the direction of future research (Diamond 1983, Keddy 1989).

Despite much research concerning negative interspecific interactions (e.g., competition & predation) in ecology, far less attention has been given to beneficial interactions (e.g. commensalism and mutualism) among species (see Boucher et al. 1982, Keddy 1989). Reports of beneficial associations are not uncommon and, depending on the organisms interacting, can be equally or more important than negative ones in determining size, composition, and diversity of communities (Boucher et al. 1982). Within mixed species assemblages, presence, abundance, and behaviour of some species can influence the behaviour of others, especially when they are foraging (Rasa 1984, Pöysä 1986a, Thompson et al. 1991, van der Wal et al. 2000). Some animals may exhibit heterospecific attraction because feeding activities of other animals enhance their ability to find or acquire food (Stamps 1988, Mönkkönen et al. 1996), whereas others may actively seek protection offered by larger groups or by certain species within those groups (Stamps 1988, Roberts 1996). Positive effects of one species' feeding activities on those of another can either arise as a direct result of their activities or as an indirect effect mediated by more complex ecological interactions (e.g., Thompson et al. 1991, van der Wal et al. 2000).

Studies of waterfowl have provided much information about interspecific interactions and their influence on community structure and foraging interactions (Nudds 1992). There has been some disagreement with respect to how important competition and food

resource partitioning are in determining waterfowl community structure (Nudds 1983, Pöysä 1983b, Nudds 1992, Nudds et al. 1994, Pöysä et al. 1994, 1996, Elmberg et al. 1997, Nudds et al. 2000) and foraging group composition and behaviour (Pöysä 1983a, 1985, 1986a, 1986b). There also has been debate over whether competition is more intense during the wintering (DuBowy 1988, 1991) or breeding seasons (Nudds and Bowlby 1984, Nudds and Wickett 1994). Regardless, interspecific interactions among waterfowl during the migration period have rarely been studied and warrant investigation (Nudds 1992).

Many species of waterfowl congregate and spend much time feeding on staging areas. It is at these staging areas where waterfowl obtain the nutrients that are necessary to build fat and protein reserves that are critical for their survival and/or reproduction (Ankney and MacInnes 1978, Wypkema and Ankney 1979). Thus, it is important to determine how species interact with each other and influence their food resources at major waterfowl staging areas. There is a growing body of evidence showing that larger community members, especially northern geese, can have large, negative effects on other species due to their population size, behaviour, or both on the breeding grounds or northern staging areas (Ankney 1996, Abraham and Jefferies 1997). Large-bodied swans may also have similar influences on aquatic plants and other waterfowl at major staging areas (Petrie et al. 2002).

Tundra Swans (*Cygnus columbianus columbianus*) are a large herbivorous waterfowl species that may adversely affect aquatic plant communities and other waterfowl (Petrie et al. 2002). Similar to populations of northern geese, Tundra Swans have increased substantially in North America since the early 1970's (Kelley et al. 1998). Little

information exists, however, concerning how this large aquatic herbivore may influence aquatic plants and other co-occurring waterfowl (Limpert and Earnst 1994, Froelich 2001), especially at important staging areas (Petrie et al. 2002). Numerous studies have shown that large, herbivorous waterfowl, mainly geese, can dramatically reduce the quantity and quality of important aquatic waterfowl food plants as a direct or indirect result of their feeding activities (e.g., Lodge 1991, Lodge et al. 1998, Froelich 2001). Such reductions in preferred foods can negatively influence large and small-scale abundance, distribution and behaviour of the primary consumers of the vegetation and possibly other species that utilize the same forage species (Cooke et al. 1995, Abraham and Jefferies 1997, Lodge et al. 1998); these types of responses are consistent with exploitative competition. Further, there is some concern that because swans are large, and potentially aggressive birds, they may directly restrict relatively smaller birds access to food via interference (Oksanen et al. 1979, Conover and Kania 1994, Pöysä and Sorjonen 2000, Petrie et al. 2002). Circumstantial evidence, however, suggests that swans may attract waterfowl and provide short-term benefits to them when foraging together in mixed species assemblages through facilitative effects on feeding (Sherwood 1960, Bailey and Batt 1974, Thomas 1982).

1.2. OVERALL HYPOTHESIS AND STUDY OBJECTIVES

I hypothesized that Tundra Swans negatively influence the abundance, distribution, and foraging behaviour of waterfowl co-occurring on small wetlands during the fall and spring staging period. Swans may cause this directly by actively restricting relatively smaller waterfowl from feeding areas by frequent use of aggressive interactions. Alternatively, Tundra Swans, through their feeding activities, may substantially reduce

amount of preferred waterfowl food plants available to other waterfowl.

Before beginning this study in fall, 1998, I set out several objectives to aid in evaluation of my overall hypothesis. These objectives were:

1. Assess small-scale removal effects of large herbivorous waterfowl (mostly swans) and smaller aquatic herbivores (mostly ducks) on above- and below ground biomass of two known important waterfowl foods, sago pondweed (*Potamogeton pectinatus*) and wild celery (*Vallisneria americana*), during fall.
2. Document interspecific interactions among staging waterfowl, but specifically those between Tundra Swans and smaller waterfowl.
3. Quantify abundance and distribution of waterfowl on small-scale observation ponds and in larger scale marsh complexes to determine if numbers of ducks decreased as numbers of Tundra Swans increased.
4. Observe and document diurnal activities and feeding methods of waterfowl in relation to proximity, activity, and abundance of Tundra Swans at different marsh locations.
5. Document foraging activity and feeding methods used by two ecologically equivalent dabbling ducks, American Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*), on ponds in relation to proximity and activity of Tundra Swans.

1.3. STUDY AREA

This general study area description is based on one that is more detailed and extensive (see Petrie 1998). This study was conducted at several different locations in the marshes associated with Long Point, Ontario (80°24'W, 42°38'N) (Figure 1.1). Long Point is a

sand spit that extends 35 km east from Ontario's south shore into Lake Erie. This sandy peninsula has facilitated the formation of about 24,000 ha of extensive, shallow emergent marsh complexes, including Big Creek Marsh, Long Point Company Marsh, and Turkey Point Marsh, and Inner and Outer Long Point Bays.

The shallow, emergent and open water marshes associated with Long Point are used extensively by hundreds of thousands of waterfowl and a large percentage of several North American waterfowl populations each fall and spring (see Petrie 1998, Petrie et al. 2002). Because of its importance as a waterfowl staging area, Long Point and its associated open water areas were designated as a Ramsar site (Convention on Wetlands, Ramsar, Iran, 1971), a World Biosphere Reserve by the United Nations Educational, Scientific, and Cultural Organization, and a Globally Important Bird Area by Bird life International and the North American Commission for Environmental Cooperation. The Canadian Wildlife Service of Environment Canada also has designated 3239 ha of marsh and upland habitat on Long Point proper and 769 ha in the Big Creek Marsh as National Wildlife Areas (Petrie 1998). A large percentage of the emergent marsh is under private ownership by waterfowl hunting clubs. The Long Point Company owns approximately 50% of the wetlands on Long Point proper, whereas the Turkey Point Company and several smaller waterfowl hunting clubs own about 95% of the Turkey Point Marsh; several smaller hunting clubs own a sizeable percentage of the emergent marsh west and adjacent to the Big Creek Marsh (Petrie 1998).

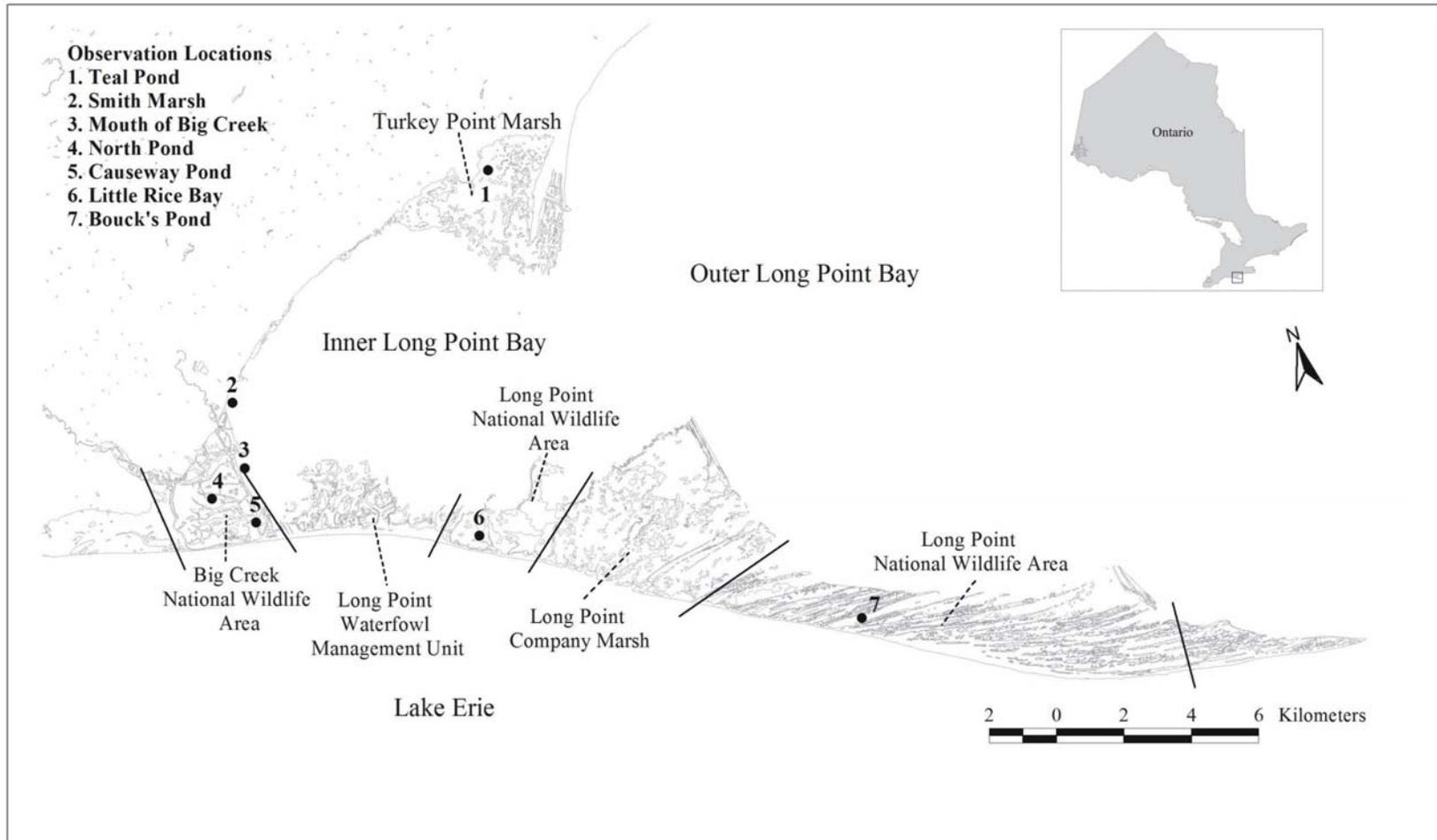


Figure 1.1. Map showing the locations of major wetland complexes and public-, private-, and government-owned areas at Long Point, Ontario. Locations where behavioural observations and vegetation sampling were conducted are shown as numbered points.

Emergent marshes and the relatively shallow (mean depth 2 m) Inner Long Point Bay are dominated by more than 90% coverage of aquatic macrophytes, making them ideal habitats for staging ducks, geese, and Tundra Swans (Knapton and Petrie 1994). Dominant emergent aquatic plants include, Cattail (*Typha angustifolia* & *Typha latifolia*), bulrush (*Scirpus* spp), and wild rice (*Zizania palustris*) and dominant floating-leaved plants include white water lily (*Nymphaea odorata*) and yellow pond lily (*Nuphar variegatum*). Major submerged aquatic macrophytes include, Canada waterweed (*Elodea canadensis*), coontail (*Ceratophyllum demersum*), pond weeds (*Potamogeton* spp), water milfoils (*Myriophyllum* spp), and wild celery (*Vallisneria americana*) (see also Knapton and Petrie 1999).

The wetlands associated with Long Point are one of the most important staging areas in Eastern North America for several species of waterfowl, including Tundra Swans (Petrie 1998, Petrie et al. 2002). The eastern population of Tundra Swans has increased substantially since the early 1970's (Kelly et al. 1998). This population growth has resulted in a substantial increase in Tundra Swan use of Long Point over the same period (Petrie et al. 2002). Coincidentally, duck use of Long Point's major marsh complexes also has changed dramatically over the past 30 years (see Petrie 1998). Increased use of some marsh complexes by swans has been associated with a decline in use of those same areas by ducks (Petrie 1998).

1.4. SCOPE OF THE DISSERTATION

This dissertation is composed of five chapters, the first of which is an introduction describing the broader ecological framework of this study. Chapter 1 also provides my overall hypothesis and study objectives, as well as a general description of the Long Point

study area. Chapters 2 through 4 are manuscript style chapters that follow the “Checklist of Instructions to Authors” provided by the American Ornithologists’ Union and its journal, *The Auk*. In Chapter 2, I investigate the influence that large aquatic herbivores (and relatively smaller consumers) have on submerged aquatic macrophytes. In Chapter 3, I report on the occurrence of interspecific aggression between swans and ducks. I also investigate the influence that Tundra Swan abundance, proximity, and activity has on large and small-scale waterfowl distributions, as well as on general diurnal feeding activities of waterfowl on ponds in Chapter 3. In Chapter 4, I evaluate the influence that Tundra Swan feeding activities (and their proximity to ducks) have on foraging activities (e.g., feeding intensity, vigilance, and mobility) and feeding methods (e.g., surface, subsurface, upend, and paddle) of two ecologically equivalent dabbling ducks, American Black Ducks and Mallards. Finally, in Chapter 5, I discuss the major conclusions of this research in a broader ecological context and propose direction and refinements for future research.

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CHAPTER 2. INFLUENCE OF TUNDRA SWANS AND OTHER LARGE HERBIVORES ON AQUATIC VEGETATION AT LONG POINT, ONTARIO

2.1. ABSTRACT

This study was done to determine if Tundra Swans (*Cygnus columbianus columbianus*) and Canada Geese (*Branta canadensis*) had a large negative influence on important aquatic plants, mainly musk grass/stoneworts (*Chara spp*), and wild celery (*Vallisneria americana*) and sago pondweed (*Potamogeton pectinatus*), during fall migration at Long Point, Lake Erie. Enclosure experiments done in fall 1998 and 1999 showed that, as compared to ducks, other relatively small vertebrate herbivores, and abiotic and natural factors, large herbivorous waterfowl did not exert a consistent or strong negative effect on these plants. In fall 1998, there was no evidence for a negative effect of small or large waterfowl herbivory on vegetation. Observations at enclosure locations suggested both ducks and muskrats (*Ondatra zibethicus*) removed aquatic vegetation and that removal effects of these animals may have a sizeable effect on aquatic plants in ponds located in shallow wetlands. During fall 1999, there was a general herbivory effect on aquatic vegetation and only weak evidence of a negative effect on over-wintering structures of wild celery and sago pondweed that was due solely to large waterfowl. Differences in large- and small-scale habitat use, feeding activity, and food preferences between large waterfowl and ducks were the most probable reasons for lack of strong negative effects of Tundra Swans and Canada Geese on aquatic plants during the two fall study seasons.

2.2. INTRODUCTION

Submerged and emergent aquatic macrophytes are important foods for many migratory waterfowl and several other species of aquatic herbivores (Thayer et al. 1984, Lodge et al. 1998, Knapton and Petrie 1999). The relationship between waterfowl and their aquatic food resources is dynamic, resulting from seasonal changes in their feeding behaviour that ultimately is a response to herbivory and other biotic and abiotic factors that affect abundance and distribution of aquatic macrophytes (Crawley 1983, Lodge 1991). Waterfowl select feeding habitats and congregate in areas with abundant macrophytes, especially those that contain preferred forage species (Dirksen et al. 1991, Wicker and Endres 1995, Mitchell and Wass 1996, Nolet et al. 2001). Waterfowl can cause large seasonal reductions in above- and below-ground biomass of their preferred forage species (Anderson and Low 1976, Giroux and Bédard 1987, Idestam-Almquist 1998, Beekman et al. 1991, Evers et al. 1998) and may even change species composition of plant communities over longer periods of time (Jefferies et al. 1994, Kotanen and Jefferies 1997). Abiotic factors, such as wave action, ice scour, or natural senescence, also contribute substantially to seasonal reductions in biomass in some aquatic macrophyte communities (Crowder and Painter 1990, Beekman et al. 1991, Idestam-Almquist 2000).

Recently, there has been concern about increasing populations of relatively large herbivorous waterfowl and the influence these birds have on food resources in critical aquatic and terrestrial habitats (Conover and Kania 1994, Ankney 1996, Petrie et al. 2002). There is a growing body of evidence showing that large numbers of geese can have pronounced and detrimental effects on the structure, quality, and quantity of

terrestrial and aquatic habitat at breeding, staging, and wintering areas (Cargill and Jefferies 1984, Bazely and Jefferies 1986, Giroux and Bédard 1987, Jefferies et al. 1994, Kotanen and Jefferies 1997). These effects not only have population level ramifications for those species that are the main consumer of foods (Cooke et al. 1995, Abraham and Jefferies 1997, Leafloor et al. 2002), but potentially also for other co-occurring or resident species that use these habitats (Abraham and Jefferies 1997). It also has been suggested that increasing populations of introduced exotic, Mute Swans in eastern North America may have a negative impact on submerged aquatic macrophytes (Reese 1975, Petrie 1998, but see Conover and Kania 1994). Furthermore, several studies of Tundra and Bewick's Swans (*Cygnus columbianus bewickii*) have shown that this species can substantially reduce wild celery (*Vallisneria americana*) or sago pondweed (*Potamogeton pectinatus*) tuber densities, preferred foods of these birds and many other waterfowl, at major staging areas in Europe and wintering areas in North America (Beekman et al. 1991, Nolet and Drent 1998, Froelich 2001, Nolet et al. 2001).

Tundra Swan populations in North America have increased since the early 1970's (Kelley et al. 1998). These large, herbivorous birds are gregarious and thousands often congregate at traditional staging and wintering areas, where they co-occur with large concentrations of many other species of waterfowl (Limpert and Earnst 1994, Petrie et al. 2002). At fall staging areas, Tundra Swans spend much time feeding in aquatic habitats where they prefer to excavate and eat subterranean over-wintering structures of several different aquatic plants (Earnst 1994, Badzinski, unpublished data), but, when available, also may consume vegetative material (Beekman et al. 1991, Earnst 1994, Limpert and Earnst 1994, Nolet et al. 2001). Some species of aquatic plants that Tundra Swans

consume (e.g., wild celery, sago pondweed, & musk grass/stoneworts, *Chara spp*) also are preferred foods of many other species of staging waterfowl (Korschgen and Green 1988, Kantrud 1990, Knapton and Petrie 1999).

The wetland complex associated with Long Point, Lake Erie is a globally important Tundra Swan and waterfowl staging area (Petrie 1998). Coincident with their continental wide increase, Tundra Swan use has substantially increased at Long Point over the past 30 years (Petrie et al. 2002). In light of their relatively recent population increase and the general lack of information concerning Tundra Swan staging ecology, there is concern that these large, herbivorous birds may substantially reduce preferred aquatic plant food availability for other staging waterfowl (Petrie 1998, Petrie et al. 2002). Staging areas, such as Long Point, are extremely important habitats for north-temperate and arctic breeding waterfowl because birds acquire body fat on these wetlands that provides energy for migration and nutrient reserves for breeding (Ankney and MacInnes 1978, Wypkema and Ankney 1979). Thus, it is important to identify and quantify factors that may reduce the quality or quantity of food available to waterfowl at these major staging areas.

In this study, a field exclosure experiment was designed to determine if large, herbivorous birds added substantially to removal of above- and below-ground biomass of aquatic vegetation caused by natural and abiotic factors and other relatively smaller aquatic herbivores (mainly ducks) during the fall staging season at Long Point, Ontario. Most importantly, I wanted to determine if activities of Tundra Swans, and to a lesser extent Canada Geese, exerted a strong additive, negative effect on total below-ground biomass and tuber mass and density of two important waterfowl foods (i.e., wild celery

and sago pondweed) at locations that traditionally receive heavy fall-use by Tundra Swans and other waterfowl.

2.3. METHODS

2.3.1. Study area

This study was conducted during fall 1998 and 1999 at Long Point, Ontario (80°24'W, 42°38'N) (see Figure 1.1). Long Point is a sand-spit extending 35 km east from the southern shore of Ontario into Lake Erie. This sandy peninsula facilitated the formation of the Inner and Outer Long Point Bays and their associated freshwater marsh complexes, which are globally important waterfowl staging areas (see Petrie 1998). Extensive wetland complexes where this study was conducted were classified as lacustrine, emergent and/or aquatic bed marshes (Cowardin et al. 1979).

During 1998, 3 study locations were used: Bouck's Pond, North Pond, and Teal Pond, whereas in 1999, 4 locations were used: Bouck's Pond, North Pond, Smith Marsh, and the Mouth of Big Creek (see Figure 1.1). North Pond and Bouck's Pond received no human disturbance because they were located within the Big Creek and Long Point National Wildlife Areas, respectively. Teal Pond was located in the Turkey Point marsh and was owned by a private hunting club, the Turkey Point Company; this location was relatively undisturbed and infrequently hunted because of its inaccessible location. The study site located near the mouth of Big Creek was accessible to the public for hunting and boating and was used relatively little by waterfowl during the day, but was used by waterfowl at night. The adjacent Smith Marsh site, however, received more use by Tundra Swans and other waterfowl during the day because it was disturbed much less

than the mouth of Big Creek. Further, hundreds (sometimes thousands) of swans and ducks were present and feeding during the night throughout most of the fall, but most of them would depart at or before sunrise each day (S. Badzinski, unpublished data).

Emergent plant species commonly found at nearly all these study locations included cattail (*Typha spp*), common reed grass (*Phragmites australis*), hard-stem bulrush (*Scirpus acutus*), Pickeralweed (*Pontedaria cordata*), wild rice (*Zizania palustris*), and arrowhead (*Sagittaria latifolia* & *S. rigida*), whereas yellow water lily (*Nuphar variegatum*) and white water lily (*Nymphaea odorata*) were common floating-leaved macrophytes. Common submerged aquatic macrophytes included, common bladderworts (*Utricularia spp*), Canada waterweed (*Elodea canadensis*), coontail (*Ceratophyllum demersum*), floating-leaved pondweed (*Potamogeton natans*), sago pondweed (*Potamogeton pectinatus*), slender pondweed (*Potamogeton pusillus*), stoneworts (*Chara spp* & *Nitella spp*), Richardson's pondweed (*Potamogeton richardsonii*), water-milfoils (*Myriophyllum spp*), water niads (*Najas spp*), and wild celery (*Vallisneria americana*).

2.3.2. Exclosure design

Three types of exclosures were designed for use in this study. Reference plots (hereafter open exclosures) were simply 6 m × 6 m square plots that were demarcated by 4 corner posts standing 1.25 m above the bottom (Figure 2.1). Open exclosures allowed all aquatic herbivores free access to aquatic vegetation. Vegetation samples collected from these plots ultimately were compared to those collected from swan and bird exclosures (see below).

Swan exclosures were designed such that only Tundra Swans, Mute Swans, and Canada Geese were excluded from aquatic vegetation (Figure 2.1). These exclosures

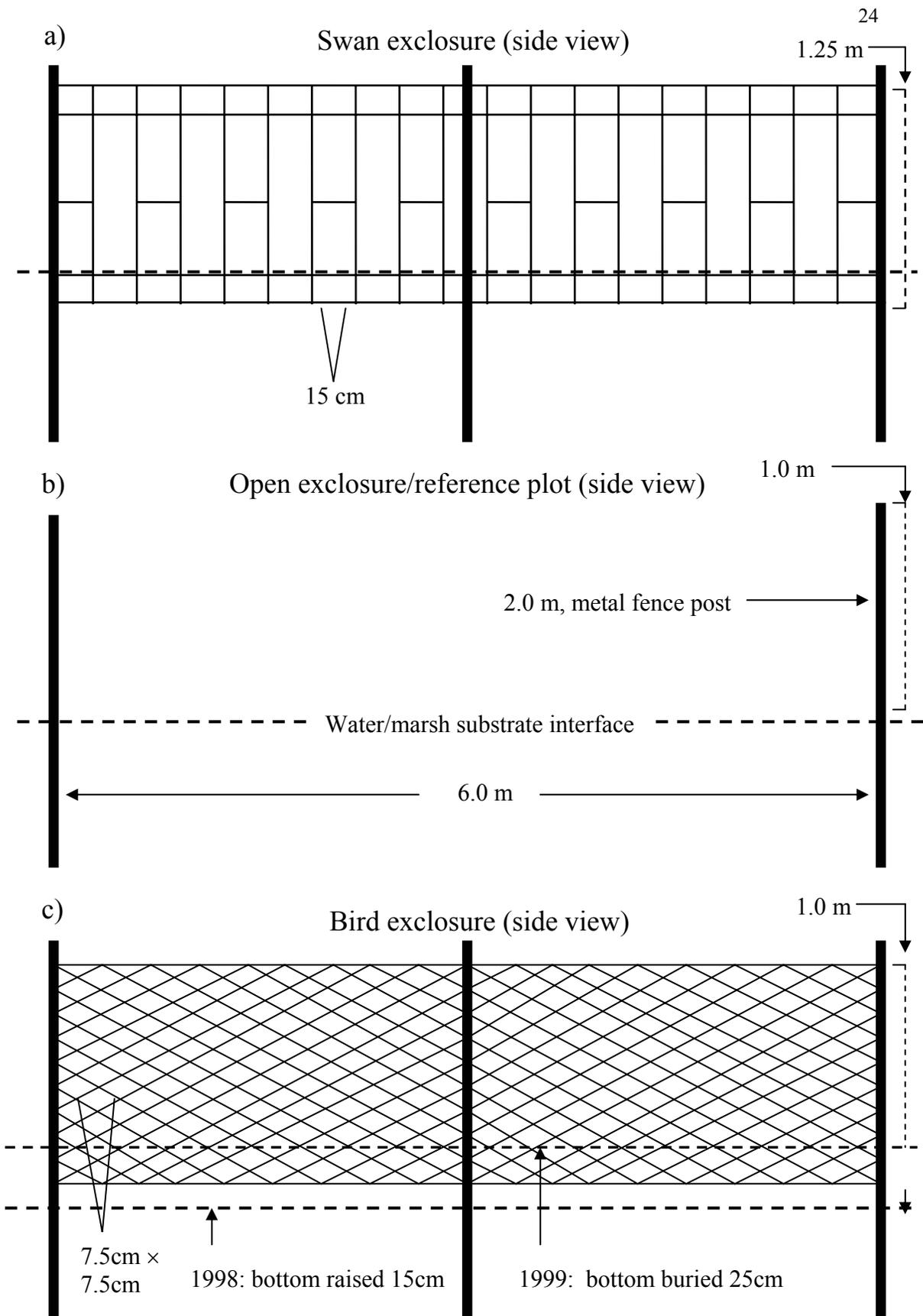


Figure 2.1. Design and dimensions of swan (a), open (b), and bird (c) enclosures used in the vegetation experiment during fall 1998 and 1999 at Long Point, Ontario.

were square structures (6 m × 6 m × 1.25 m) made by wiring concrete reinforcing mesh (mesh dimensions: 15.3 cm × 15.3 cm) to 8 fence posts. To create openings in the mesh that would allow ducks and other smaller consumers access to the vegetation inside, all horizontal wires, except for the 2 top and 2 bottom wires and every other middle wire, from each vertical column in a sheet of reinforcing mesh were removed prior to them being placed in the marsh. Once situated, the bottom 2 wires of the mesh were buried so that the entire structure was approximately 1.25 m above the bottom of the marsh. The tops of these exclosures were left open so ducks could land inside of them, but the open area of the exclosures were small enough to ensure that swans and geese would not land inside them.

Bird exclosures were constructed by wiring brown Vexar® fencing (mesh dimensions: 7.5 cm × 7.5 cm) to 8 fence posts that were situated in a 6m × 6m square (see Figure 2.1). Fine plastic mesh (mesh dimensions: 3 cm x 3 cm) was stretched across the top of the exclosure to ensure that no birds could land inside. In 1998, the bottoms of these exclosures were left 0.25 m above the water/marsh substrate interface because ponds where exclosures were placed were thought to be used only by dabbling ducks; these exclosures then should have excluded all ducks, but still allowed other herbivores such as fish, turtles, and muskrats (*Ondatra zibethicus*) access to inside exclosures. During fall 1998 at one location, however, Ring-necked Ducks (*Aythya collaris*) were observed entering these exclosures by diving beneath the fencing (see results). As a result, in 1999 the bottoms of all bird exclosures were buried 0.25m into the marsh substrate. By doing this, all aquatic herbivores theoretically should have been restricted

from accessing vegetation inside exclosures; any decrease in aquatic vegetation observed in these exclosures during fall should have been due to factors other than herbivory.

2.3.3. Exclosure placement

Early in the fall of 1998 (18 – 25 September) and 1999 (10 –19 September), three swan and bird exclosures and as many open exclosures/reference plots were grouped and placed at geographically separate study locations (see Figure 1.1). To do this, all three grouped candidate exclosure sets (i.e., 1 replicate = 1 bird, 1 swan, & 1 open exclosure) were first scouted and then marked with four fence posts (6 m × 6 m square) at each location (Figure 2.2). Candidate exclosures within a set were chosen such that all had visually similar plant species composition and biomass of dominant plants; exclosures also were situated in similar depths of water and approximately the same distance from shore or dense emergent vegetation.

All candidate exclosures were erected in water that ranged from 0.3 m to 0.9 m deep at the time of placement (see Appendix 1). Water levels in Long Point marshes can fluctuate daily by as much as 2.5 m due to precipitation, wind set-up, and seiche phenomena (Bradstreet 1977). Water levels in Lake Erie also vary annually by about 0.5 m and typically decline from spring to winter (Anonymous 1976). Thus, the range of depths chosen for exclosure placement reduced the probability that exclosures would become dry and unattractive to waterfowl throughout the fall exposure period.

All exclosure sets at a location were situated in relatively dense, contiguous patches of aquatic vegetation, especially those dominated by wild celery and sago pondweed. I chose to focus on these two species of plants because they produce subterranean overwintering carbohydrate storage structures that are consumed by both Tundra Swans and

many other waterfowl species during migration and winter (Petrie 1998, Korschgen and Green 1988, Kantrud 1990). Whenever possible, all exclosures within a set were placed in the same contiguous patch of aquatic vegetation. When the available vegetation patches were too small to allow this, each exclosure was placed in a separate, but visually similar, patch of vegetation. Exclosure sets were ≥ 24 m from every other one at a location. After each set of exclosures was finally situated, treatments were assigned at random to each exclosure. The only restriction was that an open exclosure never was placed between a swan and a bird exclosure. This, combined with the exclosure spacing restriction mentioned above, was done to reduce the probability that birds would avoid using open exclosures. The actual exclosure materials were then wired to the fence posts approximately 1 week before obtaining the early season vegetation sample.

2.3.4. Aquatic vegetation sampling

The fall staging period was divided each year into an early and late sampling period. In 1998, the early sampling period was 27 September to 8 October and the late sampling period was 5 to 13 December. During fall 1999, the early sampling period was 20 September to 7 October and the late period was 3 to 10 December. The placement of exclosures and the early sample period were timed as such because large numbers of waterfowl usually begin arriving at Long Point during the second week of October each year; this enabled me to collect a sample from exclosures before vegetation was exposed to potentially destructive activities of large numbers of waterfowl. The late sample period was late enough in the fall to allow large numbers of Tundra Swans, Canada Geese, and ducks to use ponds where exclosures were located for several weeks, but was

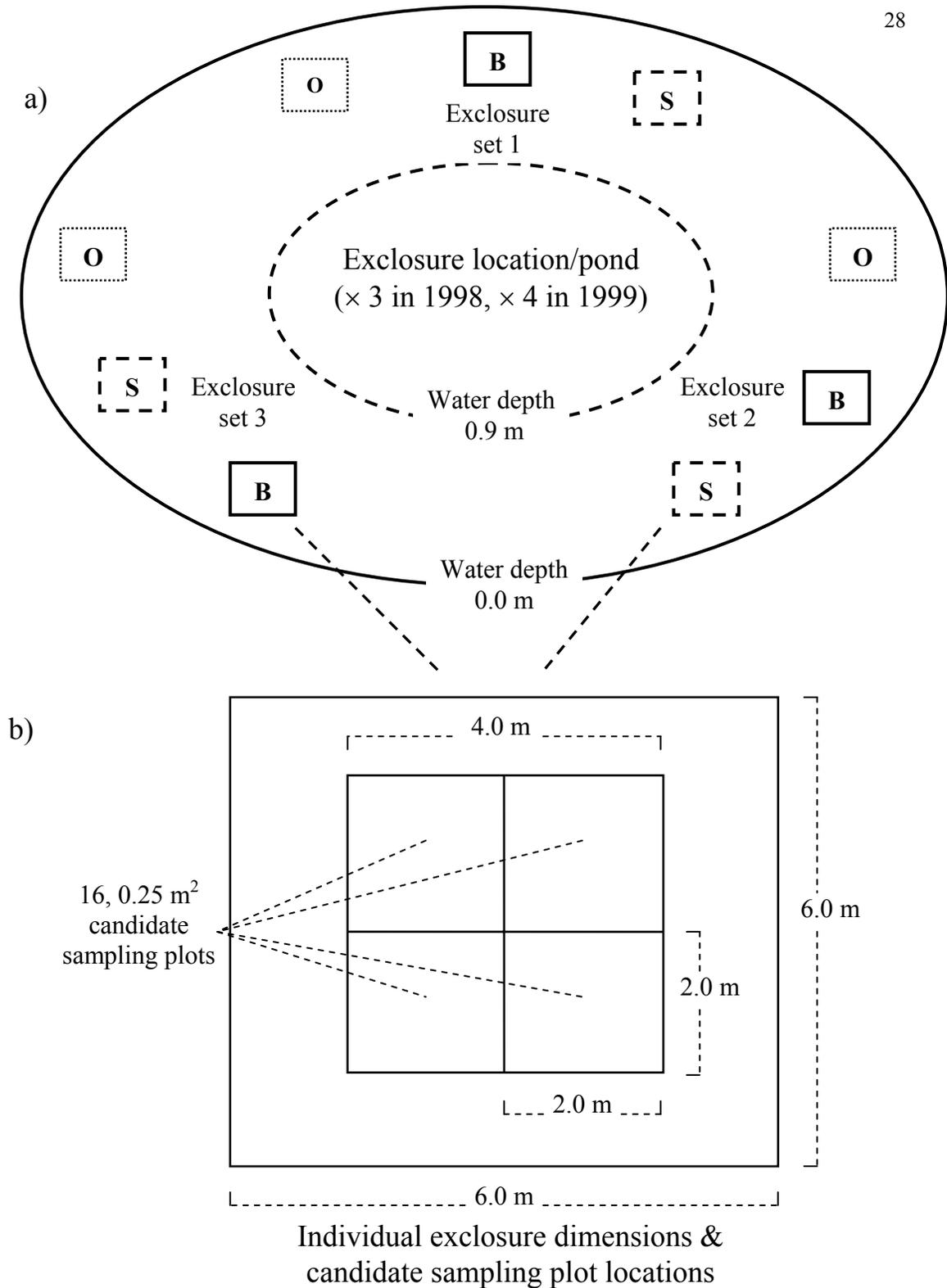


Figure 2.2. An example of the: a) experimental design for the within season vegetation study at one geographic location at Long Point, Ontario, and b) dimensions of bird (B), swan (S), and open (O) exclosures, including the dimensions of the sampling area and number of candidate sampling plots within exclosures.

early enough to reduce the probability that ponds would freeze. Mainly, however, sampling during these two periods allowed for determination of the seasonal impact that herbivores have on above- and below-ground biomass of aquatic plants at each site.

To ensure that the vegetation samples were representative of the treatment, samples were taken ≥ 1.0 m from the edge of exclosures. Doing this effectively left a $4.0 \text{ m} \times 4.0$ m area available to sample vegetation (see Figure 2.2). This sampling area was further sub-divided into $2.0 \text{ m} \times 2.0$ m quadrants. Each of these quadrants was then divided into 16 (0.25 m^2) possible sampling locations, which subsequently were sequentially numbered from 1 to 64. Sampling locations within each exclosure were chosen at random by drawing numbers, without replacement, between 1 and 64 until two sampling locations were assigned in each quadrant for each sampling period. A grid system using three ropes marked at 0.5 m increments was used to locate each designated sample location in the field. To do this, two ropes were stretched across the top (north) and bottom (south) of an exclosure, while the third rope was stretched perpendicular to the other two; this enabled me to find the coordinates for the proper sampling locations during each sampling period.

A small flat-bottomed boat was used to float equipment and the person collecting samples into an exclosure. This ensured that vegetation would not be inadvertently destroyed by human disturbance, especially during the early sampling period. A metal sampling box ($0.5 \text{ m} \times 0.5 \text{ m} \times 0.75 \text{ m}$) was pushed into the marsh substrate at each predetermined sampling location in an exclosure. Water depth (± 1 cm) was recorded in the upper right corner of the box before sampling aquatic vegetation. Above-ground vegetation samples were obtained by clipping all plant stems within the sampling box at

the substrate level. Above-ground samples were sorted by species and placed into separate plastic bags along with a tag with identifying information such as, date, sampling period, site, enclosure number, enclosure type, sampling coordinates, water depth, and plant species.

Below-ground samples were obtained by taking nine horizontal scoops of the marsh substrate with a perforated coffee can (total sample volume: 0.03 m³) at each of the eight sampling locations in an enclosure. Sampling in this way effectively created a crater within the sampling box that approximated the size and depth of the feeding craters created by Tundra Swans (S. Badzinski, personal observation). To separate the roots, rhizomes, and turions/tubers of aquatic plants from the marsh substrate, below-ground samples were passed through a fine mesh (2 mm × 2 mm) sieve. Below-ground plant parts (roots, turions/tubers, and rhizomes) were sorted by species and placed into separate plastic bags that were labeled the same way as the above-ground samples. At the end of the sampling day, all above and below-ground samples were kept cool (approx. 5°C) until they could be processed later in the laboratory. Some of the large, heterogeneous samples also were sorted later in the laboratory.

2.3.5. Laboratory procedures

All species-specific above-ground vegetation samples were thawed, blotted dry with paper towels, and then weighed on a digital balance (± 0.01 g) to obtain the wet mass. Approximately 30 sub-samples of each species above-ground parts from the 1998 vegetation sample were selected and then separately oven-dried at 80°C to constant mass (± 0.01 g) in a drying oven. These sub-samples encompassed a wide range of wet masses observed in the vegetation samples for each species. Determining the dry mass for this

sub-sample of plants was done so dry mass of the above-ground parts for each species in all samples could be estimated from their wet masses via ordinary least-squares regression (see Appendix 2). All species-specific below-ground plant parts (tubers, rhizomes, and roots) were processed separately and oven-dried the same way as were the above ground samples. Prior to drying, the number of tubers of each species were counted and recorded so their densities could be calculated later.

2.3.6. Waterfowl use of enclosure locations

Several aerial surveys, conducted by the Long Point Waterfowl and Wetlands Research Fund each fall (1998: $N = 10$ from 24 September - 10 December; 1999: $N = 5$, 25 September - 28 November), were used to estimate the number of Tundra Swans, Mute Swans, Canada Geese, dabbling ducks (*Anas spp*), and diving ducks (*Aythya spp*) on ponds or in other survey areas where enclosures were located. These surveys were done between 10:00 and 14:00 hours EST by flying a series of predetermined transects over major wetland complexes. Normally, two observers (S. Petrie & R. Ridout) would estimate waterfowl numbers on each transect without reference to individual ponds (see Petrie 1998, Badzinski, Chapter 3). However, during fall 1998 and 1999, the normal sampling design of these surveys was modified such that the same two observers would also estimate all waterfowl present on individual ponds where enclosures were located (i.e., North Pond, Bouck's Pond, and Teal Pond). This allowed for calculation of a seasonal index of waterfowl use at each enclosure location. Because Inner Long Point Bay is an extensive, open water area that could not be reduced into discrete "ponds" within an existing aerial survey transect, estimates of waterfowl numbers counted on an entire single transect flown over the Smith Marsh and mouth of Big Creek were used to

calculate and approximate waterfowl-use for these two adjacent “areas” (Dennis et al. 1984). Survey data were included in waterfowl-use calculations only if they were collected after initial exclosure placement and before late season sampling was done at each location. Numbers of waterfowl were converted to use-days by multiplying the average number of birds (by species or group) counted between successive surveys by the number of days between those surveys; percentages of total use days also were reported for each species or waterfowl group present at exclosure locations.

2.4. STATISTICAL ANALYSES

2.4.1. Data restrictions, calculations, and transformations

Before performing any data analysis, the individual vegetation samples (above-ground = 0.25 m² quadrats & below-ground = 0.03 m³ scoop samples) in each exclosure were combined and averaged to provide one sample for above-ground, below-ground, and species-specific biomass estimates for each exclosure in a sampling period. Biomass estimates for above-ground samples were reported as g/m², while those for below-ground biomass were reported as g/m³; tuber density estimates were reported as number (#) of tubers/m³.

Several different response variables were used in the statistical analyses that follow. Above-ground biomass was the total dry mass of the plant parts for all species that were above the marsh substrate in an exclosure, whereas below-ground biomass was the total dry mass of all subterranean plant parts (i.e., roots, turions/tubers, rhizomes, etc.) of all species in an exclosure. The above-ground and below-ground biomass of wild celery and sago pondweed (combined) were analyzed separately; combined tuber dry mass and tuber

density of these species also were included in analyses. All response variables mentioned above were used to determine if plant biomass differed among treatments in the early and late sampling periods, but another set of response variables was used to determine if the treatments showed different relative changes in biomass estimates from the early to late sampling periods. This proportional change was calculated by using the formula: $\exp(\log + \min [a] - \log + \min [b]) - 1$, where $\exp =$ is the natural logarithm raised to a specified power and $\log + \min =$ the logarithm plus the minimum observed value for the variable of interest in the late [a] and early [b] sample periods.

2.4.2. Model selection and parameter estimation

An information-theoretic approach was used to select the most parsimonious model from an a priori candidate set of models that best described the information contained within these data (Burnham and Anderson 1998, Anderson et al. 2000). This approach to data analysis emphasizes the strength of evidence for a given model or effect and reduces bias in estimation of effect sizes and their precision, especially when it is combined with model averaging techniques (Burnham and Anderson 1998). Akaike's Information Criterion with correction for small sample size (AIC_c) was used to select the best model from a priori candidate set of biologically meaningful models. Competing candidate models were ranked from lowest to highest AIC_c . Akaike differences (ΔAIC_c) were then calculated by subtracting the lowest AIC_c from every other one in the candidate set; ΔAIC_c of zero indicates the "best" candidate model. Models with $\Delta AIC_c \leq 2.0$ were considered to have the most support for being the best model, while those with values much > 2.0 had progressively less support. Akaike weights ($^w AIC_c$) were calculated from ΔAIC_c and were normalized to sum to 1.0. These values were considered the

weight of evidence in favor of a given model being the actual best model in the candidate set. Whenever possible, model selection uncertainty was incorporated into estimation of treatment effect and its measure of precision (\pm SE) by reporting unconditional estimates calculated from $^W\text{AIC}_c$ in a model-averaging technique (see Burnham and Anderson 1988).

Statistical analyses were done separately on 1998 and 1999 vegetation data. Statistical models were designed using PROC MIXED (SAS Institute 1990) and model selection information was obtained using the IC (METHOD = ML [maximum likelihood]) option in this procedure. Model selection was done separately for variation in (1) initial plant biomass and tuber density (early season sample), (2) post-grazing plant biomass and tuber density (late season sample), and (3) proportional seasonal change in plant biomass or tuber density. Analysis of initial plant biomass and tuber density was done to determine if these estimates varied between treatments, especially within each location. This analysis also was used to show differences in initial biomass or tuber density estimates at each location and to further aid in interpreting differences observed in the amount of vegetation remaining in exclosures later that fall (see 2 above). Late season biomass estimates from exclosures (corrected for biomass originally present in exclosures) was a measure of how much vegetation remained after exposure to activities of herbivores or other natural and abiotic factors during fall. The seasonal proportional change in aquatic vegetation was analyzed because it was a relative measure of plant removal intensity among exclosure types, i.e., herbivore groups.

The primary reason for conducting this study was to test the hypothesis that large herbivorous waterfowl have a negative influence on above- and below-ground vegetation

in addition to destructive forces resulting from other consumers and abiotic or natural factors. Because vegetation in swan and bird exclosures was not exposed to the additional grazing or destructive activities of large herbivorous waterfowl, I predicted that open exclosures would have substantially lower late season biomass and tuber densities and substantially larger proportional decreases in these variables during fall as compared to estimates obtained from both swan and bird exclosures. During 1998, I also wanted to determine if duck removal effects were more pronounced than those of other relatively small aquatic herbivores. Thus, I predicted that, as compared to bird exclosures, swan exclosures should have lower plant biomass and tuber densities and higher proportional decreases in biomass or tuber densities. In 1999, this pattern in exclosure differences could only be interpreted as an effect of “small” herbivores because there was no way to determine the relative importance of ducks and other relatively small aquatic herbivores. An overall herbivory effect in fall 1999 could be ascertained from among exclosure differences in both late season biomass/tuber density (bird > swan = open) and proportional change (bird < swan = open) data.

Two different sets of three candidate models were specified to evaluate the strength of evidence for these predictions and to determine among treatment variation in each of the three response variables listed above, both within and over all sampling locations. To assess variation in initial biomass/tuber density and in proportional seasonal decline in biomass/tuber density of aquatic vegetation, three candidate models were developed that included effects and interactions of location (1998: North Pond, Bouck’s Pond, & Teal Pond; 1999: North Pond, Bouck’s Pond, Mouth of Big Creek, & Smith Marsh), exclosure set (1, 2, & 3) nested within location, and treatment (bird, swan, & open exclosure). The

largest specified model contained the nested term and all main effects, as well as an interaction among locations and enclosure types. The second model contained the nested term and all main effects. The smallest model lacked the interaction term and treatment effect, but it included the nested term and the remaining main effects. This model served as the candidate set null model because it lacked the effect of interest (i.e., treatment effect), but contained all other specified factors that could influence the response variables. Including this model in the candidate set allowed for determination of the strength of evidence for a real treatment effect in these data.

Three additional candidate models were specified to assess variation in late sample period biomass. These models were identical to those listed above, except that biomass of aquatic plants (total above-ground, total below-ground, or species-specific estimates) obtained from each enclosure early in the season was added as an additional effect in each of the three models. This was done to control for any initial differences in biomass of vegetation among enclosures.

To aid in assessing the strength of evidence for each candidate model, all relevant model selection information (R^2 , K [number of parameters], N , ΔAIC_c , & $^w AIC_c$) were reported in tables. Model averaged least-squares means (\pm SE) for the treatment effect were reported in all tables, even if the best model was the candidate set null model.

2.5. RESULTS

2.5.1. Waterfowl and other herbivore use of enclosure locations

All study locations received much use by waterfowl during 1998 (range: 45764 - 1009313 waterfowl use-days) and 1999 (range: 57393 - 924623) (Table 2.1). During fall

Table 2.1. Use of exclosure locations by waterfowl during fall 1998 and 1999 at Long Point, Ontario. Species/group-specific and total number of use-days (average number of birds counted between two successive aerial surveys at a location multiplied by the number of days between surveys) and the percentage of use-days are shown for each exclosure location.

Year	Location	Waterfowl use-days (%)					Total
		Tundra Swan	Swan ^a	Goose	<i>Anas</i> spp	<i>Aythya</i> spp	
1998	North Pond ^b	2625	2688	899	42177	0	45764
		(6)	(6)	(2)	(92)	(0)	
	Bouck's Pond ^c	43523	44135	435	735305	229438	1009313
		(4)	(4)	(< 1)	(73)	(23)	
	Teal Pond ^d	2500	2640	2156	63970	0	68766
		(4)	(4)	(3)	(93)	(0)	
1999	North Pond ^b	28000	28058	10390	87985	0	126433
		(22)	(22)	(8)	(70)	(0)	
	Bouck's Pond ^c	35315	36913	9549	557912	320250	924623
		(4)	(4)	(1)	(60)	(35)	
	Mouth of Big Creek ^e	5422	5837	0	1926	49630	57393
	& Smith Marsh	(10)	(11)	(0)	(3)	(86)	

^a Swan = combined use-days for Tundra Swans and Mute Swans (*Cygnus olor*) combined; as a result, percentages in this table will not sum to 100%.

^b pond area = 0.02km²

^c pond area = 0.25km²

^d pond area = 0.05km²

^e survey areas = 0.75km², respectively.

1998 and 1999, Bouck's Pond had the highest number of waterfowl use-days, largely as a result of relatively greater use by diving ducks as compared to the other locations; this site also had the highest use by Tundra Swans during each year. Ducks, especially dabbling ducks, showed much higher use of exclosure ponds than did larger herbivores (95% - 70% of duck use-days vs. 5% to 30% of swan and goose use-days); this pattern was evident at each location during both study seasons. Further, a notable number and percentage of all waterfowl (1998 = 29538 – 152876 waterfowl use-days & 16% – 69% of waterfowl use-days; 1999 = 1044 – 53650 waterfowl use-days & 2% - 22% of waterfowl use-days) and duck use-days (1998 = 29070 – 152816 duck use-days & 16% – 69% of duck use-days; 1999 = 1044 – 50185 duck use-days & 2% - 21% of duck use-days) were recorded at each of these locations before peak swan migration each year (Table 2.2).

Although I did not quantify numbers of other potential herbivores at exclosure locations, it was evident that organisms other than birds were present and potentially also could remove aquatic vegetation. Carp (*Cyprinus carpio*) were present in large numbers during spring in these areas, but none were observed during the early or late season sampling periods. Snapping turtles (*Chelydra serpentina*) were observed during early and late sampling periods at all study sites, with the exception of Inner Long Point Bay, several were found within exclosures while sampling vegetation.

The most prevalent herbivore that was present at many exclosure locations, other than waterfowl, was muskrats. Muskrats were often observed at North Pond (1998 & 1999) and several bird exclosures each season showed some evidence of muskrat use (i.e., small holes chewed through the plastic fencing at or below the water surface; one exclosure in 1998, three exclosures in 1999). No muskrats were observed at Teal Pond (1998), but

Table 2.2. Waterfowl use of exclosure locations before (pre) and after (post) Tundra Swan arrival during fall 1998 and 1999 at Long Point, Ontario. Species/group-specific and total number of use-days (average number of birds counted between two successive aerial surveys at a location multiplied by the number of days between surveys) and the percentage of use-days are shown for each exclosure location.

		Waterfowl use-days (% of use-days)									
		Goose		<i>Anas</i> spp		<i>Aythya</i> spp		Total duck		Total waterfowl	
Year	Location	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
1998	North Pond	468	431	29070	13107	0	0	29070	13107	29538	13538
		(52)	(48)	(69)	(31)	(0)	(0)	(69)	(31)	(69)	(31)
	Bouck's Pond	60	375	144341	590964	8475	220963	152816	811927	152876	812302
		(14)	(86)	(20)	(80)	(4)	(96)	(16)	(84)	(16)	(84)
	Teal Pond	2156	0	40430	23540	0	0	40430	23540	32597	33529
		(100)	(0)	(63)	(37)	(0)	(0)	(63)	(37)	(49)	(51)

Table 2.2. Continued.

		Waterfowl use-days (% of use-days)									
		Goose		<i>Anas</i> spp		<i>Aythya</i> spp		Total duck		Total waterfowl	
Year	Location	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
1999	North Pond	2900	7490	18633	69353	0	0	18633	69353	21533	76843
		(28)	(72)	(21)	(79)	(0)	(0)	(21)	(79)	(22)	(78)
	Bouck's Pond	3466	6083	50185	507728	0	320250	50185	827978	53650	834061
		(36)	(64)	(9)	(91)	(0)	(100)	(6)	(94)	(6)	(94)
	Mouth of Big Creek	0	0	1044	882	0	49630	1044	50512	1044	50512
	& Smith Marsh	(0)	(0)	(54)	(46)	(0)	(100)	(2)	(98)	(2)	(98)

one bird exclosure showed evidence of muskrat entry at this location. No muskrat activity was documented at Bouck's pond during the 1998 or 1999 field seasons. There was no evidence of muskrat activity in or around exclosures in the mouth of Big Creek. Muskrats were present at the adjacent Smith Marsh location; three muskrat lodges were present along shore > 100m from exclosures. No bird exclosures in the Smith Marsh showed any evidence of muskrat entry.

2.5.2. Waterfowl exclosure observations

Exclosures were continually monitored for use by herbivores whenever observers were documenting activities of Tundra Swans and other waterfowl at Bouck's pond (1998 & 1999), North Pond (1999), and Smith Marsh (1999) (see methods, Chapter 3). These behavioral and exclosure observations documented that ducks, Tundra Swans and, to a lesser extent, Canada Geese fed at these locations (see also Chapter 3, Table 3.10). Observations also showed that: 1) ducks entered and fed in both swan and open exclosures, 2) Tundra Swans and Canada Geese occasionally fed in open exclosures, 3) swans and geese did/could not enter any swan or bird exclosure, and 4) Ring-necked Ducks were able to enter bird exclosures (Bouck's Pond 1998 only) by diving underwater. Further, ducks and swans both often were observed feeding \leq 1m from bird exclosures, which showed that waterfowl apparently did not avoid these structures.

During fall 1999, muskrats were observed inside bird exclosures at North Pond, but not at any other observation area. Muskrats often chewed small holes in bird exclosures late in the fall in order to gain access to vegetation. Once inside, they removed large amounts of vegetation and piled it in one corner of the exclosure. Further, dabbling

ducks sometimes were observed entering bird exclosures that had visible muskrat holes in them at North Pond.

2.5.3. Waterfowl exclosure and vegetation study

Early season biomass and tuber density estimates in exclosures.-There was no support that any initial above- and below ground biomass or tuber density estimate differed substantially among treatments within locations during the fall 1998 and 1999 field seasons (Table 2.3). There was some weak support ($^W\text{AIC}_c$: 0.01 – 0.03) that total above ground biomass (1998 & 1999), dry mass of musk grass, total below-ground biomass, and below-ground biomass and tuber estimates of combined wild celery and sago pondweed (total biomass, tuber dry mass and tuber density) differed among treatments over all exclosure locations in 1998 (Table 2.3). For each of the response variables included in these analyses, the best candidate models consistently were those that did not contain the treatment effect or the interaction between treatment and location (i.e., there was overwhelming support [$^W\text{AIC}_c$: 0.99 - 1.0] for the candidate set null model in each set of analyses). Despite only weak support of a treatment effect, I still chose to include initial biomass or tuber density estimates as explanatory variables in all analyses of variation in late season biomass present in exclosures (see below). Doing this controlled for any effect that among exclosure differences, no matter how small, potentially had on amount of biomass remaining after exposure to herbivory and other destructive forces.

Late season biomass and tuber density estimates in exclosures.-In the fall 1998 data, late season above-and below-ground biomass and tuber density estimates did not differ substantially among exclosures within study sites because there was no support for

Table 2.3. Dry biomass of above- and below-ground plants initially present in bird, swan and open enclosures during fall 1998 and 1999 at Long Point, Ontario. Under Model, L = location (3 in 1998 & 4 in 1999), S = enclosure set (1, 2, & 3), S(L) = enclosure sets nested within locations, T = enclosure treatment (bird, swan, & open), L×T = interaction among locations and treatments. Proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$) are shown for each candidate model. Enclosure estimates (least-squares $0 \pm SE$) under “Enclosure” account for model selection uncertainty.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Enclosure ($0 \pm SE$)		
								Bird	Swan	Open
1998	Above-ground (g/m^2)									
	Total above-ground	{L, S(L)}	0.85	10	27	0.00	0.98			
		{L, S(L), T}	0.87	12	27	8.30	0.02	222.15	239.83	266.73
		{L, S(L), T, L×T}	0.89	16	27	43.80	0.00	(14.79)	(14.79)	(14.79)

Table 2.3. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Musk grass	{L, S(L)}	0.90	6	27	0.00	0.99			
		{L, S(L), T}	0.92	8	27	8.50	0.01	174.79	195.80	216.02
		{L, S(L), T, L×T}	0.93	12	27	44.40	0.00	(13.98)	(13.98)	(13.98)
	Wild celery & sago pondweed	{L, S(L)}	0.84	6	21	0.00	1.00			
		{L, S(L), T}	0.85	8	21	13.20	0.00	18.44	21.56	22.58
		{L, S(L), T, L×T}	0.86	12	21	67.00	0.00	(3.35)	(3.35)	(3.35)
1998	Below-ground (g/m^3)									
	Total below-ground	{L, S(L)}	0.61	10	27	0.00	0.99			
		{L, S(L), T}	0.66	12	27	9.20	0.01	15.86	19.03	33.77
		{L, S(L), T, L×T}	0.74	16	27	41.70	0.00	(7.12)	(7.12)	(7.12)

Table 2.3. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Wild celery & sago	{L, S(L)}	0.57	6	21	0.00	0.99			
	pondweed	{L, S(L), T}	0.65	8	21	10.10	0.01	18.30	23.60	42.95
		{L, S(L), T, L×T}	0.79	12	21	55.20	0.00	(8.94)	(8.94)	(8.94)
	Wild celery & sago	{L, S(L)}	0.79	6	21	0.00	0.99			
	pondweed tuber mass	{L, S(L), T}	0.84	8	21	9.00	0.01	17.60	22.90	29.73
		{L, S(L), T, L×T}	0.90	12	21	55.00	0.00	(3.67)	(3.67)	(3.67)
	Wild celery & sago	{L, S(L)}	0.69	6	21	0.00	0.99			
	pondweed tubers ($\#/m^3$)	{L, S(L), T}	0.74	8	21	10.00	0.01	18	19	29
		{L, S(L), T, L×T}	0.85	12	21	55.00	0.00	(4)	(4)	(4)

Table 2.3. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1999	Above-ground (g/m^2)									
	Total above-ground	{L, S(L)}	0.79	13	36	0.00	0.99			
		{L, S(L), T}	0.80	15	36	8.90	0.01	105.04	122.47	115.24
		{L, S(L), T, L×T}	0.81	21	36	60.70	0.00	(9.78)	(9.78)	(9.78)
	Musk grass	{L, S(L)}	0.75	11	14	0.00	1.00			
		{L, S(L), T}	0.79	13	14	18.50	0.00	75.00	46.65	60.45
		{L, S(L), T, L×T}	0.80	19	14	65.80	0.00	(13.99)	(11.70)	(11.70)
	Wild celery & sago	{L, S(L)}	0.69	13	33	0.00	0.99			
	pondweed	{L, S(L), T}	0.71	15	33	9.90	0.01	33.90	44.62	42.59
		{L, S(L), T, L×T}	0.75	21	33	64.00	0.00	(5.92)	(5.92)	(5.92)

Table 2.3. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1999	Below-ground (g/m^3)									
	Total below-ground	{L, S(L)}	0.68	13	36	0.00	1.00			
		{L, S(L), T}	0.68	15	36	11.10	0.00	134.82	137.22	126.46
		{L, S(L), T, L×T}	0.71	21	36	61.20	0.00	(13.77)	(13.77)	(13.77)
	Wild celery & sago	{L, S(L)}	0.75	13	33	0.00	1.00			
	pondweed	{L, S(L), T}	0.75	15	33	11.70	0.00	106.74	108.87	108.12
		{L, S(L), T, L×T}	0.81	21	33	60.80	0.00	(10.98)	(10.98)	(10.98)
	Wild celery & sago	{L, S(L)}	0.70	13	33	0.00	1.00			
	pondweed tuber mass	{L, S(L), T}	0.70	15	33	11.30	0.00	34.92	31.26	32.73
		{L, S(L), T, L×T}	0.89	21	33	37.70	0.00	(4.04)	(4.04)	(4.04)

Table 2.3. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Wild celery & sago	{L, S(L)}	0.74	11	33	0.00	1.00			
	pondweed tubers ($\#/m^3$)	{L, S(L), T}	0.74	13	33	11.80	0.00	44	44	44
		{L, S(L), T, L×T}	0.86	19	33	50.60	0.00	(6)	(6)	(6)

models that contained the location \times treatment effect (Table 2.4). In addition, there was no consistent evidence in support of models that contained only the treatment effect in these analyses. Thus, inspection of least-squares means from models containing only the treatment effect showed that estimates of above-and below ground biomass of all plants did not substantially differ among exclosures during late fall. Most importantly, however, combined below ground biomass, tuber dry mass, and tuber density estimates of preferred waterfowl foods (i.e., wild celery and sago pondweed) did not differ substantially among exclosures after several months of exposure or protection from herbivores.

Results of analyses for variation in biomass remaining in exclosures during late fall 1999 also showed that there was no evidence to support a location \times treatment interaction (Table 2.4). However, there was some, albeit extremely weak ($^W\text{AIC}_c = 0.01$), support for a treatment effect over all exclosure locations for analyses of variation in total above-ground biomass, total below-ground biomass, combined below-ground biomass of wild celery and sago pondweed, dry mass of wild celery and sago pondweed tubers, and number of wild celery and sago pondweed tubers remaining in late fall. Late season estimates for each of these response variables were highest in bird exclosures, lowest in open exclosures, while estimates in swan exclosures were between those of bird and open exclosures. There was, however, fairly large variability about exclosure estimates relative to effect size in each of these analyses, which undoubtedly contributed to the extremely weak support this model received in the model selection process.

Table 2.4. Dry biomass of above- and below-ground plants remaining in bird, swan, and open exclosures during late fall 1998 and 1999 at Long Point, Ontario. Under Model, L = location (3 locations in 1998 & 4 locations in 1999), S = exclosure set (1, 2, & 3), S(L) = exclosure sets nested within locations, P = biomass estimate of Y in exclosures at initial sampling, T = exclosure treatment (bird, swan, & open), L×T = interaction among locations and treatments. Proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$) are shown for each candidate model. Exclosure estimates (least-squares $0 \pm SE$) under “Exclosure” account for model selection uncertainty.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1998	Above-ground (g/m^2)									
	Total above-ground	{L, S(L), P}	0.67	11	27	0.00	1.00			
		{L, S(L), P, T}	0.67	13	27	14.20	0.00	39.93	39.21	42.91
		{L, S(L), P, T, L×T}	0.76	17	27	53.60	0.00	(5.78)	(5.39)	(5.64)

Table 2.4. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Musk grass	{L, S(L), P}	0.69	7	27	0.00	1.00			
		{L, S(L), P, T}	0.70	9	27	13.80	0.00	34.97	34.66	39.72
		{L, S(L), P, T, L×T}	0.76	13	27	55.50	0.00	(5.32)	(5.11)	(5.31)
	Wild celery & sago	{L, S(L), P}	0.26	7	21	0.00	1.00			
	pondweed	{L, S(L), P, T}	0.31	9	21	15.50	0.00	0.01	0.01	0.01
		{L, S(L), P, T, L×T}	0.59	13	21	79.10	0.00	(0.01)	(0.01)	(0.01)
1998	Below-ground (g/m^3)									
	Total below-ground	{L, S(L), P}	0.38	11	27	0.00	1.00			
		{L, S(L), P, T}	0.80	13	27	10.70	0.00	-2.35	30.37	6.59
		{L, S(L), P, T, L×T}	0.58	17	27	51.60	0.00	(9.66)	(9.54)	(9.89)

Table 2.4. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Wild celery & sago	{L, S(L), P}	0.59	7	21	0.00	1.00			
	pondweed	{L, S(L), P, T}	0.60	9	21	16.70	0.00	1.30	1.32	1.09
		{L, S(L), P, T, L×T}	0.85	13	21	70.40	0.00	(0.36)	(0.35)	(0.37)
	Wild celery & sago	{L, S(L), P}	0.60	7	21	0.00	1.00			
	pondweed tuber mass	{L, S(L), P, T}	0.60	9	21	16.60	0.00	1.36	1.32	1.08
		{L, S(L), P, T, L×T}	0.84	13	21	72.20	0.00	(0.38)	(0.35)	(0.37)
	Wild celery & sago	{L, S(L), P}	0.72	7	21	0.00	1.00			
	pondweed tuber (#/m ³)	{L, S(L), P, T}	0.72	9	21	16.60	0.00	2	2	3
		{L, S(L), P, T, L×T}	0.92	13	21	64.20	0.00	(1)	(1)	(1)

Table 2.4. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1999	Above-ground (g/m^2)									
	Total above-ground	{L, S(L), P}	0.51	14	36	0.00	0.99			
		{L, S(L), P, T}	0.55	16	36	9.90	0.01	31.30	25.46	21.03
		{L, S(L), P, T, L×T}	0.76	22	36	48.10	0.00	(4.30)	(4.30)	(4.30)
	Musk grass	{L, S(L), P}	0.61	12	14	0.00	1.00			
		{L, S(L), P, T}	0.85	14	14	17.00	0.00	31.52	13.90	7.02
		{L, S(L), P, T, L×T}	0.97	20	14	85.40	0.00	(3.99)	(3.88)	(3.46)
	Wild celery & sago	{L, S(L), P}	0.24	14	33	0.00	0.99			
	pondweed	{L, S(L), P, T}	0.32	16	33	9.50	0.01	0.11	0.05	0.01
		{L, S(L), P, T, L×T}	0.54	22	33	64.30	0.00	(0.04)	(0.04)	(0.03)

Table 2.4. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1999	Below-ground (g/m^3)									
	Total below-ground	{L, S(L), P}	0.48	14	36	0.00	0.99			
		{L, S(L), P, T}	0.53	16	36	9.40	0.01	42.89	30.68	26.47
		{L, S(L), P, T, L×T}	0.72	22	36	52.10	0.00	(6.52)	(6.52)	(6.53)
	Wild celery & sago	{L, S(L), P}	0.48	14	33	0.00	0.99			
	pondweed	{L, S(L), P, T}	0.52	16	33	10.20	0.01	38.95	28.80	22.94
		{L, S(L), P, T, L×T}	0.74	22	33	57.70	0.00	(6.63)	(6.63)	(6.63)
	Wild celery & sago	{L, S(L), P}	0.47	14	33	0.00	0.99			
	pondweed tuber mass	{L, S(L), P, T}	0.51	16	33	10.10	0.01	36.24	27.02	22.15
		{L, S(L), P, T, L×T}	0.73	22	33	59.10	0.00	(6.47)	(6.50)	(6.47)

Table 2.4. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Wild celery & sago	{L, S(L), P}	0.70	12	33	0.00	0.99			
	pondweed tuber (#/m ³)	{L, S(L), P, T}	0.72	14	33	10.10	0.01	37	33	26
		{L, S(L), P, T, L×T}	0.83	20	33	60.90	0.00	(4)	(5)	(5)

Proportional change in biomass and tuber density in exclosures.- In all analyses of proportional change in above- and below-ground biomass and tuber density during fall 1998 and 1999, model selection criterion showed overwhelming support ($^W\text{AIC}_c$: 0.93 – 1.0) for models that did not have the location \times treatment or treatment effects (Table 2.5). Similar to analyses of late season biomass, there was no support for models that only contained the treatment effect in all analyses of variation for proportional change in biomass and number of tubers in fall 1998 data set. In the fall 1999 data set, several response variables, including proportional change in total below-ground biomass, combined below-ground biomass of wild celery and sago pondweed, wild celery and sago pondweed tuber mass, and wild celery and sago pondweed tuber density, showed some, but extremely weak ($^W\text{AIC}_c$: 0.01 - 0.07), support for an overall treatment effect.

During 1999, total below-ground biomass, on average, declined by 59% ($\pm 5\%$) in bird exclosures, which was about 15-17% ($\pm 5\%$) less than that observed in both swan (-74%) and open (-76%) exclosures. Total combined below-ground biomass of wild celery and sago pondweed, on average, declined by 66% in both bird and swan exclosures and only decreased by an additional 8% ($\pm 6\%$) in open exclosures during fall. However, dry mass of wild celery and sago pondweed tubers increased slightly by about the same amount in both bird and swan exclosures, but tuber dry mass decreased by about 22% ($\pm 19\%$) from the early to late fall sampling periods in open exclosures; the average estimate from open exclosures was 58% and 42% lower than those from bird and swan exclosures, respectively. On average, number of wild celery and sago pondweed tubers in bird and swan exclosures essentially did not change during fall, but density of tubers in open exclosures showed a 22% ($\pm 19\%$) decrease during fall 1999.

Table 2.5. Proportional change in dry biomass of above- and below-ground plants in bird, swan, and open enclosures from early to late fall 1998 and 1999 at Long Point, Ontario. Under Model, L = location (3 locations in 1998 & 4 locations in 1999), S = enclosure set (1, 2, & 3), S(L) = enclosure sets nested within locations, T = enclosure treatment (bird, swan & open), L×T = interaction among locations and treatments. Proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$) are shown for each candidate model. Change in biomass estimates (least-squares $0 \pm SE$) under “Enclosure” account for model selection uncertainty.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Enclosure ($0 \pm SE$)		
								Bird	Swan	Open
1998	Above-ground (g/m^2)									
	Total above-ground	{L, S(L)}	0.70	10	27	0.00	1.00			
		{L, S(L), T}	0.72	12	27	10.30	0.00	-0.80	-0.82	-0.84
		{L, S(L), T, L×T}	0.80	16	27	41.40	0.00	(0.02)	(0.02)	(0.02)

Table 2.5. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Musk grass	{L, S(L)}	0.63	6	27	0.00	0.98			
		{L, S(L), T}	0.68	8	27	8.10	0.02	-0.69	-0.74	-0.78
		{L, S(L), T, L×T}	0.81	12	27	34.30	0.00	(0.03)	(0.03)	(0.03)
	Wild celery & sago pondweed	{L, S(L)}	0.58	6	21	0.00	1.00			
		{L, S(L), T}	0.63	8	21	11.00	0.00	-1.00	-1.00	-1.00
		{L, S(L), T, L×T}	0.74	12	21	59.60	0.00	(<0.01)	(<0.01)	(<0.01)
1998	Below-ground (g/m^3)									
	Total below-ground	{L, S(L)}	0.30	10	27	0.00	1.00			
		{L, S(L), T}	0.40	12	27	10.30	0.00	-0.73	0.63	-0.63
		{L, S(L), T, L×T}	0.53	16	27	42.00	0.00	(0.88)	(0.88)	(0.88)

Table 2.5. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Wild celery & sago	{L, S(L)}	0.31	6	21	0.00	1.00			
	pondweed	{L, S(L), T}	0.36	8	21	12.30	0.00	-0.86	-0.92	-0.82
		{L, S(L), T, L×T}	0.67	12	21	54.60	0.00	(0.06)	(0.06)	(0.06)
	Wild celery & sago	{L, S(L)}	0.27	6	21	0.00	1.00			
	pondweed tuber mass	{L, S(L), T}	0.33	8	21	12.10	0.00	-0.89	-0.94	-0.82
		{L, S(L), T, L×T}	0.64	12	21	54.90	0.00	(0.06)	(0.06)	(0.06)
	Wild celery & sago	{L, S(L)}	0.86	6	21	0.00	1.00			
	pondweed tuber (#/m ³)	{L, S(L), T}	0.86	8	21	13.90	0.00	-0.53	-0.54	-0.52
		{L, S(L), T, L×T}	0.91	12	21	59.90	0.00	(0.04)	(0.04)	(0.04)

Table 2.5. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1999	Above-ground (g/m^2)									
	Total above-ground	{L, S(L)}	0.49	13	36	0.00	1.00			
		{L, S(L), T}	0.52	15	36	10.50	0.00	-0.71	-0.78	-0.78
		{L, S(L), T, L×T}	0.63	21	36	54.00	0.00	(0.04)	(0.04)	(0.04)
	Musk grass	{L, S(L)}	0.30	11	14	0.00	1.00			
		{L, S(L), T}	0.37	13	14	19.40	0.00	-0.61	-0.69	-0.71
		{L, S(L), T, L×T}	0.91	19	14	41.40	0.00	(0.07)	(0.06)	(0.06)
	Wild celery & sago	{L, S(L)}	0.28	13	33	0.00	1.00			
	pondweed	{L, S(L), T}	0.38	15	33	16.80	0.00	-0.99	-1.00	-1.00
		{L, S(L), T, L×T}	0.72	21	33	39.70	0.00	(<0.01)	(<0.01)	(<0.01)

Table 2.5. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
1999	Below-ground (g/m^3)									
	Total below-ground	{L, S(L)}	0.44	13	36	0.00	0.93			
		{L, S(L), T}	0.53	15	36	5.10	0.07	-0.59	-0.74	-0.76
		{L, S(L), T, L×T}	0.69	21	36	44.20	0.00	(0.05)	(0.05)	(0.05)
	Wild celery & sago	{L, S(L)}	0.32	13	33	0.00	0.99			
	pondweed	{L, S(L), T}	0.35	15	33	9.90	0.01	-0.66	-0.65	-0.74
		{L, S(L), T, L×T}	0.53	21	33	58.10	0.00	(0.06)	(0.06)	(0.06)
	Wild celery & sago	{L, S(L)}	0.51	13	33	0.00	0.97			
	pondweed tuber mass	{L, S(L), T}	0.57	15	33	6.90	0.03	0.36	0.20	-0.22
		{L, S(L), T, L×T}	0.84	21	33	33.80	0.00	(0.19)	(0.19)	(0.19)

Table 2.5. Continued.

Year	Response (Y)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Exclosure ($0 \pm SE$)		
								Bird	Swan	Open
	Wild celery & sago	{L, S(L)}	0.50	11	33	0.00	0.99			
	pondweed tuber (#/m ³)	{L, S(L), T}	0.54	13	33	9.00	0.01	0.08	-0.05	-0.22
		{L, S(L), T, L×T}	0.80	19	33	39.80	0.00	(0.13)	(0.13)	(0.13)

2.6. DISCUSSION

During fall 1998, there was no evidence for an effect of duck herbivory or, more importantly, no negative effect of large waterfowl herbivory on aquatic vegetation in shallow, undisturbed ponds; I will propose possible reasons for the lack of the latter effect later in discussion of results of the 1999 vegetation study. Determination of the relative impact that non-waterfowl herbivores and ducks had on vegetation was originally a secondary objective during 1998 (see methods). However, ducks could not consistently be restricted from feeding inside the bird exclosures. Bird exclosures were compromised in two different ways: 1) diving ducks at Bouck's Pond were able to feed in exclosures simply by diving under fencing and 2) dabbling ducks entered exclosures by way of holes chewed through fencing by muskrats. This essentially exposed vegetation in both swan and bird exclosures to the same groups of herbivores (i.e., muskrats or other non-waterfowl herbivores and ducks), thus eliminating the possibility of detecting an additive waterfowl removal effect. Despite the limitations of the experimental design in 1998, I could still reliably conclude that large herbivorous waterfowl did not add substantially to removal of vegetation due to natural events and relatively smaller herbivores that season because large waterfowl could not enter bird exclosures even after muskrats had compromised them.

The fact that muskrats removed vegetation from inside bird exclosures late in the fall (1998 & 1999) suggested that they may be an important direct or indirect factor in determining the abundance or distribution of some aquatic plants (De Szalay and Cassidy 2001, Connors et al. 2000). Herbivory by muskrats alone, however, probably was less important as compared to the destructive activities that the large number of waterfowl

that were present at these locations had on aquatic vegetation. Determination of which group of small herbivores had the greatest impact on vegetation was not possible, but data and observations in this study suggested that muskrats and waterfowl both were potentially important predators on aquatic vegetation in shallow, cattail-dominated marshes at Long Point. Future plant-herbivore studies in such habitats could determine the relative impact that each of these consumers has on the structure of aquatic plant communities and investigate more subtle indirect effects, such as compensatory herbivory, by designing a more complex enclosure experiment (e.g., see Evers et al. 1998, Hamilton 2000).

During 1999, muskrats only were abundant and caused damage to bird enclosures at 1 (North Pond) of 4 study locations. Further, bird enclosure design also was changed that year to exclude all herbivores so that decline of vegetation due to factors other than herbivory could be determined. Among enclosure differences in most 1999 late-season below-ground biomass estimates agreed with the pattern predicted if large herbivores had an additive, negative effect on over-wintering structures of those plants (i.e., bird < swan < open); proportional decline in below ground biomass (all plants) during fall also showed the same pattern in among enclosure differences. However, these differences were much more consistent with removal effects caused by all herbivores because treatment effect sizes were not really large enough, relative to the variability in these data, to discern strong differences between bird and swan enclosures or between swan and open enclosures. This also agreed with the very weak support that models that generated these estimates received during the model selection process.

Differences between bird and open enclosures showed that, on average, 16.4

$\pm 6.5\text{g}/\text{m}^3$ of total below ground biomass were removed by aquatic herbivores, which represented a $17 \pm 5\%$ seasonal decline. Total below ground vegetation protected from all herbivores, however, declined by $59 \pm 5\%$ during fall, showing that natural and/or abiotic factors have a sizeable effect on total below ground biomass of plants remaining in late fall (Jupp and Spence 1977, Anderson 1978, Crowder and Painter 1992). Late season estimates of wild celery and sago pondweed tubers also showed that about $14.1 \pm 6.5\text{g}$ dry mass/ m^3 or approximately 11 ± 5 tubers/ m^3 were removed by aquatic herbivores during fall.

Estimates for proportional change in total below-ground biomass and tuber dry mass of wild celery and sago pondweed were consistent with a weak additive, large-waterfowl herbivory effect. For example, estimates of proportional change for these variables in bird and swan exclosures did not differ, whereas estimates from open exclosures decreased more than did those from swan exclosures. But, the difference in proportional changes between swan and open exclosures (i.e., the additive large herbivore effect) was only $9 \pm 6\%$ for below-ground biomass of wild celery and sago pondweed, which was especially small relative to the $66 \pm 6\%$ decline due to natural factors. Wave action was one explanation for this relatively large decline because 3 of 4 sites (Bouck's Pond, Smith Marsh, and mouth of Big Creek) potentially were exposed to much wind (Anderson 1978, Idestam-Almquist 2000), but it was probably mostly caused by disintegration of rhizomes after nutrients had been incorporated into the developing tubers (Korschgen and Green 1988, Kantrud 1990). Despite open exclosures showing slightly higher grazing intensity than other types of exclosures, actual biomass of wild celery and sago pondweed remaining in each type of exclosure at the end of the season

was similar. This further suggested that there was no strong or consistent additive removal effect on these species by the end of the season.

Even though the estimated proportional changes in number of tubers in exclosures during fall all were in the directions predicted, the large variability about those estimates showed no strong herbivory effect on the number of over-wintering structures. These estimates conflicted with those of proportional changes in tuber dry mass during fall, which, out of all below-ground response variables, showed the most support for an additive effect attributable to destructive activities of large waterfowl. If in fact tuber mass increased, as was shown in swan and bird exclosures and which was consistent with these plant species life cycles (Stephen and Titus 1983, van Wijk 1988, Korschgen and Green 1988, Kantrud 1990), large herbivorous waterfowl (mostly Tundra Swans) removed, on average, 42% of tuber dry mass during fall. This sizable amount of removal did not appear to strongly affect the mass or numbers of tubers present later that fall because tuber estimates in swan and open exclosures essentially were identical during the late sample period. Given the extremely weak evidence in support of the statistical models used to generate these estimates, combined with the conflicting results of analyses of late season biomass and proportional change over fall in biomass/density of tubers, these findings can be only interpreted as suggestive of an additive effect of large herbivores.

The lack of strong additive effects of large waterfowl on preferred waterfowl foods during fall (1998 & 1999) can be attributed to large- and small-scale habitat use, food preferences, and feeding activities of geese and swans. Behavioural observations of waterfowl done at Bouck's Pond (1998), Little Rice Bay (1998), and North Pond (1999,

2000, & 2001) should be representative of all undisturbed areas where exclosures were located in 1998 & 1999. These observations showed that waterfowl feeding activity generally declined throughout fall (see Chapter 3), which was consistent with the decline in aquatic plants in exclosures at these locations. They also revealed that Canada Geese used ponds primarily as roosting sites between foraging bouts in surrounding agricultural fields (see Chapter 3). Thus, Canada Geese probably had little influence on aquatic vegetation during the time frame involved in this study.

Tundra Swans had more potential to affect aquatic plants because they feed almost exclusively in aquatic habitats during fall at Long Point (Petrie et al. 2002, Badzinski, unpublished data) and can substantially reduce tuber producing plants preferred by them and other waterfowl during migration and winter (Beekman et al. 1991, Froelich 2001, Nolet et al. 2002). During fall 1998 and 1999, Tundra Swans spent, on average, between 5% and 29% of the day feeding on shallow ponds (see Chapter 3), but spent much more time feeding (> 60% of diurnal and nocturnal hours) at the exclosure locations in Inner Long Point Bay. Observations of swan feeding activity and foraging micro-habitats within locations, however, showed that they had very different food preferences than did dabbling and diving ducks. For example, Tundra Swans occasionally were observed feeding in relatively deep water on wild celery and sago pondweed tubers in open exclosures, but most often they fed in shallower areas that were dominated by aquatic plants that produced relatively large rhizomes and/or tubers. Direct observation documented that Tundra Swans fed on subterranean, over-wintering structures of *Sagittaria latifolia*, *Sagittaria rigida*, *Nuphar variegatum*, and possibly on *Scirpus acutus* (S. Badzinski, personal observation). Dabbling ducks and diving ducks at Long Point

rarely feed on rhizomes or tubers of these plants, but commonly eat seeds of aquatic plants and relatively smaller tubers of wild celery and sago pondweed (Petrie 1998, Knapton and Petrie 1999).

This differential habitat use and food preference was most evident in the Smith Marsh, which was a major feeding area for Tundra Swan on my study area, where hundreds (sometimes thousands) of Tundra Swans congregated to feed in extensive shallow water beds of *Sagittaria* spp and stands of *Scirpus* spp each night from their arrival in late October (S. Badzinski, unpublished data). Once they had depleted this area several weeks later, Tundra Swans typically moved east along the shoreline to other locations in Inner Long Point Bay with similar foods, while some remained and began feeding in progressively deeper water where extensive beds of wild celery and sago pondweed, and thus my exclosures, were located (S. Badzinski, unpublished data). A similar phenomenon has been observed in Bewick's Swans; birds fed in deeper water and upended more as their preferred shallow water feeding locations were depleted during spring migration (Nolet and Drent 1998). Thus, the weak, large-waterfowl herbivory effect present in 1999 may have been due to swans only feeding for a short time on these "less preferred" foods. In fact, Tundra Swans tend to feed in deeper water during spring, as compared to fall, and likely feed more intensively on wild celery and sago pondweed tubers at that time of year. Thus, it is likely that swans and/or diving ducks substantially further reduce the tuber bank during spring, which may in turn decrease plant production later in the year (Anderson and Low 1976, Tubbs and Tubbs 1983, Beekman et al. 1991, Idestam-Almquist 1998). This hypothesis remains to be tested at Long Point, but one that is necessary to evaluate in order to better understand plant-herbivore dynamics at staging

areas used by swans and other waterfowl during both fall and spring.

Relatively high rates of human disturbance during fall in Inner Long Point Bay, a preferred feeding area for Tundra Swans and diving ducks, causes waterfowl to feed there at night, while each morning birds return to areas with low diurnal disturbance, relatively high densities of birds, and lower food availability (Knapton et al. 2000, Badzinski, unpublished data). The predictable daily disturbance regime that Tundra Swans and other waterfowl in my study area experienced may have indirectly influenced the results of this study by reducing the amount of time each day that Tundra Swans and other waterfowl could feed on their preferred foods, thus extending their availability later into fall than would be allowed in the absence of disturbance (Knapton et al. 2000). In the absence of such disturbance, however, foraging pressure would increase on foods that were used later in the fall and during spring, such as wild celery and sago pondweed. This also could increase the potential for competition between Tundra Swans and diving ducks. Relatively high rates of herbivory on wild celery and sago pondweed may occur at some areas at Long Point and at other staging or wintering areas, where these plants grow in relatively large, shallow areas and where large numbers of Tundra Swans and ducks both can access their tubers (see Froelich 2001).

Even though results of this two season study did not show strong or even consistent support for Tundra Swans (or geese) having a negative influence on important waterfowl foods, additional investigations should be done to determine potential effects that large numbers of Tundra Swans and other waterfowl have on vegetation at this and other important staging and wintering areas. Future studies should strive to determine the extent to which different consumer groups overlap in use of specific aquatic plants and

how herbivores affect these plant species relative abundances, compositions, and distributions in the short-term (i.e., fall and spring staging or winter periods) and over the longer term (i.e., over several years of exposure). Studies of aquatic herbivory during spring, when aquatic food availability is at its lowest, also should be undertaken in wetlands that are used by large numbers of staging Tundra Swans. Use of well designed enclosure experiments that minimize unintended herbivory or avoidance effects will aid in understanding complex herbivore-plant and herbivore-herbivore interactions and provide data necessary to guide management of waterfowl populations and their preferred aquatic foods at critical staging areas.

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CHAPTER 3. INFLUENCE OF TUNDRA SWANS ON THE ABUNDANCE, DISTRIBUTION, AND BEHAVIOUR OF STAGING WATERFOWL AT LONG POINT, ONTARIO

3.1. ABSTRACT

Large or dominant species, such as Tundra Swans, could have pronounced negative effects on the abundance, distribution, or behaviour of other waterfowl species, especially when birds are concentrated in space and time at their major staging areas. In this study, I used waterfowl survey and behavioural observation data to evaluate the hypothesis that Tundra Swans, which are large birds that can be aggressive toward con- and heterospecifics, negatively influence the abundance, distribution, or behaviour of other staging waterfowl that co-occur at Long Point, Ontario. This study showed that Tundra Swans were infrequently aggressive toward other waterfowl species and were so only when feeding. Ducks and geese were supplanted by use of low intensity acts of aggression, but these birds were never observed leaving a pond after an altercation with a swan. These findings suggested that: 1) Tundra Swans did not view other waterfowl as strong competitors for food or space and 2) interference competition was not common between Tundra Swans and other staging waterfowl. Indirect evidence also suggested that Tundra Swans did not drastically reduce food available to other waterfowl on ponds (i.e., exploitative competition) because both swans and other waterfowl generally showed similar rates of seasonal decline in their feeding activities, but swans spent much less time feeding during the day on ponds than did co-occurring dabbling ducks. There was little evidence to suggest any negative influence of large numbers of Tundra Swans on the densities of other waterfowl in large marsh complexes or on relatively small,

individual ponds. In fact, several species of dabbling ducks showed positive relationships with Tundra Swan densities. These results did not support spatial exclusion or habitat saturation due to high densities of swans in diurnal habitats. Waterfowl did not tend to avoid active or inactive Tundra Swans on ponds, but finer scale observations suggested some avoidance when feeding because birds would feed out of neck's reach and often behind swans. The number of swans present during observations did not negatively influence time waterfowl spent feeding on ponds, nor was feeding negatively affected by a swan's proximity or by the nearest swan's activity (feeding/not feeding). Furthermore, waterfowl did not substantially alter their feeding methods while foraging with swans, but individuals of several species did spend more time feeding when near active, as compared to their conspecifics near inactive, Tundra Swans. This suggested that foraging activities of swans may positively influence short-term feeding activities of other waterfowl on ponds. Thus, results of this study generally showed that Tundra Swans did not have substantial negative effects on the abundance, distribution, or behaviour of other staging waterfowl. In contrast to my initial hypothesis, results also indicated that waterfowl, especially dabbling ducks, may benefit by their association with Tundra Swans while feeding on ponds during migration.

3.2. INTRODUCTION

Interspecific interactions among animals and how they influence the abundance, distribution, and behaviour of individuals has been a prominent area of research in the field of ecology (Keddy 1989, Pusey and Packer 1997). Competitive interactions among ecologically similar species often have been cited as the primary mechanism determining ecological community or guild structure in some animals (Lack 1968, Diamond 1976, Connell 1983, Schoener 1983). Much less attention, however, has been given to other forms of negative (e.g., predation and parasitism) and positive interspecific interactions (e.g., mutualistic, commensalistic, and heterospecific attraction) that also can influence the abundance, distribution, and behaviour of some animals (Keddy 1989, Ricklefs 1990, Nummi et al. 1994, Elmberg et al. 1997).

There is some evidence that competitive interactions have been central in structuring waterfowl communities in both evolutionary (Nudds 1983, Nudds 1992, Nudds and Wickett 1994) and ecological time (Toft et al. 1982, DuBowy 1988, 1991, Pöysä 1983a, Pöysä 1986, Nudds 1992, but see Pöysä 1983b, Nummi et al. 1995, Elmberg et al. 1997). In ecological time, both harmful (e.g., interference and exploitative competition) and beneficial interspecific interactions (e.g., heterospecific attraction and feeding facilitation) may be important in modifying pond-level interspecific foraging associations and distributions among some dabbling duck species (Bailey and Batt 1974, Toft et al. 1982, Pöysä 1986, Elmberg et al. 1997). In some waterfowl studies, however, mutually beneficial or commensalistic interactions have been observed more often than indications of interspecific competition (Bailey and Batt 1974, Pöysä 1986, Elmberg et al. 1997, Mathers and Montgomery 1996).

Overt aggression often is cited as evidence of interference competition between species (Connell 1983, Schoener 1983). In addition, aggression between competitors generally increases as their densities increase (Huntingford and Turner 1987, Kaufmann 1983). Because of this, large numbers of dominant aggressive animals may reduce space/habitat available for subordinates (Burger et al. 1979, Nudds 1981, Metcalf and Furness 1987). Aggressive activities of dominant individuals may negatively influence foraging behaviour, thus energetic condition, spatial distribution, or abundance of subordinates, especially when densities of potential competitors are high (Zwarts 1976, Burger et al. 1979, Metcalf and Furness 1987, Pusey and Packer 1997). It has been suggested that the largest, and often the most dominant, members of a waterfowl community can affect the structure of that community or the foraging associations and activities among its members via interference (interspecific aggression) or exploitative (resource depletion) competition, both of which can exclude other individuals from food, space, or preferred habitats (Oksanen et al. 1974, Conover and Kania 1994, Pöysä and Sorjonen 2000).

Tundra Swans are one of the largest migratory waterfowl species in North America (Limpert et al. 1994) and can be aggressive toward conspecifics and other waterfowl throughout the annual cycle (Ely et al. 1987, Burgess and Stickney 1994, Limpert et al. 1994, Badzinski 2003). Outside of the breeding season, Tundra Swans are extremely gregarious and thousands often congregate at traditional staging and wintering areas, where they co-occur with large numbers of many other species of waterfowl (Limpert et al. 1994, Petrie et al. 2002). During the past several decades, Tundra Swan populations have grown substantially in North America (Kelley et al. 1998), which has resulted in

their increased use of major waterfowl staging areas (Petrie 1998, Thorson et al. 2002). While in aquatic habitats at staging areas, Tundra Swans feed primarily on above- and below-ground parts of aquatic plants (Earnst 1994, Limpert et al. 1994), many of which also are important foods for many other waterfowl during migration (Korschgen and Green 1988, Kantrud 1990). Because of the high energy demands associated with migration, Tundra Swans spend much time feeding in aquatic and terrestrial habitats while at staging areas (Earnst 1994, Limpert et al. 1994). Feeding activities of these large birds during migration can dramatically reduce preferred waterfowl forage species (Beekman et al. 1991, Nolet and Drent 1998). Thus, large numbers of Tundra Swans could have important effects on other species of waterfowl at traditional staging areas.

There is little information concerning how Tundra Swans interact with and influence the abundance, behaviour, or activities of other waterfowl (Limpert et al. 1994). Some studies have suggested that waterfowl may benefit by their co-occurrence and interaction with swans (Sherwood 1960, Bailey and Batt 1974, Pöysä and Sorjonen 2000). But, given the information in the paragraph above and evidence or speculation from other swan studies (Rees 1990, Conover and Kania 1994, Petrie et al. 2002), Tundra Swans, through aggressive interactions, resource depletion, or spatial/habitat limitation, may have negative influences on co-occurring waterfowl, especially on staging areas where waterfowl tend to congregate in large, mixed species assemblages. Therefore, in this study I used observational and waterfowl survey data to test the hypothesis that Tundra Swans negatively influence the abundance, distribution, and behaviour of other staging waterfowl.

3.3. METHODS

3.3.1. Study area

Behavioural and survey data on Tundra Swans and other waterfowl used in this study were collected during fall and spring at Long Point, Ontario (80°24'W, 42°38'N). Long Point is a sand-spit extending east 35 km from the southern shore of Ontario into Lake Erie (see Chapter 1, Figure 1.1.). This peninsula facilitated the formation of the Inner and Outer Long Point Bays and their associated marsh complexes, which are globally important waterfowl staging areas (see Petrie 1998).

3.3.2. Waterfowl surveys

Large-scale waterfowl counts.- The number and distribution of Tundra Swans and other staging waterfowl using Long Point's wetlands were determined from mid-day aerial surveys conducted by the Canadian Wildlife Service (1971, 1975, 1979, 1984, 1986, and 1988) and the Long Point Waterfowl and Wetlands Research Fund (annually from 1991-2001) during the fall and spring migration periods. Surveys flights were conducted between 10:00 and 14:00 (EST) along a regular route of 27 separate transects (>250 km) by two observers in a fixed-wing aircraft at an altitude of 100 m (see Petrie 1998). Survey transects were flown over all the major marsh complexes at Long Point. Two observers estimated numbers of each waterfowl species on opposite sides of the aircraft; in most cases, the same pair of observers did all surveys throughout the season in a given year. For each survey, the total number of each waterfowl species in a marsh complex was determined by summing species-specific waterfowl counts over all transects for that marsh complex. Approximate areas of each major marsh complex or survey area

(km²) were determined from Ontario Wetland Survey Base Maps using ArcView and were as follows: Inner Long Point Bay (69.9), Big Creek National Wildlife Area (6.4), Turkey Point Marsh (14.8), Long Point Waterfowl Management Unit (12.7), Long Point Company Marsh (30.4), Long Point National Wildlife Area (27.8), Lake Erie shoreline (32.0), and Outer Long Point Bay (11.0).

Small-scale waterfowl counts.-Tundra Swans and other waterfowl were counted on several ponds during daily behavioural observation sessions (see below). These counts represented abundances of birds at a much smaller geographical scale than did those collected during aerial surveys. Waterfowl counts were obtained from five different observation ponds during five seasons of study: Bouck's Pond (fall 1998), Little Rice Bay (fall 1998), Big Creek North Impoundment (spring 1999), Big Creek North Pond (fall 1999 & 2000), and Biosphere Pond (spring 2000). Counts were done at 09:00, 12:00, and 15:00, but only on days when observers were documenting diurnal activities of waterfowl at these ponds.

3.3.3. Diurnal behavioural observations

Locations, dates, and times of observations.- Diurnal activities of Tundra Swans and other staging waterfowl were documented during fall 1998, 1999, 2000 and spring 2000. During 1998, data were collected from observation blinds at two separate locations in the Long Point National Wildlife Area (Little Rice Bay & Bouck's Pond) from 7 November – 1 December. During fall 1999, observations were done at Bouck's Pond and Big Creek North Pond from 25 October – 30 November. During the 2000 field season, observations were done from 8 November – 6 December only at Big Creek North Pond; spring observations were done from 1 March – 15 April at Biosphere Pond in the Big Creek

National Wildlife Area. Successively fewer ponds were used each season because water levels declined substantially over the three study seasons, which also was the reason why the same observation ponds were not used throughout the study (i.e., they were nearly dry). All observation ponds were chosen because they traditionally received heavy use by Tundra Swans and dabbling ducks plus they had similar disturbance regimes and wetland characteristics such as, pond size, water depth, and aquatic plant assemblages.

Observations were done each day from either one half hour before sunrise until noon (morning) or from noon to one half hour after sunset (evening). The first observation period at a site was determined at random; subsequent observation periods at a site alternated between mornings and evenings so both time periods would be equally represented in analyses. The same two observers did all behavioural observations throughout each season (1998: SB and KP, 1999: SB and SM, 2000: SB and SM) and other individuals were employed throughout the season to record data.

Definitions of waterfowl activities.- During behavioural observations, six general activities were recorded for all waterfowl: aggression, alert, feed, locomotion, maintenance, and head-up. Aggression (inter- and intraspecific) included threat displays, pecks, chases, and fights directed at other individuals. Alert was an extreme head-up posture with the neck extended straight up. Maintenance included sleep/rest (with head on back), preen, bathe, drink, scratch, and stretch. Locomotion included swimming or walking in shallow water. Head-up was recorded when a bird was not in motion and the head was up and in a relaxed position. Feeding included 3 specific acts to obtain aquatic foods: surface feeding, subsurface feeding, and treading. Each of these specific behaviours was recorded separately and then later combined into a general category

called “feeding” for activity calculations. Surface feeding was picking food from the surface or feeding with only the bill submerged under water. Subsurface feeding was when a bird was feeding with the entire head or neck submerged under water and included upending or tip-up feeding postures. Treadling was a feeding method characterized by a rocking motion of the body resulting from birds pumping their feet into the marsh substrate; this activity presumably dislodges food buried in the marsh substrate and facilitates waterfowl feeding.

In some analyses, several of these activity categories were combined into general variables termed, active and inactive. Active Tundra Swans were those that were feeding, involved in an aggressive interaction, or were likely searching for food (locomotion). Inactive swans were birds that were not involved in activities associated with feeding, such as maintenance (e.g., sleep & preen) activities. Birds that were recorded as “alert” were removed from analyses because it could not be determined if that bird was feeding or not.

Tundra Swan activity.- Tundra Swan activity data were collected hourly using modified scan sampling technique (Altman 1974). Activity data were obtained from samples of entire flocks of Tundra Swans. To do this, the spotting scope was first placed on a bird at the extreme edge of the flock and a stopwatch was set to chime at 3-second intervals. The observer watched an individual swan, determined its activity, and called out this activity when the stopwatch chimed so a recorder could enter it into a portable computer. The observer then moved to a different individual swan and repeated the process, thereby effectively scanning through a flock on an observation pond.

Waterfowl-Tundra Swan associations on ponds.- A variation of the activity sampling

technique described above also was used to obtain hourly activity data on waterfowl and also to document species associations near active or inactive swans. During these observations, a random point on a pond was picked and the nearest “focal” Tundra Swan was identified. On the first chime of the watch, that swan’s activity was recorded. Three seconds later, on the next chime, the species, sex and activity of the nearest duck or goose and its distance in species-specific body lengths to the focal swan was recorded. On the next chime, the spotting scope was moved, a new random swan was identified, and the entire process repeated until at least 25 different Tundra Swan-waterfowl associations were observed. This procedure provided a random sample and showed which species were closest to active and inactive swans. These data were combined with those on relative abundance of each waterfowl species on ponds to determine if waterfowl species abundances in samples were random with respect to activity of swans.

Waterfowl activity in relation to proximity and activity of Tundra Swans.-During daily observation sessions, two sets of hourly scan samples were done on each waterfowl species present on a pond; the most common waterfowl species included American Black Duck (*Anas rubripes*), American Wigeon (*Anas americana*), Canada Geese (*Branta canadensis*), Gadwall (*Anas strepera*), Green-winged Teal (*Anas crecca*), Mallard (*Anas platyrhynchos*), Northern Pintail (*Anas acuta*), and Ring-necked Duck (*Aythya collaris*). By restricting all observations of waterfowl only to ponds where both swans and other waterfowl co-occur in time and space reduced the chance that some inherent feature of ponds influenced the behaviour or activity of waterfowl other than the swans themselves. One set of observations was done on birds that were ≤ 3 meters (hereafter, close) away from a Tundra Swan. This criterion was chosen because waterfowl behaviour and

foraging could be directly affected by swan activity or aggression at this distance (Bailey and Batt 1974). Another set of observations was done on waterfowl that should not have been affected by the immediate activity or disposition of a swan; birds that were > 30 meters away (hereafter, far) were chosen to satisfy this criterion. These two sets of observations of each species were done immediately after one another, but the starting order was randomly determined each hour. These activity data were collected using the same method described above (see *Tundra Swan activity*), except observers were looking for birds that were either close or far from swans. In addition to waterfowl activity, I also recorded the activity of the closest Tundra Swan to the “focal” individual, but this was done only when observing waterfowl within 3 meters of swans. These data allowed me to test if Tundra Swan activity (active or inactive) influenced waterfowl activities or foraging behaviour when they were close to swans.

Interspecific interactions.- All interspecific interactions observed between waterfowl were recorded during formal observation sessions or opportunistically between observations. Information recorded during interactions included: species of the initiating and recipient birds, intensity of the agonistic act (high = fight & chase, medium = bite, peck, attempted peck, & low = threat posture), and the recipient bird’s reaction (e.g., did it remain at the pond or did it leave the pond).

3.4. STATISTICAL ANALYSES

3.4.1. Calculations and data transformations

Activity data were converted to proportions by dividing the counts of each activity by the total number of observations for each waterfowl species during a daily observation

period at each site. Data on waterfowl foraging methods (i.e., surface & subsurface) also were converted to proportions, but were calculated by dividing the number of each feeding method recorded for each species by the total number of feeding acts they employed during a daily observation period at each site. Pooling and averaging activity data for each species over daily observation periods at each site was done to minimize problems with pseudoreplication. Using pooled average values, as compared to those calculated from one randomly selected hourly observation, also provided a better estimate of time waterfowl spent in activities because activity levels can change over several hours of observation (Baldassarre et al. 1988).

Proportion data were not normally distributed so they were arcsine square root transformed (Zar 1996); doing this improved the distributions of these data but did not entirely normalize the residuals generated from linear models. All statistical analyses using activity data were done using transformed values, but percentages were reported in tables to allow easier and more meaningful interpretation of results. Nonparametric analyses were not used because parametric statistics are fairly robust to deviations from normality (Johnson 1995; Smith 1995; Stewart-Oaten 1995). Covariates also can be used in parametric models to obtain more precise estimates of effect sizes. Unless otherwise noted, General Linear Models (Proc Mixed, SAS Institute 1990) were used to calculate model selection information, parameter estimates, and measures of precision for specified effects.

3.4.2. Information theoretic approach

Rather than using *P*-values and a traditional stepwise modeling approach to obtain final statistical models, an information-theoretic approach, which is based on criteria that

estimates Kullback-Leibler (K-L) information loss (Kullback & Leibler 1951), was used to select the most parsimonious model from an *a priori* candidate set of models that best described the information contained within these data (see Burnham & Anderson 1998; Anderson et al. 2000). This approach emphasizes the strength of evidence for a given model or effect; it also reduces bias in estimation of effect sizes and their precision, especially when it is combined with model averaging techniques (Burnham & Anderson 1998).

Akaike's Information Criterion corrected for small sample size (AIC_c) was used to select the best model from each *a priori* candidate set of biologically meaningful models I specified. The model with the lowest AIC_c was considered the "best" model in that candidate set. Because AIC_c is on a relative scale, competing models within a candidate set were ordered from lowest to highest AIC_c . Akaike differences (ΔAIC_c) were then calculated by subtracting the lowest AIC_c from every other one in the candidate set. These AIC_c differences allow for comparison and ranking of candidate models. Models with $\Delta AIC_c \leq 2.0$ were considered to have the most support for being the best model, while those with values much > 2.0 had progressively less support. Akaike weights ($^w AIC_c$) also were calculated from ΔAIC_c and have been normalized to sum to 1.0 (see Burnham & Anderson 1998). These values were considered the weight of evidence in favor of a given model being the actual K-L best model, given that one of the models is actually the K-L best model for that candidate set.

A null model was included in each set of candidate models for all analyses. This model was one that contained all relevant and biologically important covariates that may influence a response variable but lacked the effect(s) of interest. When a candidate set

contained only one model, and that model simply was the effect interest, a “true” null or intercept model was included to determine the strength of evidence for that effect. If a “null” model was determined to be the best one, then the parameter estimates from the model with the lowest AIC_c containing the effect of interest were reported in the appropriate tables. Whenever possible, model selection uncertainty was incorporated into parameter estimates and their measures of precision. These unconditional estimates of model parameters and precision ($\pm 95\%$ CI or SE) were calculated by using $^W AIC_c$ in a model-averaging technique (see Burnham and Anderson 1988).

To aid in assessing the strength of evidence for each candidate model, I reported all relevant model selection information, including R^2 , K , N , ΔAIC_c , & $^W AIC_c$. Further, conditional or unconditional slope ($b \pm 95\%$ CI) estimates, least-squares means (\pm SE), and effect sizes were reported in tables and text to allow assessment of differences due to the specified effects of interest.

3.4.3. Data restrictions, predictions, and statistical models

Relationships between densities of Tundra Swans and other waterfowl: wetland complex scale.- Long-term aerial survey data were used to investigate the relationship between densities of Tundra Swans and other waterfowl in each major marsh complex. Several restrictions, however, were imposed on this data set prior to analysis. First, data were included only if at least six Tundra Swans were observed on a survey. This restriction ensured that only surveys conducted during Tundra Swans residency at Long Point were included and enough swans were present to have been counted at any of the six marsh complexes. The next restriction applies only to the species-specific analyses. Data were included only if at least six individuals of a given species were recorded on a

survey. This ensured that both swans and each duck species of interest were present at Long Point and that both were numerous enough so they could have been counted in any of the marsh complexes. The final restriction was that only data from Big Creek National Wildlife Area (BCNWA), Long Point Waterfowl Management Unit (LPWMU), Long Point Company Marsh (LPCM), Long Point National Wildlife Area (LPNWA), Inner Long Point Bay (ILPB), and Turkey Point Marsh (TPM) were included in analyses; counts from Lake Erie and Outer Long Point Bay were not included because these deep, open-water habitats rarely were used by swans.

Several response variables (Y) were used in these analyses, including the density of: 1) common waterfowl (Canada Geese *Branta canadensis*, American Black Duck *Anas rubripes*, American Wigeon *Anas americana*, Green-winged Teal *Anas crecca*, Mallard *Anas platyrhynchos*, Canvasback *Aythya valisineria*, Greater & Lesser Scaup *Aythya marila* & *Aythya affinis*, Redhead *Aythya americana*, and Ring-necked Ducks *Aythya collaris*), 2) dabbling ducks (see above, *Anas* spp), 3) diving ducks (see above, *Aythya* spp), 4) individual species of waterfowl.

For these analyses, two linear models were developed and assessed separately by season (fall & spring), to determine the relationship between densities of Tundra Swans and those of other waterfowl. These models included class effects of year (1971- 2001), and marsh complex (BCNWA, LPWMU, LPCM, LPNWA, ILPB, & TPM) and continuous effects of Julian date, total density of individuals of species Y at Long Point, and density of Tundra Swans. The largest candidate model was one that had all the above main effects, whereas the null model included all the effects above except the Tundra Swan density effect.

Relationships between densities of Tundra Swans and other waterfowl: pond-scale.- Pond-level waterfowl count data were restricted to surveys done only at noon each day. This standardized survey times and ensured that only one survey each day was used in analyses. Data for each observation pond were analyzed separately. By doing this, differences in area/size among ponds were controlled for and counts became approximations of waterfowl densities. Response variables included in these analyses were numbers of: 1) waterfowl (Canada Geese, American Black Duck, American Wigeon, Green-winged Teal, Mallard, Northern Pintail (*Anas acuta*), Northern Shoveler (*Anas clypeata*), and Ring-necked Ducks), 2) ducks (all species above except Canada Geese), 3) dabbling ducks (*Anas* spp), and 4) individual species.

I predicted that numbers of waterfowl would decrease with increasing numbers of Tundra Swans because high densities of large bodied or potentially aggressive birds, such as swans, increases aggression between potential competitors (Huntingford and Turner 1987), which in turn could limit space or habitat available for other waterfowl on ponds (Nudds 1981). Two models were developed and included in the candidate set to assess this prediction. The largest model contained both Julian date and Tundra Swan numbers as main effects, while the null model contained only Julian date.

Waterfowl-Tundra Swan associations.- Chi-square analyses were used to determine if any waterfowl species was: 1) less (or more) likely to be close to a swan and 2) less (or more) likely to be close to active or inactive swans given their abundance on observation ponds. The observed values for these analyses were the actual counts of species closest to Tundra Swans recorded during daily sampling sessions (see Methods: *Waterfowl-Tundra Swan associations on ponds*). Expected values for each species were calculated

by multiplying the total number of all birds in a waterfowl-Tundra Swan sample by the percentage of each species that were on that pond; these percentages were obtained from pond-level waterfowl surveys that were done as close as possible to the time when species association samples were taken. To ensure independence in analyses, only one species association sample was used from each pond per day.

Species-specific heterogeneity chi-square analyses were done to determine if the individual chi-square analyses could be combined into one overall analysis (Zar 1996). A pooled analysis was not appropriate if this test was rejected ($P < 0.05$). Regardless of the significance of this test, results from a pooled analysis always were presented in tables to show the overall tendency in these data. In such cases, however, I based my conclusions on the percentage of the contributing individual chi-square analyses that had observed values that were greater than, equal to, and less than those expected; these numbers also were reported in tables.

Interactions between Tundra Swans and other waterfowl.- Daily aggression rates of pairs of interacting species (e.g., initiator-recipient: swan-swan, swan-mallard, mallard-swan, mallard-mallard, etc.) or groups interacting waterfowl (e.g., initiator-recipient: swan-swan (i.e., Tundra Swan-Tundra Swan), swan-geese (i.e., Tundra Swan-Canada Goose), goose-geese, goose-swan, swan-duck, duck-swan, duck-duck) were calculated by dividing the total number of interactions observed for each species pair or group by the total number of daily observation hours at each site. The group “duck” includes data for following species: ABDU, GADW, GWTE, MALL, NOPI, and RNDU. These rates were used as response variables to assess intensity of interference competition between Tundra Swans and other waterfowl. If Tundra Swans consistently viewed other

waterfowl as equal competitors, then rates of Tundra Swan initiated aggression toward other waterfowl (i.e., swan-species or swan-group aggression) should \geq than those initiated with conspecifics (swan-swan aggression). Data used in these analyses were pooled over years and ponds. Two candidate models were used to determine if aggression rates differed between pairs of selected interacting species and waterfowl groups. For each of these two sets of analyses, one model contained the “group” effect and the other simply was a true null or intercept model.

Feeding activity of co-occurring waterfowl on ponds.-To determine if there was any indirect evidence supporting exploitative competition or other negative effects between swans and other waterfowl, I compared time that all waterfowl spent feeding while on the same ponds during fall. Waterfowl feeding activity should decline during fall because they collectively deplete their food resources. However, if Tundra Swans were substantially reducing food available for other waterfowl then ducks and geese should spend less time feeding or show a more dramatic seasonal decline in feeding activity than did swans. Thus, three models were included in the candidate set to assess the strength of evidence for these predictions, which included effects of Species (ABDU, AMWI, CAGO, GADW, GWTE, MALL, NOPI, RNDU, TUSW) and Date. The largest model included effects of species and Julian date, while also including a species \times Julian date interaction. Another model contained the species and Julian date effects, while the null model only had the Date effect.

Waterfowl behaviour in relation to Tundra Swan proximity.-These analyses were done to determine if individuals of each species that were close to swans, regardless of swan activity, spent substantially more time vigilant than did conspecifics that were far

from swans. Specifically, this tests if waterfowl view Tundra Swans as a potential threat or source of physical harm. These “proximity” analyses also were done to assess if individuals close to swans generally spent less time feeding and more time in locomotion than did conspecifics far from swans, results that both indicate an energetic cost of being close to active/inactive swans. To evaluate these predictions, I developed and assessed two candidate models. The first was a model that contained effects of year, observation location (site), and Julian Date; these effects were not of interest, but were included because I wanted to account for their influence on duck behaviour and to increase model R^2 to provide more precise estimates of the effect of interest (i.e., the swan proximity effect). This first model also was included as a candidate set “null” model and allowed me to determine the strength of evidence for the swan proximity effect. The second model was the one of biological interest because it contained all the previous effects plus the swan proximity effect (ducks that were close to [$< 3\text{m}$] versus ducks that were far from [$> 30\text{m}$] swans).

Waterfowl behaviour in relation to Tundra Swan activity.- Negative effects between potential competitors should occur when species are active or involved in acquiring food resources (Connell 1983, Schoener 1983). The “proximity” analyses above do not take into consideration the activity of the swan that was closest to the “focal” waterfowl. If foraging activity of Tundra Swans has a large negative effect on behaviour of other waterfowl it should be most easily observed when these birds were close to each other. Therefore, these analyses assessed energetic costs to waterfowl by comparing time spent feeding, vigilant and in locomotion between individuals of each species that were close to active and inactive Tundra Swans. Data used in these analyses were restricted to include

only observations where waterfowl were close ($\leq 3\text{m}$) to swans. For these “activity” analyses, I predicted that waterfowl close to active swans, as compared to conspecifics near inactive swans, would spend less time feeding and more time in vigilance and locomotion. Further, waterfowl also may alter their feeding methods when foraging close to Tundra Swans (Bailey and Batt 1974). Specifically, birds may use shallow feeding methods (dabbling, surface straining) more often when foraging near feeding and active swans, as compared to those conspecifics near inactive swans. To test these predictions, again, two candidate models were developed and evaluated. The candidate set “null” model contained year, site, and Julian date; the second model also contained effects of year, site, and Julian date, but included a swan activity effect (i.e., ducks that were close to active or feeding swans versus ducks close to inactive or non-feeding swans). Because only two models are compared in the swan proximity (see above) and activity analyses I have provided 95% confidence intervals for parameter estimates and base my interpretation of differences on whether or not the effect sizes of interest fall within or outside of those calculated values.

Waterfowl behaviour in relation to Tundra Swan abundance.-Increased density of competitors increases the potential for interspecific interactions, which may in turn reduce time individuals spend feeding (Huntingford and Turner 1987). Thus, these analyses were done to evaluate the strength of evidence for my predictions that time waterfowl spent feeding would decrease, while time spent in locomotion would increase, with increasing abundance of Tundra Swans on each pond. There were two main effect models developed for this candidate set that included effects of Julian date, number of conspecifics, number of Tundra Swans, and number of waterfowl other than conspecifics

and Tundra Swans. One candidate contained all the main effects mentioned above, while the null model had all main effects except that of Tundra Swan numbers.

3.4. RESULTS

3.4.1. Relationships between densities of Tundra Swans and other waterfowl: wetland complex scale

None of the analyses showed substantial evidence to support negative relationships between densities of Tundra Swans and those of other waterfowl in major marsh complexes during fall or spring (Tables 3.1 and 3.2, respectively). In fact, the candidate model containing the Tundra Swan effect was ranked as the best model in only 1 (i.e., Mallard) of 13 analyses in fall data set (Table 3.1). Further, inspection of the slope and 95% confidence intervals for the relationship showed that there was no actual increase ($b_T = 0$) in densities of Mallards with increasing densities of Tundra Swans. However, several analyses in the spring data set showed relatively strong evidence ($^W AIC_c$: 0.74 – 1.0) for small, but positive increases in densities of all waterfowl, all ducks, all dabbling ducks (*Anas* spp.), American Black Ducks, American Wigeon, Green-winged Teal, and Mallards with increased densities of Tundra Swans (Table 3.2).

3.4.2. Relationships between densities of Tundra Swans and other waterfowl: pond scale

Analyses of waterfowl count data collected at individual ponds did not support a decrease in waterfowl abundances with increasing numbers of Tundra Swans at any of the observation ponds (Table 3.3). In the Bouck's Pond (BK) data set, the candidate model containing the Tundra Swan effect was ranked as the best model in 5 of 7 analyses, but these models all had relatively low weight of evidence in support of any

Table 3.1. Relationships between densities of waterfowl and Tundra Swans (*Cygnus columbianus*) in six major marsh complexes at Long Point, Ontario, during fall 1971, 1975, 1979, 1984, 1986, 1988, and 1991 – 2001. Under Model, Yr = year, D = Julian date, M = marsh complex (Big Creek National Wildlife Area, Crown Marsh, Long Point Company Marsh, Long Point National Wildlife Area, Inner Long Point Bay, and Turkey Point Marsh), Yt = total density of Y individuals counted over all marsh locations at Long Point, and T = density of Tundra Swans counted in marsh complexes. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^w AIC_c$). The slopes for the Tundra Swan effects (b_T) and the 95% confidence intervals ($\pm 95\%$ CI) are shown for each model containing that effect regardless of whether or not it was the best model.

Response / Y (#/km ²)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_T	95% CI
Waterfowl ^a	{Yr, D, M, Yt}	0.40	25	360	0.00	0.75		
	{Yr, D, M, Yt, T}	0.40	26	360	2.20	0.25	0.0068	0.0376
Ducks ^b	{Yr, D, M, Yt}	0.35	25	360	0.00	0.76		
	{Yr, D, M, Yt, T}	0.35	26	360	2.30	0.24	0.0052	0.0374
<i>Anas</i> spp ^c	{Yr, D, M, Yt}	0.60	25	360	0.00	0.65		
	{Yr, D, M, Yt, T}	0.60	26	360	1.20	0.35	0.0107	0.0203
<i>Aythya</i> spp ^d	{Yr, D, M, Yt}	0.16	25	360	0.00	0.76		
	{Yr, D, M, Yt, T}	0.16	26	360	2.30	0.24	-0.0031	0.0297

Table 3.1. Continued.

Response / Y (#/km ²)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_T	95% CI
CAGO	{Y _r , D, M, Y _t }	0.38	25	360	0.00	0.72		
	{Y _r , D, M, Y _t , T}	0.38	26	360	1.90	0.28	0.0018	0.0058
ABDU	{Y _r , D, M, Y _t }	0.57	25	348	0.00	0.54		
	{Y _r , D, M, Y _t , T}	0.58	26	348	0.30	0.46	0.0040	0.0054
AMWI	{Y _r , D, M, Y _t }	0.39	25	306	0.00	0.72		
	{Y _r , D, M, Y _t , T}	0.39	26	306	1.90	0.28	-0.0025	0.0069
GWTE	{Y _r , D, M, Y _t }	0.39	25	288	0.00	0.76		
	{Y _r , D, M, Y _t , T}	0.39	26	288	2.30	0.24	-0.0006	0.0041
MALL	{Y _r , D, M, Y _t , T}	0.60	26	360	0.00	0.51	0.0084	0.0110
	{Y _r , D, M, Y _t }	0.60	25	360	0.10	0.49		
CANV	{Y _r , D, M, Y _t }	0.19	25	360	0.00	0.61		
	{Y _r , D, M, Y _t , T}	0.20	26	360	0.90	0.39	-0.0107	0.0177
GRSC & LESC	{Y _r , D, M, Y _t }	0.09	25	342	0.00	0.74		
	{Y _r , D, M, Y _t , T}	0.09	26	342	2.10	0.26	-0.0040	0.0159
REDH	{Y _r , D, M, Y _t }	0.27	25	348	0.00	1.00		
	{Y _r , D, M, Y _t , T}	0.27	26	348	12.20	0.00	-0.0012	0.0072
RNDU	{Y _r , D, M, Y _t }	0.41	25	324	0.00	0.51		
	{Y _r , D, M, Y _t , T}	0.42	26	324	0.10	0.49	0.0042	0.0054

^a Combined number of CAGO, ABDU, AMWI, GWTE, MALL, CANV, GRSC/LESC, REDH, & RNDU.

^b Combined number of ABDU, AMWI, GWTE, MALL, CANV, GRSC/LSCP, REDH, & RNDU.

^c Combined number of ABDU, AMWI, GWTE, & MALL.

^d Combined number of CANV, GRSC/LESC, REDH, & RNDU.

Table 3.2. Relationships between densities of waterfowl and Tundra Swans (*Cygnus columbianus*) in six major marsh complexes at Long Point, Ontario, during spring 1971, 1975, 1979, 1984, 1986, 1988, and 1991 – 2002. Under Model, Yr = year, D = Julian date, M = marsh complex (Big Creek National Wildlife Area, Crown Marsh, Long Point Company Marsh, Long Point National Wildlife Area, Inner Long Point Bay, and Turkey Point Marsh), Yt = total density of Y individuals counted over all marsh locations at Long Point, and T = density of Tundra Swans counted in marsh complexes. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$). The slopes for the Tundra Swan effects (b_T) and the 95% confidence intervals ($\pm 95\% \text{ CI}$) are shown for each model containing that effect regardless of whether or not it was the best model.

Response / Y (#/km ²)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	b_T	95% CI
Waterfowl ^a	{Yr, D, M, Yt, T}	0.33	25	300	0.00	0.79	0.1041	0.0917
	{Yr, D, M, Yt}	0.32	24	300	2.60	0.21		
Ducks ^b	{Yr, D, M, Yt, T}	0.30	25	300	0.00	0.74	0.0960	0.0892
	{Yr, D, M, Yt}	0.28	24	300	2.10	0.26		
<i>Anas</i> spp ^c	{Yr, D, M, Yt, T}	0.58	25	300	0.00	1.00	0.0965	0.0292
	{Yr, D, M, Yt}	0.52	24	300	37.20	0.00		
<i>Aythya</i> spp ^d	{Yr, D, M, Yt}	0.28	24	300	0.00	0.75		
	{Yr, D, M, Yt, T}	0.28	25	300	2.20	0.25	-0.0168	0.0861

Table 3.2. Continued.

Response / Y (#/km ²)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_T	95% CI
CAGO	{Yr, D, M, Yt}	0.43	24	300	0.00	0.75		
	{Yr, D, M, Yt, T}	0.43	25	300	2.20	0.25	0.0046	0.0212
ABDU	{Yr, D, M, Yt, T}	0.45	25	300	0.00	1.00	0.0212	0.0092
	{Yr, D, M, Yt}	0.41	24	300	17.60	0.00		
AMWI	{Yr, D, M, Yt, T}	0.49	25	264	0.00	1.00	0.0166	0.0081
	{Yr, D, M, Yt}	0.46	24	264	13.30	0.00		
GWTE	{Yr, D, M, Yt, T}	0.39	25	192	0.00	0.74	0.0033	0.0030
	{Yr, D, M, Yt}	0.38	24	192	2.10	0.26		
MALL	{Yr, D, M, Yt, T}	0.50	25	300	0.00	1.00	0.0559	0.0199
	{Yr, D, M, Yt}	0.45	24	300	26.90	0.00		
CANV	{Yr, D, M, Yt}	0.29	24	288	0.00	0.76		
	{Yr, D, M, Yt, T}	0.29	25	288	2.30	0.24	-0.0046	0.0309
GRSC & LESC	{Yr, D, M, Yt}	0.27	24	270	0.00	0.77		
	{Yr, D, M, Yt, T}	0.27	25	270	2.40	0.23	0.0072	0.0470
REDH	{Yr, D, M, Yt}	0.23	24	270	0.00	0.68		
	{Yr, D, M, Yt, T}	0.24	25	270	1.50	0.32	-0.0175	0.0361
RNDU	{Yr, D, M, Yt}	0.27	24	252	0.00	0.76		
	{Yr, D, M, Yt, T}	0.27	25	252	2.30	0.24	0.0010	0.0066

^a Combined number of CAGO, ABDU, AMWI, GWTE, MALL, CANV, GRSC/LESC, REDH, & RNDU.

^b Combined number of ABDU, AMWI, GWTE, MALL, CANV, GRSC/LSCP, REDH, & RNDU.

^c Combined number of ABDU, AMWI, GWTE, & MALL.

^d Combined number of CANV, GRSC/LESC, REDH, & RNDU.

Table 3.3. Relationships between number of waterfowl and number of Tundra Swans (*Cygnus columbianus*) counted on spring and fall observation ponds at Long Point, Ontario. Data from the following locations were used in these analyses: Bouck's pond (BK: fall 1998), Little Rice Bay (LRB: fall 1998), Biosphere pond (BIO: spring 1999), Big Creek North Pond (BCNP: fall 1999 & 2000), Big Creek North Impoundment (NI: spring 2000). Under Model, D = Julian date and T = number of Tundra Swans. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$). Slope of the Tundra Swan effect (b_{Tuc}) and 95% confidence intervals ($\pm 95\% CI_{uc}$) reported are unconditional estimates calculated by accounting for model uncertainty.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	b_{Tuc}	$\pm 95\% CI_{uc}$
BK	Waterfowl ^a	{T}	0.23	3	8	0.00	0.71	3.37	5.59
		{D}	0.03	3	8	1.90	0.28		
		{D, T}	0.30	4	8	8.70	0.01		
	Ducks ^b	{T}	0.23	3	8	0.00	0.71	3.36	5.59
		{D}	0.03	3	8	1.90	0.28		
		{D, T}	0.30	4	8	8.60	0.01		
	<i>Anas</i> spp ^c	{D, T}	0.80	4	8	0.00	0.40	3.97	3.54
		{D}	0.32	3	8	0.60	0.30		
		{T}	0.33	3	8	0.60	0.30		

Table 3.3. Continued.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	$b_{\Gamma_{uc}}$	$\pm 95\% CI_{uc}$
ABDU		{T}	0.22	3	8	0.00	0.67	0.36	0.62
		{D}	0.05	3	8	1.50	0.32		
		{D, T}	0.32	4	8	8.20	0.01		
AMWI		{D, T}	0.87	4	8	0.00	0.50	0.12	0.07
		{T}	0.59	3	8	0.10	0.48		
		{D}	0.14	3	8	6.00	0.02		
GADW		{D}	0.33	3	8	0.00	0.54		
		{T}	0.24	3	8	1.00	0.33	0.30	0.41
		{D, T}	0.71	4	8	2.70	0.14		
GWTE		{D}	0.34	3	8	0.00	0.78		
		{T}	0.08	3	8	2.70	0.20	0.76	2.18
		{D, T}	0.51	4	8	7.00	0.02		
MALL		{T}	0.42	3	8	0.00	0.54	1.62	1.46
		{D, T}	0.79	4	8	1.30	0.28		
		{D}	0.22	3	8	2.30	0.17		
NOPI		{T}	0.53	3	8	0.00	0.52	0.48	0.33
		{D, T}	0.85	4	8	0.40	0.43		
		{D}	0.17	3	8	4.50	0.05		

Table 3.3. Continued.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_{Tuc}	$\pm 95\% CI_{uc}$
LRB	Waterfowl	{D}	0.11	3	17	0.00	0.47		
		{T}	0.09	3	17	0.40	0.39	0.12	0.21
		{D, T}	0.16	4	17	2.40	0.14		
	Ducks	{T}	0.09	3	17	0.00	0.57	0.12	0.19
		{D}	0.03	3	17	1.20	0.32		
		{D, T}	0.10	4	17	3.30	0.11		
	<i>Anas</i> spp	{T}	0.09	3	17	0.00	0.57	0.11	0.19
		{D}	0.03	3	17	1.10	0.33		
		{D, T}	0.10	4	17	3.30	0.11		
ABDU	{D}	0.01	3	17	0.00	0.47			
	{T}	0.01	3	17	0.10	0.44	< 0.01	0.03	
	{D, T}	0.03	4	17	3.30	0.09			
AMWI	{T}	0.01	3	17	0.00	0.47	0.01	0.03	
	{D}	0.00	3	17	0.10	0.45			
	{D, T}	0.01	4	17	3.50	0.08			
CAGO	{D}	0.15	3	17	0.00	0.70			
	{T}	< 0.01	3	17	2.80	0.17	< 0.01	0.10	
	{D, T}	0.16	4	17	3.50	0.12			
GWTE	{T}	0.19	3	17	0.00	0.73	0.12	0.13	
	{D}	0.02	3	17	3.30	0.14			
	{D, T}	0.19	4	17	3.40	0.13			

Table 3.3. Continued.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_{Tuc}	$\pm 95\% CI_{uc}$
MALL		{D}	0.05	3	17	0.00	0.48		
		{T}	0.02	3	17	0.40	0.39	-0.02	0.07
		{D, T}	0.09	4	17	2.70	0.12		
NOPI		{D}	0.11	3	17	0.00	0.64		
		{T}	0.01	3	17	1.90	0.25	< 0.01	0.01
		{D, T}	0.11	4	17	3.50	0.11		
BIO	Waterfowl	{T}	0.24	3	11	0.00	0.71	-0.07	0.09
		{D}	0.03	3	11	2.60	0.19		
		{D, T}	0.32	4	11	3.90	0.10		
Ducks		{T}	0.24	3	11	0.00	0.73	-0.07	0.08
		{D}	0.02	3	11	2.80	0.18		
		{D, T}	0.30	4	11	4.30	0.09		
<i>Anas</i> spp		{T}	0.24	3	11	0.00	0.73	-0.07	0.09
		{D}	0.02	3	11	2.80	0.18		
		{D, T}	0.30	4	11	4.30	0.09		
ABDU		{D}	0.14	3	11	0.00	0.51		
		{T}	0.11	3	11	0.30	0.44	-0.01	0.02
		{D, T}	0.20	4	11	4.30	0.06		
MALL		{D}	0.18	3	11	0.00	0.39		
		{T}	0.17	3	11	0.10	0.37	-0.03	0.03
		{D, T}	0.44	4	11	1.00	0.24		

Table 3.3. Continued.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_{Tuc}	$\pm 95\% CI_{uc}$
BCNP	Waterfowl	{T}	0.07	3	20	0.00	0.54	0.60	0.98
		{D}	0.01	3	20	1.20	0.29		
		{D, T}	0.11	4	20	2.30	0.17		
	Ducks	{T}	0.07	3	20	0.00	0.47	0.64	1.00
		{D}	0.02	3	20	0.90	0.30		
		{D, T}	0.15	4	20	1.40	0.23		
	<i>Anas</i> spp	{T}	0.07	3	20	0.00	0.51	0.64	1.00
		{D}	0.02	3	20	1.20	0.28		
		{D, T}	0.14	4	20	1.70	0.22		
ABDU	{T}	0.15	3	20	0.00	0.67	0.22	0.25	
	{D}	0.04	3	20	2.60	0.18			
	{D, T}	0.15	4	20	3.10	0.14			
AMWI	{T}	0.01	3	20	0.00	0.47	0.02	0.10	
	{D}	0.00	3	20	0.20	0.43			
	{D, T}	0.01	4	20	3.20	0.10			
CAGO	{D}	0.17	3	20	0.00	0.69			
	{D, T}	0.20	4	20	2.40	0.21	-0.05	0.19	
	{T}	< 0.01	3	20	3.70	0.11			
GADW	{T}	0.06	3	20	0.00	0.51	0.13	0.22	
	{D}	0.01	3	20	1.00	0.31			
	{D, T}	0.12	4	20	2.00	0.19			

Table 3.3. Continued.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_{Tuc}	$\pm 95\% CI_{uc}$
GWTE		{D}	0.02	3	20	0.00	0.49		
		{T}	< 0.01	3	20	0.40	0.40	< 0.01	0.06
		{D, T}	0.02	4	20	3.10	0.10		
MALL		{D}	0.08	3	20	0.00	0.45		
		{T}	0.03	3	20	0.90	0.28	0.31	0.60
		{D, T}	0.17	4	20	1.00	0.27		
BCNI	Waterfowl	{D}	0.37	3	8	0.00	0.80		
		{T}	0.09	3	8	2.80	0.20	- 0.25	0.72
		{D, T}	0.38	4	8	9.10	0.01		
Ducks		{D}	0.13	3	8	0.00	0.58		
		{T}	0.05	3	8	0.70	0.41	- 0.02	0.72
		{D, T}	0.14	4	8	9.20	0.01		
<i>Anas</i> spp		{D}	0.08	3	8	0.00	0.53		
		{T}	0.05	3	8	0.30	0.46	- 0.16	0.68
		{D, T}	0.10	4	8	9.20	0.01		
ABDU		{D}	0.26	3	8	0.00	0.76		
		{T}	0.01	3	8	2.40	0.23	- 0.01	0.13
		{D, T}	0.27	4	8	9.20	0.01		
AMWI		{D}	0.02	3	8	0.00	0.51		
		{T}	< 0.01	3	8	0.10	0.49	< 0.01	0.05
		{D, T}	0.02	4	8	9.30	0.00		

Table 3.3. Continued.

Site	Response (#)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_{Tuc}	$\pm 95\% CI_{uc}$
CAGO		{D}	0.54	3	8	0.00	0.93		
		{T}	0.08	3	8	5.50	0.06	-0.07	0.25
		{D, T}	0.54	4	8	9.30	0.01		
MALL		{T}	0.09	3	8	0.00	0.57	-0.10	0.30
		{D}	0.02	3	8	0.60	0.42		
		{D, T}	0.09	4	8	9.40	0.01		
NOPI		{D}	0.06	3	8	0.00	0.55	-0.03	0.26
		{T}	0.01	3	8	0.40	0.45		
		{D, T}	0.06	4	8	9.30	0.01		

^a Combined number of ABDU, AMWI, CAGO, GADW, GWTE, MALL, NOPI, & RNDU.

^b Combined number of ABDU, AMWI, GADW, GWTE, MALL, NOPI, & RNDU.

^c Combined number of ABDU, AMWI, GADW, GWTE, MALL, & NOPI.

kind of Tundra Swan effect ($^W\text{AIC}_c$: 0.40 – 0.73). Further, only two (*Anas* spp & American Wigeon) out of those five analyses had Tundra Swan effect (slope) estimates that were different than zero and in both of these cases the estimates were positive.

Data collected at the four remaining ponds also did not support a strong influence of Tundra Swan abundance on those of other waterfowl. The candidate model containing the Tundra Swan effect was the highest ranked model in 4 of 9, 3 of 5, 6 of 9, and 1 of 8 analyses of data collected at Little Rice Bay, Biosphere Pond, Big Creek North Pond, and Big Creek North Impoundment, respectively, but the strength of evidence was relatively weak that this model was actually the best one ($^W\text{AIC}_c$: 0.47 – 0.73 [LRB], 0.71 – 0.73 [BIO], 0.47 – 0.67 [BCNP], & 0.57 [BCNI]). Further, 95% confidence intervals about the Tundra Swan effect estimates included zero in each of these models, which showed that there was no relationship between numbers of Tundra Swans and those of other waterfowl on these ponds.

3.4.3. Waterfowl-Tundra Swan associations

All species-specific heterogeneity chi-square analyses showed that daily samples should not be pooled (Table 3.4). Given this, a large percentage of species-specific chi-square analyses showed that numbers of individuals observed as the closest bird to swans were either greater than or equal to the numbers expected given that species relative abundance on ponds. Based on this, no waterfowl species appeared to be strongly avoiding Tundra Swans, although there was some indication from the pooled chi-square analysis that Green-winged Teal and American Wigeon tended to “avoid” Tundra Swans.

The following analyses were restricted to the number of waterfowl counted only around active swans (Table 3.5). Pooled chi-square analyses were valid for American

Table 3.4. Number of each waterfowl species recorded as the closest individual to random Tundra Swans relative to the expected abundance of each waterfowl species present on observation ponds during fall at Long Point, Ontario.

Species	Chi-square ^a		Pooled Chi-square				% of samples (<i>N</i>)					
					Total	Direc						
	Π^2	<i>P</i> ^b	Π^2	<i>P</i> ^c	<i>N</i>	birds	# Obs	# Exp	-tion	> Exp	= Exp	< Exp
ABDU	316.443	***	12.555	***	25	1610	409	343.3	>	40%	40%	20%
AMWI	33.495	***	13.779	***	25	1610	26	53.0	<	4%	84%	12%
CAGO	541.613	***	3.431	NS	18	1610	173	150.3	=	39%	44%	17%
GADW	200.828	***	0.820	NS	25	1610	150	161.0	=	20%	60%	20%
GWTE	294.350	***	36.525	***	25	1610	126	214.5	<	16%	48%	36%
MALL	220.558	***	0.947	NS	25	1610	568	545.3	=	20%	64%	16%
NOPI	152.839	***	42.332	***	25	1610	48	19.4	>	20%	80%	0%
RNDU	3735.117	***	0.671	NS	8	465	77	84.5	=	25%	37%	38%

^aHomogeneity of samples was rejected ($P < 0.05$) for analyses of all species. The percentage (%) of samples (*N*) from the pooled analysis for each species shows the distribution of the individual Chi-square analyses where observed (Obs) values were <, =, & > those expected (Exp) given each species relative abundance on ponds.

^bDegrees of freedom (*df*) = 17 & 7 for CAGO & RNDU, respectively; *df* = 24 for the remaining species.

^c*df* = 1 for all analyses.

Table 3.5. Number of each active waterfowl species recorded as the closest individual to random active Tundra Swans relative to the expected abundance of each waterfowl species present on observation ponds during fall at Long Point, Ontario.

Heterogeneity												
Species	Chi-square ^a		Pooled Chi-square					% of samples (<i>N</i>)				
	Π^2	<i>P</i> ^b	Π^2	<i>P</i> ^c	<i>N</i>	birds	# Obs	# Exp	tion	> Exp	= Exp	< Exp
ABDU	31.441	NS	0.390	NS	21	200	31	34.6	=	10%	90%	0%
AMWI	27.384	NS	0.077	NS	21	200	2	2.4	=	5%	95%	0%
CAGO	563.351	***	2.279	NS	15	77	3	7.0	=	13%	80%	7%
GADW	31.103	NS	3.700	NS	21	200	21	13.8	=	10%	90%	0%
GWTE	42.150	**	28.429	***	21	200	7	41.2	<	10%	71%	19%
MALL	59.441	***	0.440	NS	21	200	60	55.1	=	19%	76%	5%
NOPI	0.960	NS	1.132	NS	21	200	1	2.8	=	0%	100%	0%
RNDU	3710.410	***	29.753	***	7	133	71	37.6	>	71%	29%	0%

^aHomogeneity of samples was rejected ($P < 0.05$) for analyses of CAGO, GWTE, MALL, and RNDU, but was not rejected ($P > 0.05$) for the remaining species. The percentage (%) of samples (*N*) from the pooled Chi-square analysis for each species is presented to show the distribution of the individual component Chi-square analyses where observed (Obs) values were less than, equal to, and greater than those expected (Exp) given each species relative abundance on ponds.

^bDegrees of freedom (*df*) = 14 & 6 for CAGO & RNDU, respectively; *df* = 20 for the remaining species.

^c*df* = 1 for all analyses.

Black Duck, American Wigeon, Gadwall, and Northern Pintail (Table 3.5), but interpretation of results for remaining species were done by assessing the percentages of individual chi-square analyses that showed observed counts that were greater than, equal to, or less than those expected given that species relative abundance on a pond. Given this, numbers of American Black Duck, Green-winged Teal, American Wigeon, Canada Geese, Gadwall, Mallard, and Northern Pintail in samples around active swans were similar to values expected based on each species relative abundance on ponds (i.e., they did not appear to be attracted to nor avoiding active swans). However, a large percentage of individual chi-square analyses (71%) showed that numbers of Ring-necked Ducks counted in samples around active swans were higher than those expected given their relative abundance on a pond (i.e., they appeared to be attracted to active swans).

The analyses of waterfowl-Tundra Swan associations that follow were done using data collected on birds that were counted only around inactive Tundra Swans. Individual chi-square analyses could not be pooled for any waterfowl species except Green-winged Teal (Table 3.6). Given this, waterfowl species did not appear to strongly avoid inactive Tundra Swans because an overwhelming percentage of individual chi-square analyses for each species showed numbers of waterfowl observed around such swans were higher than or equal to values expected given each species relative abundance on ponds. In fact, there was some indication that American Black Ducks may even be attracted to Tundra Swans because more than half of individual chi-square analyses showed greater than expected numbers of these ducks around inactive birds.

Table 3.6. Number of each inactive waterfowl species recorded as the closest individual to random inactive Tundra Swans relative to the expected abundance of each waterfowl species present on observation ponds during fall at Long Point, Ontario.

Species	Chi-square ^a		Pooled Chi-square				% of samples (N)					
					Total	Direc						
	Π^2	P^b	Π^2	P^c	N	birds	# Obs	# Exp	-tion	> Exp	= Exp	< Exp
ABDU	223.551	***	31.927	***	24	934	311	226.1	>	54%	46%	0%
AMWI	47.310	***	4.516	*	24	934	19	30.8	<	4%	92%	4%
CAGO	132.177	***	27.668	***	17	722	149	97.2	>	24%	65%	12%
GADW	224.882	***	18.382	***	24	934	60	103.7	<	17%	62%	21%
GWTE	21.350	NS	35.899	***	24	934	30	85.3	<	0%	87%	13%
MALL	92.646	***	0.197	NS	24	934	322	330.1	=	13%	66%	21%
NOPI	77.099	***	15.742	***	24	934	21	9.1	>	13%	87%	0%
RNDU	149.866	***	7.751	***	8	182	15	30.3	<	12%	75%	13%

^aHomogeneity of samples was rejected ($P < 0.05$) for analyses of all species except GWTE ($P > 0.05$). The percentage (%) of samples (N) from the pooled Chi-square analysis for each species is presented to show the distribution of the individual component Chi-square analyses where observed (Obs) values were less than, equal to, and greater than those expected (Exp) given each species relative abundance on ponds.

^bDegrees of freedom (df) = 16 & 7 for CAGO & RNDU, respectively; df = 23 for the remaining species.

^c df = 1 for all analyses.

3.4.4. Interactions between Tundra Swans and other waterfowl

Rates of aggression between Tundra Swans and other waterfowl were extremely low during migration at Long Point (Tables 3.7 and 3.8). Tundra Swans initiated interactions with ducks and Canada Geese at much lower rates than they did with conspecifics (Table 3.7). Further, Canada Geese only rarely initiated interactions with Tundra Swans ($CAGO - TUSW = 0.0028$ acts/hr), while ducks never initiated or won an altercation with a Tundra Swan (Table 3.7 and 3.8). Tundra Swans were successful in all interactions they initiated with other waterfowl. Individuals supplanted by swans always left the immediate area where the interaction occurred (usually a feeding site), but they never immediately left a pond.

3.4.5. Feeding activity of co-occurring waterfowl on ponds

There was a tendency for all waterfowl feeding activity to decrease by about 1% each day at all ponds during the staging season (Table 3.9). Given this, there was no support for feeding activity of ducks and geese to decrease at a faster rate than that of Tundra Swans over the staging season at any pond. All waterfowl species spent similar amounts of time feeding during the day at Big Creek North Impoundment (spring 2000), but evidence for differences in feeding activity among species was much stronger at other ponds. For example, Tundra Swans spent less time feeding than did each dabbling duck species at Bouck's Pond (fall 1998), Little Rice Bay (fall 1998), and Big Creek North Pond (fall 1999). During fall 1998, Tundra Swans and Ring-necked Ducks spent the same time feeding at Bouck's Pond, but Tundra Swans and Canada Geese spent an identical amount of time foraging on all ponds where they co-occurred. Overall, these

Table 3.7. Aggression rates (acts/observation hour) recorded between waterfowl groups during 302 diurnal hours of observation during spring and fall at Long Point, Ontario.

Under Model, G = Groups (initiator – recipient) of interacting waterfowl.

Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Interacting groups	Aggression rate estimates		
							Acts/hr	\pm SE	\pm 95% CI
{G}	0.15	9	560	0.00	1.00	TUSW-TUSW	0.5238	0.0476	0.0936
{Null}	0.00	2	560	78.40	0.00	TUSW-Goose	0.0248	0.0476	0.0936
						Goose-TUSW	0.0028	0.0476	0.0936
						Goose-Goose	0.0337	0.0476	0.0936
						Goose-Duck	0.0030	0.0476	0.0936
						TUSW-Duck	0.2098	0.0476	0.0936
						Duck-TUSW	—	—	—
						Duck-Goose	0.0025	0.0476	0.0936
						Duck-Duck	0.1356	0.0476	0.0936

Table 3.8. Aggression rates (acts/observation hour) recorded between waterfowl species during 302 diurnal hours of observation during spring and fall at Long Point, Ontario.

Under Model, S = species (initiator - recipient) of interacting waterfowl.

Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Interacting species	Aggression rate estimates		
							Acts/hr	\pm SE	\pm 95% CI
{S}	0.16	16	1104	0.00	1.00	TUSW-TUSW	0.5314	0.0341	0.0669
{Null}	0.00	2	1104	167.50	0.00	TUSW-CAGO	0.0251	0.0341	0.0669
						CAGO-CAGO	0.0342	0.0341	0.0669
						TUSW-MALL	0.1114	0.0341	0.0669
						MALL-MALL	0.0451	0.0341	0.0669
						MALL-ABDU	0.0173	0.0341	0.0669
						TUSW-ABDU	0.0558	0.0341	0.0669
						ABDU-ABDU	0.0052	0.0341	0.0669
						ABDU-MALL	0.0029	0.0341	0.0669
						TUSW-NOPI	0.0035	0.0341	0.0669
						NOPI-NOPI	—	—	—
						TUSW-GADW	—	—	—
						GADW-GADW	0.0112	0.0341	0.0669
						TUSW-GWTE	0.0031	0.0341	0.0669
						GWTE-GWTE	0.0172	0.0341	0.0669
						TUSW-RNDU	0.0304	0.0341	0.0669
						RNDU-RNDU	0.0032	0.0341	0.0669

Table 3.9. Comparisons of the percentage of time waterfowl spent feeding at observation ponds at Long Point, Ontario, during spring and fall. Data from the following locations were used in these analyses: Bouck’s pond (BK: fall 1998), Little Rice Bay (LRB: fall 1998), Big Creek North Pond (BCNP: fall 1999), BK (fall 1999), Big Creek North Impoundment (BCNI: spring 2000), & BCNP (fall 2000). Under Model, D = Julian date and S = Species effects (see methods for abbreviations). Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$). Date effect and least squares means ($\pm SE$) are shown for the percentage (%) of time spent feeding for each species; these values are unconditional estimates that take into account model selection uncertainty.

Site	Response (%)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	effect	Date						
									TUSW	ABDU	AMW	CAG	GADW	GWTE	MALL
BK 1998	Feed	{D S}	0.69	7	41	0.00	0.92	-1	23	39			57	54	26
		{S}	0.62	6	41	5.90	0.05	(< 1)	(3)	(3)			(3)	(3)	(4)
		{S×D}	0.74	11	41	6.90	0.03								
		{D}	0.05	3	41	35.40	0.00								

Table 3.9. Continued.

Site	Response (%)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	effect	Date	Least squares means (\pm SE) for % time spent feeding						
									TUSW	ABDU	AMWI	CAGO	GADW	GWTE	MALL	NOPI
LRB 1998	Feed	{S}	0.82	7	71	0.00	0.74	-1	10	46		3	62	28	75	
		{D S}	0.82	8	71	2.50	0.21	(1)	(3)	(3)		(3)	(3)	(3)	(4)	
		{S×D}	0.85	13	71	5.30	0.05									
		{D}	0.01	3	71	114.00	0.00									
BCNP1999	Feed	{S×D}	0.61	15	119	0.00	0.78	-1	6	16	15	2	22	42	26	
		{D S}	0.55	9	119	2.50	0.22	(1)	(5)	(2)	(4)	(3)	(3)	(4)	(2)	
		{S}	0.46	8	119	21.80	0.00									
		{D}	0.09	3	119	71.90	0.00									

Table 3.9. Continued.

Site	Response (%)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	effect	Date									
									Least squares means (\pm SE) for % time spent feeding									
									TUSW	ABDU	AMWI	CAGO	GADW	GWTE	MALL	NOPI	RNDU	
BCNP 2000	Feed	{S}	0.58	7	24	0.00	0.78	-1	8	11			< 1				23	
		{D S}	0.61	8	24	2.70	0.20	(1)	(3)	(5)			4				(4)	
		{D}	0.04	3	24	7.20	0.02											
		{S×D}	0.67	9	24	16.80	0.00											
BCNI 2000	Feed	{D}	0.05	3	22	0.00	0.97	-1	18	26			33				14	
		{S×D}	0.78	11	22	8.40	0.01	(1)	(5)	(8)			(8)				(6)	
		{S}	0.12	6	22	8.70	0.01											
		{D S}	0.17	7	22	11.70	0.00											

results showed that Tundra Swans did not feed substantially more than did other waterfowl species that were present on the same ponds. In fact, out of all waterfowl species present at observation ponds, Tundra Swans (and Canada Geese) consistently spent the lowest amount of time feeding during the day.

3.4.6. Waterfowl behaviour in relation to Tundra Swan proximity

With a few exceptions, Tundra Swan proximity did not have a large influence on the amount of time that ducks spent feeding on ponds during the day (Table 3.10). Analyses for American Wigeon, Canada Geese, Mallard, and Ring-necked ducks each showed some support for an effect of Tundra Swan proximity on time each spent feeding on ponds (i.e., {Y, S, D, P} was the “best” model in each of these analyses). In analyses for American Wigeon and Mallard, the model containing the swan proximity effect, {Y, S, D, P}, had relatively low model weight ($^W\text{AIC}_c = 0.54$ and 0.55 , respectively) and effect size estimates generated from these models were small relative to the variability in these data. As a result, no strong inferences could be made concerning the effect that swan proximity had on feeding activity of these species. However, analyses for variation in time spent feeding by Canada Geese and Ring-necked Ducks showed much stronger support for an effect of swan proximity ($^W\text{AIC}_c = 0.98$ and 1.00 , respectively). Given this, feeding activity of Canada Geese decreased by 58% ($[(19\% - 8\%) / 19\%] \times 100$) when individuals of this species were close to, as opposed to far from, Tundra Swans (both active and inactive). Conversely, Ring-necked Ducks that were close to swans spent, on average, 48% of the day feeding, whereas ducks far from swans only spent about 8% of diurnal hours doing so; this represented an 83% increase in diurnal feeding activity for this species.

Table 3.10. Comparisons of time (%) waterfowl spent in feed, locomotion, and vigilant activities when close (≤ 3 m) to and far (≥ 30 m) from active and inactive Tundra Swans (*Cygnus columbianus*) on observation ponds during fall at Long Point, Ontario. Under Model, Y = year, S = observation site, D = Julian date and P = swan proximity effects. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$).

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Estimates for % time spent in activity				
								Swan proximity		Effect	$\pm 95\%$	
								Close	Far		size ^a	\pm SE
ABDU	Feed	{Y, S, D}	0.48	7	106	10.00	0.57					
		{Y, S, D, P}	0.49	8	106	0.60	0.43	39	41	- 3	3	6
	Locomotion	{Y, S, D}	0.28	7	106	0.00	0.61					
		{Y, S, D, P}	0.29	8	106	0.90	0.39	16	18	- 1	2	3
	Vigilant	{Y, S, D, P}	0.16	8	106	0.00	0.60	1.7	2.3	- 0.6	0.5	1.0
		{Y, S, D}	0.14	7	106	0.80	0.40					

Table 3.10. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Estimates for % time spent in activity				
								Swan proximity		Effect size ^a	\pm SE	CI
								Close	Far			
AMWI	Feed	{Y, S, D, P}	0.29	8	39	0.00	0.54	26	40	-14	8	17
		{Y, S, D}	0.23	7	39	0.30	0.46					
	Locomotion	{Y, S, D}	0.30	7	39	0.00	0.55					
		{Y, S, D, P}	0.34	8	39	0.40	0.45	23	16	+7	5	10
	Vigilant	{Y, S, D, P}	0.27	8	39	0.00	0.72	-1.0	2.3	-3.3	1.4	2.9
		{Y, S, D}	0.17	7	39	1.90	0.28					
CAGO	Feed	{Y, S, D, P}	0.29	7	62	0.00	0.98	8	19	-11	4	8
		{Y, S, D}	0.16	6	62	7.90	0.02					
	Locomotion	{Y, S, D}	0.21	6	62	0.00	0.78					
		{Y, S, D, P}	0.21	7	62	2.50	0.22	19	19	+1	4	8
	Vigilant	{Y, S, D}	0.20	6	62	0.00	0.78					
		{Y, S, D, P}	0.20	7	62	2.50	0.22	2.3	2.7	-0.5	1.8	3.7

Table 3.10. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Estimates for % time spent in activity				
								Swan proximity		Effect size ^a	\pm SE	CI
								Close	Far			
GADW	Feed	{Y, S, D}	0.57	6	27	0.00	0.75					
		{Y, S, D, P}	0.59	7	27	2.20	0.25	7	16	-10	8	16
	Locomotion	{Y, S, D}	0.30	6	28	0.00	0.68					
		{Y, S, D, P}	0.35	7	28	1.50	0.32	13	8	+5	4	7
	Vigilant	{Y, S, D}	0.28	6	27	0.00	0.74					
		{Y, S, D, P}	0.32	7	27	2.10	0.26	2.8	0.6	+2.2	1.3	2.7
GWTE	Feed	{Y, S, D}	0.26	6	56	0.00	0.78					
		{Y, S, D, P}	0.26	7	56	2.50	0.22	54	55	-1	5	9
	Locomotion	{Y, S, D, P}	0.26	7	56	0.00	0.71	20	14	+6	3	6
		{Y, S, D}	0.20	6	56	1.80	0.29					
	Vigilant	{Y, S, D}	0.04	6	56	0.00	0.78					
		{Y, S, D, P}	0.04	7	56	2.50	0.22	0.1	0.1	0.0	0.1	0.2

Table 3.10. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Estimates for % time spent in activity				
								Swan proximity		Effect size ^a	\pm SE	CI
								Close	Far			
MALL	Feed	{Y, S, D, P}	0.27	8	119	0.00	0.55	38	44	-6	3	7
		{Y, S, D}	0.25	7	119	0.40	0.45					
	Locomotion	{Y, S, D, P}	0.31	8	119	0.00	0.90	25	18	+7	2	4
		{Y, S, D}	0.27	7	119	4.40	0.10					
	Vigilant	{Y, S, D, P}	0.30	8	119	0.00	0.86	1.4	2.3	-0.9	0.5	1.0
		{Y, S, D}	0.27	7	119	3.70	0.14					
NOPI	Feed	{Y, S, D}	0.38	5	24	0.00	0.72					
		{Y, S, D, P}	0.42	6	24	1.90	0.28	71	74	-2	6	13
	Locomotion	{Y, S, D, P}	0.28	6	24	0.00	0.82	14	6	+9	3	7
		{Y, S, D}	0.05	5	24	3.00	0.18					
	Vigilant	{Y, S, D}	0.45	5	24	0.00	0.61					
		{Y, S, D, P}	0.51	6	24	0.90	0.39	2.5	5.4	-2.9	1.6	3.2

Table 3.10. Continued.

Species Response (%) Model		R^2	K	N	ΔAIC_c	$W AIC_c$	Estimates for % time spent in activity				
							Swan proximity		Effect size ^a	\pm SE	CI
							Close	Far			
RNDU Feed	{Y, D, P}	0.75	5	17	0.00	1.00	48	8	+ 40	5	12
	{Y, D}	0.04	4	17	19.00	0.00					
Locomotion	{Y, D}	0.05	4	18	0.00	0.89					
	{Y, D, P}	0.06	5	18	4.10	0.11	18	18	0	3	7
Vigilant	{Y, D, P}	0.49	5	18	0.00	0.79	1.7	0.1	+ 1.6	0.6	1.2
	{Y, D}	0.24	4	18	2.60	0.21					

^aDifference between close and far estimates.

In general, Tundra Swan proximity did not have a large influence on time that most waterfowl species spent in locomotion (Table 3.10). Analyses of Green-winged Teal, Mallard, and Northern Pintail all showed some support for a Tundra Swan proximity effect because $\{Y, S, D, P\}$, was ranked higher than $\{Y, S, D\}$; model weights in each of these analyses were high ($^W AIC_c = 0.71, 90, \text{ and } 82$, respectively), suggesting relatively strong support for a swan proximity effect. Based on estimates from these models, Green-winged Teal, Mallard, and Northern Pintail that were close to swans spent only slightly more time in locomotion than did conspecifics that were far from swans (effect size $\pm 95\%$ CI: $7 \pm 6\%$, $7 \pm 4\%$, and $9 \pm 7\%$, respectively).

Time spent vigilant by Canada Geese, Gadwall, Green-winged Teal, and Northern Pintail was not greatly influenced by Tundra Swan proximity (Table 3.10). Model selection provided some support for a Tundra Swan proximity effect in analyses for American Black Ducks, American Wigeon, Mallards, and Ring-necked Ducks ($^W AIC_c = 0.60, 0.72, \text{ and } 0.86$, respectively), but effect sizes were small relative to variability in those data (effect size $\pm 95\%$ CI: $-0.6 \pm 1.0\%$, $-3.3 \pm 3.0\%$, $-0.9 \pm 1.0\%$, and $+1.6 \pm 1.2\%$, respectively). Thus, these estimates showed that Tundra Swans did not have a large influence on vigilance of these four duck species. Further, only Ring-necked Ducks showed a difference that was consistent with my prediction that ducks would be more vigilant when they were close to Tundra Swans; the other three species showed slightly higher vigilance when Tundra Swans were far away from them.

3.4.7. Waterfowl behaviour in relation to Tundra Swan activity

None of the waterfowl species observed in this study showed substantial evidence for reduced time spent feeding when they were near active, as opposed to when near inactive,

Tundra Swans (Table 3.11). Model selection for variation in time spent feeding by American Black Ducks, Mallard, and Ring-necked Ducks showed that models containing the Tundra Swan activity effect received overwhelming support over ones that did not contain such effects ($^W\text{AIC}_c = 1.00, 1.00, \text{ and } 0.91$, respectively). Estimates from those models showed that American Black Ducks, Mallards and Ring-necked ducks spent substantially more time feeding when they were close to active, as opposed to inactive, Tundra Swans. As a result, American Black Ducks, Mallards, and Ring-necked Ducks increased their feeding activity by 63%, 44%, and 49%, respectively, in response to swan feeding activity. Feeding activity of American Wigeon, Green-winged Teal, and Northern Pintail, however, was not greatly influenced by the foraging activities of the nearest Tundra Swan.

Most waterfowl species (American Black Duck, American Wigeon, Canada Geese, Green-winged Teal, and Northern Pintail) did not substantially alter time spent in locomotion in relation to Tundra Swan activity on ponds (Table 3.11). Mallards spent slightly more time (effect size \pm 95% CI: $-0.6 \pm 1.0\%$) in locomotion when near active, as compared to inactive, Tundra Swans, but the strength of evidence for such an effect was relatively weak ($^W\text{AIC}_c = 0.55$ and relatively large 95% CI) in this analysis. Ring-necked Ducks close to active, as compared to those near inactive, Tundra Swans spent $12 \pm 5\%$ more time in locomotion, which represented a 57% increase in this activity.

Contrary to my prediction, none of the duck species I regularly observed showed a large increase in vigilance when they were close to active, as opposed to inactive, Tundra Swans (Table 3.11). Canada Geese were the only waterfowl species that showed any, albeit relatively weak ($^W\text{AIC}_c = 0.54$), support for a swan activity effect on vigilance.

Table 3.11. Comparisons of time (%) waterfowl spent in feed, locomotion, and vigilant activities when close (≤ 3 m) to active and inactive Tundra Swans (*Cygnus columbianus*) on observation ponds during fall at Long Point, Ontario. Under Model, Y= year, S = observation site, D = Julian date and A = swan activity effects. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$).

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Estimates for % time spent in activity				
								Swan activity		Effect	$\pm 95\%$	
								Active	Inactive	size ^a	\pm SE	CI
ABDU	Feed	{Y, S, D, A}	0.62	7	73	0.00	1.00	61	23	+ 38	5	9
		{Y, S, D}	0.31	6	73	42.50	0.00					
	Locomotion	{Y, S, D}	0.44	6	73	0.00	0.59					
		{Y, S, D, A}	0.45	7	73	0.70	0.41	18	13	+ 4	2	4
	Vigilant	{Y, S, D}	0.27	6	73	0.00	0.65					
		{Y, S, D, A}	0.29	7	73	1.20	0.35	2.0	2.5	- 0.4	0.5	1.0

Table 3.11. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	Estimates for % time spent in activity				
								Swan activity		Effect size ^a	\pm SE	\pm 95% CI
								Active	Inactive			
AMWI	Feed	{Y, S, D}	0.45	6	15	0.00	0.97					
		{Y, S, D, A}	0.48	7	15	6.80	0.03	11	17	- 5	13	28
	Locomotion	{Y, S, D}	0.41	6	15	0.00	0.95					
		{Y, S, D, A}	0.46	7	15	6.10	0.05	37	22	+ 14	11	23
	Vigilant	{Y, S, D}	0.44	6	15	0.00	0.97					
		{Y, S, D, A}	0.47	7	15	6.70	0.03	< 0.1	0.4	- 0.4	0.4	0.9
CAGO	Feed	{Y, S, D}	0.55	6	37	0.00	0.74					
		{Y, S, D, A}	0.56	7	37	2.10	0.26	15	10	+ 5	2	5
	Locomotion	{Y, S, D}	0.28	6	37	0.00	0.62	30	18	+ 13	10	20
		{Y, S, D, A}	0.32	7	37	1.00	0.38					
	Vigilant	{Y, S, D, A}	0.44	7	37	0.00	0.54	11.0	< 0.1	+ 11.0	4.6	9.4
		{Y, S, D}	0.39	6	37	0.30	0.46					

Table 3.11. Continued.

		Estimates for % time spent in activity										
								Swan activity		Effect	± 95%	
Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	Active	Inactive	size ^a	± SE	CI
GWTE	Feed	{Y, S, D}	0.06	5	34	0.00	0.77					
		{Y, S, D, A}	0.08	6	34	2.40	0.23	65	71	- 6	8	16
	Locomotion	{Y, S, D}	0.16	5	34	0.00	0.81					
		{Y, S, D, A}	0.16	6	34	2.90	0.19	23	22	+ 2	5	11
	Vigilant	{Y, S, D}	0.14	5	34	0.00	0.82					
		{Y, S, D, A}	0.14	6	34	3.00	0.18	< 0.1	< 0.1	< 0.1	0.1	0.2
MALL	Feed	{Y, S, D, A}	0.45	8	82	0.00	1.00	57	32	+ 25	4	9
		{Y, S, D}	0.28	7	82	20.30	0.00					
	Locomotion	{Y, S, D, A}	0.50	8	82	0.00	0.55	28	22	+ 6	3	6
		{Y, S, D}	0.49	7	82	0.40	0.45					
	Vigilant	{Y, S, D}	0.31	7	82	0.00	0.75					
		{Y, S, D, A}	0.32	8	82	2.20	0.25	1.8	2.0	- 0.2	0.6	1.2

Table 3.11. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	Estimates for % time spent in activity					
								Swan activity		Effect	$\pm 95\%$		
								Active	Inactive	size ^a	\pm SE	CI	
NOPI	Feed	{Y, S, D}	0.32	5	18	0.00	0.91						
		{Y, S, D, A}	0.32	6	18	4.60	0.09	62	63	- 1	6	13	
	Locomotion	{Y, S, D}	0.43	5	18	0.00	0.84						
		{Y, S, D, A}	0.47	6	18	3.30	0.16	15	8	+ 8	6	12	
	Vigilant	{Y, S, D}	0.03	5	18	0.00	0.60						
		{Y, S, D, A}	0.22	6	18	0.80	0.40	0.6	0.1	+ 0.5	0.3	0.6	
RNDU	Feed	{Y, D, A}	0.81	5	12	0.00	0.91	64	44	+ 21	4	10	
		{Y, D}	0.53	4	12	4.60	0.09						
	Locomotion	{Y, D, A}	0.60	5	12	0.00	0.80	21	9	+ 12	2	5	
		{Y, D}	0.14	4	12	2.80	0.20						
	Vigilant	{Y, D}	0.99	4	12	0.00	0.96						
		{Y, D, A}	0.99	5	12	6.30	0.04	2.4	2.4	0.0	0.2	0.5	

^aDifference between active and inactive estimates.

Canada Geese spent 11.1% and $0.1 \pm 9.4\%$ of their time vigilant, when near active and inactive Tundra Swans, respectively. This substantial increase in vigilance supported my prediction that some waterfowl may view active and feeding Tundra Swans as a formidable threat and thus increase their awareness to avoid being attacked.

3.4.8. Waterfowl foraging behaviour in relation to Tundra Swan activity

There was no evidence to suggest that any waterfowl species considerably altered its feeding methodology in response to activity of the nearest Tundra Swan (Table 3.12). Frequency in use of surface (and subsurface) feeding methods used by dabbling ducks and Canada Geese were identical regardless of whether or not conspecifics were close to active or inactive Tundra Swans. Ring-necked Ducks did not alter use of their feeding methods in relation to activities of the nearest Tundra Swan.

3.4.9. Waterfowl behaviour in relation to Tundra Swan abundance

After controlling for abundances of conspecifics and other waterfowl, I found no substantial negative (or positive) effects of Tundra Swan abundance on time each waterfowl species spent feeding or in locomotion on observation ponds (Table 3.13). There was a weak, positive relationship between feeding activity of Green-winged Teal and Tundra Swan abundance at Bouck's Pond and Little Rice Bay (i.e., 2 of 2 observation ponds where they were present). The only evidence for a negative influence of Tundra Swan abundance on waterfowl activity was observed in time spent feeding by Mallards at Big Creek North Pond, but the strength of evidence for this effect was relatively weak ($^W\text{AIC}_c = 0.54$).

Table 3.12. Comparisons of relative (%) use of feeding methods employed by waterfowl foraging close (≤ 3 m) to active and inactive Tundra Swans (*Cygnus columbianus*) on observation ponds during fall at Long Point, Ontario. Under Model, Y = year, S = observation site, D = Julian date and A = swan activity effects. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$).

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Estimates for % of feed acts used					
								Swan activity		Effect	$\pm 95\%$		
								Active	Inactive	size ^a	\pm SE	CI	
ABDU	Surface	{Y, S, D}	0.50	6	42	0.00	0.74						
		{Y, S, D, A}	0.51	7	42	2.10	0.26	25	29	- 4	5	10	
	Subsurface	{Y, S, D}	0.59	6	42	0.00	0.76						
		{Y, S, D, A}	0.59	7	42	2.30	0.24	75	71	+ 4	5	10	

Table 3.12. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Estimates for % of feed acts used					
								Swan activity		Effect size ^a	$\pm 95\%$		
								Active	Inactive		$\pm SE$	CI	
GWTE	Surface	{Y, S, D}	0.52	4	28	0.00	0.71						
		{Y, S, D, A}	0.54	5	28	1.80	0.29	16	22	- 6	7	15	
	Subsurface	{Y, S, D}	0.52	4	28	0.00	0.71						
		{Y, S, D, A}	0.54	5	28	1.80	0.29	84	78	+ 6	7	15	
MALL	Surface	{Y, S, D}	0.35	7	44	0.00	0.51						
		{Y, S, D, A}	0.39	8	44	0.10	0.49	25	38	- 12	6	12	
	Subsurface	{Y, S, D}	0.35	7	44	0.00	0.51						
		{Y, S, D, A}	0.39	8	44	0.10	0.49	75	62	+ 12	6	12	

Table 3.12. Continued.

Species	Response (%)	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Estimates for % of feed acts used				
								Swan activity		Effect size ^a	\pm SE	CI
								Active	Inactive			
NOPI	Surface	{Y, S, D}	0.12	4	16	0.00	0.90					
		{Y, S, D, A}	0.13	5	16	4.30	0.10	5	8	- 3	6	13
	Subsurface	{Y, S, D}	0.12	4	16	0.00	0.90					
		{Y, S, D, A}	0.13	5	16	4.30	0.10	95	92	+ 3	6	13
RNDU	Surface	{Y, D}	0.07	4	12	0.00	0.51					
		{Y, D, A}	0.44	5	12	0.10	0.49	2	0	+ 2	1	2
	Subsurface	{Y, D}	0.14	4	12	0.00	0.95					
		{Y, D, A}	0.15	5	12	6.10	0.05	0	< 1	< - 1	2	5
	Dive	{Y, D}	0.17	4	12	0.00	0.91					
		{Y, D, A}	0.28	5	12	4.60	0.09	98	100	- 2	2	5

^aDifference between active and inactive estimates.

Table 3.13. Relationships between time spent feeding and in locomotion by waterfowl and abundance of Tundra Swans (*Cygnus columbianus*) on ponds during fall at Long Point, Ontario. Under Model, D = Julian date, C = number of conspecifics, W = number of waterfowl other than conspecifics and Tundra Swans, and T = number of Tundra Swans. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^w AIC_c$). Slopes for Tundra Swan effects (b_T) and 95% confidence intervals ($\pm 95\%$ CI) are shown for each model containing that effect regardless of whether or not it was the best model.

Site	Species Response (%)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_T	$\pm 95\%$ CI
BK (1998)	ABDU Feed	{D, W, C}	0.20	5	16	0.00	0.69		
		{D, W, C, T}	0.37	6	16	1.60	0.31	-0.15	0.15
	Locomotion	{D, C, W}	0.25	5	16	0.00	0.93		
		{D, C, W, T}	0.25	6	16	5.30	0.07	< 0.01	0.05
	GWTE Feed	{D, W, C, T}	0.35	6	16	0.00	0.54	0.18	0.16
		{D, W, C}	0.08	5	16	0.30	0.46		
Locomotion	{D, C, W}	0.15	5	16	0.00	0.90			
	{D, C, W, T}	0.20	6	16	4.40	0.10	-0.04	0.08	
MALL	Feed	{D, W, C}	0.41	5	16	0.00	0.82		
		{D, W, C, T}	0.48	6	16	3.10	0.18	-0.17	0.24
	Locomotion	{D, C, W}	0.41	5	16	0.00	0.82		
		{D, C, W, T}	0.48	6	16	3.10	0.18	-0.01	0.09

Table 3.13. Continued.

Site	Species Response (%)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_T	$\pm 95\% CI$
RNDU	Feed	{D, W, C}	0.08	5	8	0.00	1.00		
		{D, W, C, T}	0.34	6	8	53.40	0.00	7.26	11.35
	Locomotion	{D, C, W}	0.45	5	8	0.00	1.00		
		{D, C, W, T}	0.98	6	8	29.50	0.00	2.64	0.63
LRB (1998)	ABDU Feed	{D, W, C}	0.20	5	23	0.00	0.86		
		{D, W, C, T}	0.20	6	23	3.70	0.14	< 0.01	0.03
	Locomotion	{D, C, W, T}	0.29	6	23	0.00	0.51	0.02	0.02
		{D, C, W}	0.17	5	23	0.10	0.49		
CAGO	Feed	{D, W, C}	0.69	5	14	0.00	0.95		
		{D, B, C, T}	0.70	6	14	5.80	0.05	< 0.01	0.01
	Locomotion	{D, C, W}	0.49	5	14	0.00	0.87		
		{D, C, W, T}	0.58	6	14	3.80	0.13	0.03	0.05
GWTE	Feed	{D, W, C, T}	0.41	6	20	0.00	0.92	0.04	0.02
		{D, W, C}	0.09	5	20	4.80	0.08		
	Locomotion	{D, C, W}	0.09	5	20	0.00	0.89		
		{D, C, W, T}	0.09	6	20	4.20	0.11	< 0.01	0.02
MALL	Feed	{D, W, C}	0.18	5	23	0.00	0.86		
		{D, W, C, T}	0.18	6	23	3.60	0.14	< 0.01	0.02
	Locomotion	{D, C, W}	0.18	5	23	0.00	0.86		
		{D, C, W, T}	0.18	6	23	3.60	0.14	< 0.01	0.03

Table 3.13. Continued.

Site	Species Response (%)	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	b_T	$\pm 95\% CI$
NOPI	Feed	{D, W, C}	0.08	5	11	0.00	0.98		
		{D, W, C, T}	0.33	6	11	7.50	0.02	-0.02	0.03
	Locomotion	{D, C, W}	0.06	5	11	0.00	0.94		
		{D, C, W, T}	0.43	6	11	5.50	0.06	0.02	0.02
BCNP (1999)	ABDU Feed	{D, W, C}	0.35	5	27	0.00	0.84		
		{D, W, C, T}	0.35	6	27	3.30	0.16	< 0.01	0.03
	Locomotion	{D, C, W}	0.17	6	27	0.00	0.51	-0.03	0.03
		{D, C, W, T}	0.06	5	27	0.10	0.49		
CAGO	Feed	{D, W, C}	0.21	5	20	0.00	0.89		
		{D, W, C, T}	0.21	6	20	4.20	0.11	< 0.01	0.02
	Locomotion	{D, C, W}	0.04	5	20	0.00	0.79		
		{D, C, W, T}	0.11	6	20	2.70	0.21	-0.04	0.06
GADW	Feed	{D, W, C}	0.38	5	12	0.00	0.99		
		{D, W, C, T}	0.38	6	12	8.80	0.01	-0.01	0.14
	Locomotion	{D, C, W}	0.06	5	12	0.00	0.99		
		{D, C, W, T}	0.09	6	12	8.40	0.01	-0.02	0.08
MALL	Feed	{D, W, C, T}	0.35	6	28	0.00	0.52	-0.05	0.04
		{D, W, C}	0.26	5	28	0.20	0.48		
	Locomotion	{D, C, W, T}	0.35	6	28	0.00	0.52	0.02	0.03
		{D, C, W}	0.26	5	28	0.20	0.48		

3.5. DISCUSSION

3.5.1. Aggression and potential for competition between swans and other waterfowl

The increase in Tundra Swan populations in North America has raised the question of whether Tundra Swans adversely affect other ecologically similar waterfowl species, especially when concentrated at their major staging areas. Large birds, such as swans, often are assumed to be competitively superior to other co-occurring members of the waterfowl community (Oksanen et al. 1979, Conover and Kania 1994, Pöysä and Sorjonen 2000). Such size or dominance based competitive asymmetries are common among members of the same ecological guild and especially are prevalent during interference competition (Connell 1983, Schoener 1983, Persson 1985). Despite this, results of my study generally showed that aggressive behaviour, feeding activities, and increased abundance of Tundra Swans did not have a major negative influence on the abundance, associations, or behaviour of other staging waterfowl at Long Point, Ontario.

Interference competition, via interspecific aggression, could adversely influence waterfowl on breeding grounds because Tundra Swans (and other swans) commonly and aggressively defend territories and feeding ponds from heterospecifics (Oksanen et al. 1974, Ely et al. 1987, Burgess and Stickney 1994, Limpert et al. 1994). Staging Tundra Swans, however, rarely initiated aggressive interactions with other waterfowl. Further, Tundra Swans only used low intensity (threats & pecks) acts of aggression simply to displace other foraging waterfowl. Similar findings were reported between wintering Bewick's Swans (*Cygnus columbianus bewickii*) and field-feeding waterfowl (Reese 1990). Even though Tundra Swans displayed some interspecific aggression or

territoriality while feeding, my results further indicated that they did not perceive other waterfowl as strong or even equal competitors for food or space because they initiated interactions much more often with conspecifics than they did with any other waterfowl species. This result was not surprising because conspecifics do share more resource dimensions (e.g., macrohabitat preferences, feeding microhabitat preferences, forage species, food size, etc.) than do heterospecifics (MacArthur and Levins 1967). Despite relatively low prevalence of interspecific aggression between swans and ducks, potential still exists for interference competition to be an important factor for foraging swans and ducks. Interference may be most important when food is highly concentrated in wetlands and when dietary overlap between swans and ducks is relatively large. Intensive behavioural observations combined with detailed dietary and small-scale habitat use studies of foraging swans and waterfowl over a range of waterfowl densities in wetlands could provide better information on the potential for interference competition between swans and other waterfowl.

Several lines of indirect observational evidence argued against Tundra Swans having a strong or immediate exploitative effect on food resources potentially used by other waterfowl. First, interspecific comparisons of waterfowl feeding activity on ponds showed that Tundra Swans generally spent much less time feeding than did co-occurring duck species. I also found that feeding activity of geese and ducks, as compared to that of swans, did not decline more rapidly during fall. Rather, feeding activity of all species on ponds declined at about the same rate (approx. 1% day⁻¹), which at least suggested that food availability declined during fall (Chapter 2). Lastly, feeding activity of other waterfowl did not decline with increasing abundance of Tundra Swans on ponds.

Given these results, and combined with the heavy waterfowl use that observation ponds received before (approx. ≤ 1.5 months) Tundra Swan arrival (Chapter 2), I suggest that other waterfowl species actually may have reduced food available to Tundra Swans (see also Rees 1990). This may account for low diurnal feeding activity of swans on ponds and partly explain why these birds fed (ave. 67% of nocturnal hours, Badzinski, unpublished data) extensively at night in Inner Long Point Bay where food availability was much higher (Chapter 2). Low food availability in aquatic habitats may also explain the increased use of terrestrial habitats and the high prevalence of agricultural grains in diets of Tundra Swans during spring (Petrie et al. 2002). It remains to be determined, however, if widespread interspecific interference or exploitation competition occurs in nocturnal feeding areas used by Tundra Swans and ducks at Long Point. These findings were interesting because swans often are assumed to be superior competitors that adversely affect waterfowl and their habitats (Conover and Kania 1994, Petrie 1998, Pöysä and Sorjonen 2000).

Even though there was little evidence of competition and widespread interspecific territoriality in Tundra Swans, there was some behavioural evidence to suggest that other waterfowl “recognized” the physical capabilities and potential hazards of interacting with larger and more powerful swans. First, during three fall field seasons, a duck never was observed initiating an interaction with a Tundra Swan and only one instance was documented where Canada Geese initiated an interaction with a Tundra Swan. Even though some avoidance behaviour was observed, it was very subtle and occurred at an extremely small scale (i.e., between individual Tundra Swans and waterfowl). For example, analyses of waterfowl-Tundra Swan associations showed that waterfowl species

did not avoid active or inactive Tundra Swans. However, when swans and other waterfowl were feeding, individuals of most species stayed at least 1 meter or more away (see Appendix 1: Table A1.1) and almost always remained behind swans (personal observation). Presumably, waterfowl reduced their probability of being attacked by staying out of direct view or just out of necks reach from feeding swans (Bailey and Batt 1974). These subtle types of avoidance were not a substantial cost for most species because there was no widespread or substantially increased vigilance or locomotion nor did I find reduced time spent feeding by waterfowl that were close to swans or by those close to active (or feeding) swans. In fact, most waterfowl appeared to benefit from association or co-occurrence with Tundra Swans (see below).

3.5.2. Influence of swans on feeding waterfowl

Several of the more abundant species of waterfowl appeared to be positively influenced by feeding activities of Tundra Swans. American Black Ducks, Mallard, and Ring-necked Ducks that were close to active and feeding swans spent considerably more time feeding than did conspecifics that were close to inactive, non-feeding swans. Positive effects of swans on other waterfowl have been implied in several studies (Bailey and Batt 1974, Thomas 1982, Pöysä and Sorjonen 2000), but, to my knowledge, this is the first quantitative evidence suggestive of foraging enhancement or facilitation by swans (see Chapter 4). Even though I did not specifically quantify the possible effect of duck feeding activity on swans, there was no obvious trade-off in feeding time for vigilance or increased aggression toward ducks, which suggests that their foraging relations may be commensalistic in nature (Mathers and Montgomery 1996).

Swans possess some unique features that might enable them to inadvertently increase

food available to other waterfowl species. First, swans are large birds with extremely long necks. These morphological features allow partitioning of available feeding niche space among waterfowl community members, which theoretically reduces potential for interspecific competition (Lack 1971, Pöysä 1983a, Nudds 1992, Pöysä and Sorjonen 2000). However, long necks enable swans to easily reach aquatic plants that are not available (i.e., too deep) to relatively smaller, shorter necked, dabbling ducks (Pöysä and Sorjonen 2000). When swans feed on vegetative parts of plants in deep water they often either drop or dislodge vegetation from the bottom, which would allow ducks access to food that they normally cannot attain. Although uncommon in this study, others have reported that ducks pick floating vegetation off the water's surface around feeding swans (Sherwood 1960, Bailey and Batt 1974, Thomas 1982). Secondly, staging and wintering Tundra Swans commonly use a specialized feeding behaviour called "treadling" when feeding in shallow water (Earnst 1994, Limpert et al. 1994). To perform this activity, swans repeatedly thrust their large, powerful feet into the marsh substrate in order to uncover, breakup, or dislodge subterranean, carbohydrate storage structures (turions, tubers, & rhizomes) of aquatic plants that they subsequently eat (Limpert et al. 1994, Badzinski, unpublished data). By doing this, swans turnover and disturb the marsh substrate, which likely brings seeds, invertebrates, or plant tubers that once were buried deep in the substrate closer to the surface where ducks can reach them. This may be one interpretation for the increase in feeding activity and high prevalence of subsurface feeding methods used by many dabbling ducks when they were near feeding swans.

Treadling also creates large relatively deep craters in the marsh bottom (approximate dimensions: $\leq 1 \text{ m} \times 1 \text{ m} \times 0.5 \text{ m}$; personal observation), which may represent a novel

foraging microhabitat for dabbling, but especially diving ducks. For Ring-necked Ducks, which was the only species that appeared to be strongly attracted to feeding Tundra Swans, exploiting swan's foraging craters may be an energetically efficient way to find and obtain seeds and tubers and likely the only way that they could reach foods buried deeper than they normally probe with their bills into the substrate. The feeding enhancement effect around Tundra Swans was very pronounced in this species. For example, Ring-necked Ducks often rested in large rafts in the middle of ponds throughout the day, but when swans began feeding near or among them, numerous individuals would begin diving directly beneath them.

It has also been implied that Tundra Swans (and other swans) may alter the feeding methods used by other waterfowl (Bailey and Batt 1974, Thomas 1982). For example, Bailey and Batt (1974) noted dabbling ducks picking floating fragments of aquatic plants from the surface of the water around swans and diving ducks frequently diving underneath feeding swans. I also saw similar behaviours in waterfowl foraging with swans, but there was no substantial change in relative use of surface or subsurface feeding methods employed by individuals foraging near active or inactive Tundra Swans in this study (but see Chapter 4). Ducks that feed with their eyes below the water surface are less aware of their surroundings and incur a higher risk of predation or swan attack than those employing surface feeding methods (Pöysä 1987). Thus, the generally high prevalence of subsurface feeding observed in dabbling ducks in this study could be interpreted as additional evidence that waterfowl did not view feeding Tundra Swans as overly formidable threats to their well being. These results also were consistent with evidence that ducks are more likely to employ a risk-prone foraging strategy in response

to low food availability on ponds (Guillemain et al. 2000, see Chapter 2).

Besides their potential behavioural influences (e.g. aggression, interference) on waterfowl, large numbers of Tundra Swans also may reduce the habitat available for other species through spatial limitation (Zwarts 1976, Burger et al. 1979). I was unable to document any adverse impact of large numbers of Tundra Swans on densities of other staging waterfowl on individual ponds or in large wetland complexes at Long Point. Lack of evidence for spatial limitation at the scale of the wetland complex was not surprising because there were many different ponds available that species could redistribute to if densities of birds became too high at any given pond. This, at least generally, indicated that densities of Tundra Swans and other waterfowl were not consistently high enough to cause habitat saturation in these large wetland complexes (or individual ponds) during fall or spring (see also Pöysä 1984). On the contrary, some data from spring waterfowl surveys of large marsh complexes at Long Point showed a positive relationship between numbers of several common waterfowl species, including Mallard, American Black Duck, and American Wigeon, and Tundra Swans. This not only provided more evidence against negative or competitive associations between Tundra Swans and these common ducks, but also suggested that these species had similar spring migration chronologies (Petrie 1998) or consistently displayed heterospecific attraction (Stamps 1988, Elmberg et al. 1997).

Circumstantial evidence of food resource partitioning may provide another plausible explanation for lack of strong negative effects observed between Tundra Swans and other waterfowl, especially dabbling ducks. Not only does their large body size and long neck separate (although not entirely) swans from dabbling ducks in foraging microhabitat

(Pöysä 1983a, Pöysä and Sorjonen 2000), but they also appear to prefer different foods and possibly larger sized items during migration. At staging areas during fall, Tundra Swans will eat vegetative matter but prefer the high energy subterranean carbohydrate storage structures of aquatic plants (Limpert and Earnst 1994, Earnst 1994). These large birds also feed extensively on rhizomes and tubers of plants that often are much too large for most ducks to eat, including those of *Nuphar* spp, *Nymphaea* spp, *Sagittaria* spp, and *Scirpus* spp (Limpert and Earnst 1994, S. Badzinski, personal observation). Further, at Long Point during fall, Green-winged Teal, Mallard, and American Black Duck primarily consumed aquatic plant seeds and agricultural grains (e.g., aggregate dry mass in diets: 71%, 77%, & 89%, respectively) and Gadwall and American Wigeon overwhelmingly ate stems and leaves of aquatic plants (aggregate dry mass in diets: 91% & 97%, respectively) (Petrie 1998). With the exception of American Wigeon (aggregate tuber dry mass in diet: 9%), tubers, even the relatively small ones of very common plants (e.g., wild celery), were uncommon in dabbling ducks diets at Long Point (Petrie 1998).

It could be argued that Tundra Swans may be more likely to negatively influence diving ducks, namely Canvasback (*Aythya vallisineria*), Redhead (*Aythya americana*), Lesser Scaup (*Aythya affinis*), and Ring-necked Ducks (*Aythya collaris*), because these species often feed extensively on small tubers and rhizomes of aquatic plants (e.g., wild celery & sago pondweed tubers; Hohman 1985, Petrie 1998, Korschgen and Green 1988, Kantrud 1990). However, habitat separation due to mode and depth of feeding prevents extensive overlap of Tundra Swans and diving duck feeding niches and is analogous to ecological separation of dabbling and diving ducks (Lack 1968, Nudds 1990). Observations I made at Long Point also agree with habitat segregation of Tundra Swans

and *Aythya* spp. For example, during three consecutive fall field seasons in my study area, Tundra Swans always exploited very shallow (≤ 1 m deep), near-shore areas in Inner Long Point Bay that had extensive beds of *Sagittaria* spp early in the season and later would feed farther from shore in deeper water (approx. 1 m deep) where many submerged aquatic plants, including wild celery and sago pondweed occurred in higher densities (S. Badzinski, personal observation). Small numbers (≤ 500) of diving ducks rarely were observed feeding in shallow water with swans, but often tens of thousands could be seen (morning) or heard (night) feeding far off shore. Further, diving ducks potentially have access to all food in Inner Long Point Bay, but Tundra Swans only can effectively feed in areas with preferred food that is ≤ 1 meter deep. This suggests that there is low potential for Tundra Swans to substantially affect diving duck foods or feeding activity on a large scale at Long Point.

Potential for large-scale negative effects of Tundra Swans is higher for dabbling ducks and Ring-necked Ducks because they overlap more in habitat preferences and feeding microhabitats. Even though results of this study showed no short-term, negative effects on dabbling ducks, it does not imply that Tundra Swans cannot influence them in the longer-term, especially if their use of staging areas increases. For example, feeding activities of Tundra Swans positively influenced waterfowl likely by increasing access to foods (e.g., seeds and tubers) normally too deep for ducks to reach. In fact, this short-term benefit for ducks could turn into a longer-term problem. Feeding activities of Tundra Swan may provide ducks with an opportunity to deplete more of the seed and tuber bank in shallow wetlands than normally would be allowed in their absence. This type of exploitation can cause drastic changes in species composition or reductions in

food biomass in subsequent seasons (Jefferies et al. 1994, Lodge et al. 1998). Therefore, longer-term vegetation studies should be developed to better understand Tundra Swan-waterfowl interactions and the potential impacts on aquatic forage species at important waterfowl staging and wintering areas.

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CHAPTER 4. INFLUENCE OF TUNDRA SWANS ON FORAGING BEHAVIOUR OF AMERICAN BLACK DUCKS AND MALLARDS DURING FALL MIGRATION AT LONG POINT, LAKE ERIE

4.1. ABSTRACT

Foraging bout activities and feeding methods of American Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*) were documented in relation to proximity and activity of Tundra Swans (*Cygnus columbianus columbianus*). This was done to evaluate if Tundra Swan feeding activity affected time ducks spent feeding, vigilant, and in locomotion and if it influenced feeding methods used by ducks during foraging bouts. I also assessed if there were interspecific differences in foraging activity and feeding methods used by these two morphologically identical duck species. Feeding intensity of both duck species increased, but their vigilance decreased, in response to feeding activity of Tundra Swans. American Black Ducks and Mallards differed in their use of surface and subsurface feeding methods when foraging with inactive swans, but they used those feeding methods at the same frequency when foraging with feeding swans. Overall, Tundra Swans had a positive effect on duck feeding activity by increasing food availability through creation of novel foraging microhabitats that resulted from their destructive feeding activities. Despite occasional aggressive encounters between foraging ducks and swans, ducks showed reduced vigilance when swans were feeding. These results suggested that ducks did not view swans as major threats, but rather as a possible source of information on impending danger. Divergent patterns in use of feeding methods between American Black Ducks and Mallards when swans were

inactive, and their similarity when swans were active, suggested these species were partitioning resources on ponds.

4.2. INTRODUCTION

Foraging associations and interactions among animals often have been studied in context of competition over limited resources (Connell 1983, Schoener 1983, Keddy 1989). However, reports of positive associations and beneficial interactions, such as heterospecific attraction and feeding facilitation, are not uncommon among potential competitors in communities or mixed species foraging assemblages (Pöysä 1986a, Pöysä 1986b, Thompson et al. 1991, Mönkkönen et al. 1996, Elmberg et al. 1997, van der Wal et al. 2000, see Chapter 3). In mixed species feeding assemblages, presence, activities, and proximity of potential competitors cause changes in the foraging environment of each species or individual (Stephens and Krebs 1986). To cope with these changes, animals often alter their foraging behaviour by switching between habitats, forage patches, food items, and foraging methods (Brown 1988, Guillemain et al. 2000, Pöysä 1987, Pöysä 1989). The presence, abundance, or behaviour of potential competitors or predators also may affect feeding behaviour of individuals or species in foraging associations (Pöysä 1985, Pöysä 1987, Conover and Kania 1994).

Waterfowl have been the focus of numerous studies of community organization and interspecific foraging association and interaction (Nudds 1992). Waterfowl are ideal for investigation of interspecific foraging interactions because they are locally abundant, highly visible, often feed in mixed species flocks, overlap considerably in temporal and spatial use of feeding locations and food types, use several discrete feeding methods, and frequently change use of feeding methods (Thomas 1982, Pöysä 1986a, Pöysä 1986b,

Pöysä 1987, Elmberg et al. 1997). This group of birds also shows considerable variation in body size, neck length, and bill morphology (ecomorphology), all of which may affect their coexistence and interspecific foraging interactions in ecological and evolutionary time (Pöysä 1986b, Nudds 1992, Pöysä and Sorjonen 2000). Ecomorphological differences among species of ducks also influence feeding methods each use, thus the depth of water exploited, and food items consumed when they forage in mixed species assemblages (Eadie et al. 1979, Thomas 1982, Pöysä 1983a, Nudds and Bowlby 1984, Nummi 1993, Nudds et al. 1994, Nudds et al. 2000). Thus, differences in feeding methods may allow coexisting ducks to partition food resources (Pöysä 1983a, Pöysä et al. 1994, Nudds et al. 2000).

Swans are the largest waterfowl and thus differ from ducks by their larger body size and relatively long necks. It has been implied that these large aquatic birds may positively or negatively influence small-scale feeding activities or foraging environments of other co-occurring species of waterfowl (Oksanen et al. 1979, Bailey and Batt 1974, Thomas 1982, Conover and Kania 1994, Pöysä and Sorjonen 2000, Petrie et al. 2002), but there is little quantitative evidence in support of such contentions (see Chapter 3). Tundra Swans (*Cygnus columbianus columbianus*) spend more than half of their annual cycle between their arctic breeding grounds and mid-latitude wintering areas in North America, much of which is spent at a few major staging areas (Petrie et al. 2002, Petrie and Wilcox, unpublished data). While at staging areas, these birds congregate with numerous other species of waterfowl and spend considerable time feeding during the day and night at preferred foraging areas (Earnst 1994, Badzinski, unpublished data, see also

Chapter 3). As a result, potential exists for these birds to have large, possibly negative, effects on feeding activity and foraging methods used by other syntopic waterfowl.

Two of the most abundant ducks that co-occur and forage with Tundra Swans at eastern staging areas in North America are American Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*) (Petrie 1998). These two dabbling ducks are very close genetic relatives (Ankney et al. 1986, Avise et al. 1994) and are similar in overall morphology and body size (Hanson and Ankney 1994). Because of this, some researchers have suggested that American Black Ducks may simply be a melanistic morph of the Mallard (Ankney et al. 1986, Ankney and Dennis 1988, but see Hepp et al. 1988). American Black Ducks and Mallards also have the same bill and tongue morphologies (Bélanger et al. 1988), further suggesting that these species should show considerable overlap in feeding niche and behaviours (MacArthur and Levins 1967, Schoener 1974). Despite much debate and research over the evolutionary and population level relationships between American Black Ducks and Mallards (Ankney et al. 1986, Ankney et al. 1987, Merendino et al. 1993, Avise et al. 1994, Nudds et al. 1996), there has been surprisingly few comparative studies of finer scale foraging interactions between these species (Eadie et al. 1979) and none comparing how these two ecological equivalents behave in relation to feeding activities and proximity of larger potential competitors, such as Tundra Swans.

In this study, I used behavioural data to determine first if proximity and feeding activity of Tundra Swans influenced time foraging American Black Ducks and Mallards spent feeding, vigilant, and in locomotion. Second, I assessed whether the frequency of feeding methods used during foraging bouts by these two dabbling ducks differed in

relation to activity and proximity of swans. Finally, I determined if foraging American Black Ducks and Mallards displayed any large behavioural differences when swans were and were not feeding on relatively small ponds during fall migration.

4.3. METHODS

4.3.1. Study area

This study was conducted during fall 1999 and 2000 at Long Point, Ontario (80°24'W, 42°38'N). Long Point is a sand spit extending 35 km east from the southern shore of Ontario into Lake Erie (see Figure 1.1.). This peninsula facilitated the formation of 24,000 ha of emergent marsh and the Inner and Outer Long Point Bays, which are globally important waterfowl staging areas (see Petrie 1998). Wetlands of Long Point are a mixture of lacustrine and palustrine types (Cowardin et al. 1979) and support diverse stands of emergent, floating-leaved, and submerged aquatic macrophytes. Inner Long Point Bay has an area of approximately 280,000 ha, an average depth of about 2 m, and supports a diverse community of submerged aquatic macrophytes that cover over 90% of the embayment.

4.3.2. Behavioural observations

Observation locations.-During fall 1999 and 2000, behavioural observations of foraging American Black Ducks and Mallards were done at two ponds (North Pond and Causeway Pond) in the Big Creek National Wildlife Area (see Figure 1.1). These ponds were chosen because both were: 1) used by many Tundra Swans, American Black Ducks and Mallards, 2) had similar areas, water depths, emergent and submerged aquatic plant assemblages, and human disturbance regimes (see Chapter 2).

Definitions of waterfowl activities.- During behavioural observations, five general activities including aggression, maintenance, vigilance, feed, and locomotion originally were recorded for all waterfowl during foraging bouts. Aggression (intra- and inter-specific) included threat displays, pecks, chases, and fights directed at other individuals. Maintenance included sleep/rest (with head on back), preen, bathe, drink, scratch, and stretch. These two activities accounted for less than 1% of activities employed during foraging bouts, so were not included in analyses that follow. Maintenance activities were, however, used to determine the termination of a focal individual's foraging activity (see below). Vigilance was recorded when ducks were not moving and when they either displayed an extreme head-up posture by extending their head and neck straight up or when their head was up and the neck was in a relaxed, curved posture. Locomotion was recorded when ducks were swimming, but not feeding, on ponds. Feeding was separated into four specific acts ducks used to obtain aquatic foods: surface feeding, subsurface feeding, upending, and paddling. Surface feeding was categorized as ducks picking food from the surface or feeding with only the bill submerged under water. Ducks were deemed to have used a subsurface feeding method when feeding with their entire head or neck submerged under water. Upending was recorded when ducks fed below the water's surface to such an extent that their rear end deviated from its normal horizontal position. Paddling was a feeding method characterized by a rocking motion of a duck's body that resulted from pushing their feet into the marsh substrate to dislodge food items. Each of these specific feeding methods initially was recorded and later converted to a general category called "feeding" to calculate duck feeding intensities (see below).

Sampling methodology.-Observations were done using a spotting scope from

permanent blinds or vehicles situated > 100 m from ponds. Observations were done each day from either one half hour before sunrise until noon (morning) or from noon to one half hour after sunset (evening). The first observation period at a site was determined at random; subsequent observation periods at a site alternated between mornings and evenings so both time periods would be equally represented in analyses. The same two observers (1999 and 2000: SB and SM) did all behavioural observations throughout each season; other assistants simultaneously entered data into portable computers.

Focal individual sampling was used to document foraging behaviours and specific feeding acts of ducks (Altmann 1974). Behaviour of focal ducks was recorded every 15 seconds for 15 minutes, resulting in a total of 60 acts for each individual during an observation session. This sampling interval allowed ducks time to change activities of long duration and was short enough to document acts of relatively short duration, such as vigilant behaviours. Only foraging ducks were chosen as focal subjects and observations were stopped if these birds performed ≥ 10 consecutive non-foraging acts (mainly sleep & preen). Focal ducks also were selected based on their proximity to active and inactive Tundra Swans, which enabled them to be categorized as ducks that were: 1) close to (≤ 3 m) active swans (American Black Duck: $N = 49$, Mallard: $N = 58$), 2) close to inactive swans (American Black Duck: $N = 16$, Mallard: $N = 39$), and 3) far from (> 30 m) active swans (American Black Duck: $N = 23$, Mallard: $N = 29$), and 4) far from inactive swans (American Black Duck: $N = 52$, Mallard: $N = 77$). There was no established protocol for how many observations would be done each day because of uncertainty associated with finding ducks and swans that fit the activity and proximity criteria required for inclusion in this study. However, when data were collected for a bird that fit into one of the swan

proximity/activity categories, we tried to collect data for other individuals of that species in all remaining swan proximity/activity categories within hours of each other on the same pond. Focal ducks chosen for each distance-activity category always were located on different parts of ponds to minimize pseudoreplication within observation periods.

Behaviour of Tundra Swans closest to a focal duck also was monitored throughout an observation session. This was done to ensure that ducks were classified properly with respect to Tundra Swan distance and activity (i.e., treatments). In this study, active Tundra Swans were individuals that were feeding, involved in an aggressive interaction, or were searching for food (i.e., in locomotion), whereas inactive swans were those not involved in activities associated with feeding, such as sleep, preen, and other maintenance activities. Observation of a focal duck was terminated if the distance between it and the closest swan caused a change in the focal individual's classification (see above); the same applied if the closest swan's behavioural state changed (i.e., it became inactive by performing ≥ 10 consecutive non-foraging acts or active by performing ≥ 10 consecutive foraging acts). Activity state of the nearest swan to a duck was representative of what other swans on ponds were doing at the time of observation. This was possible because feeding activity of swans often was cyclical within a day.

4.4. STATISTICAL ANALYSES

4.4.1. Data restrictions, calculations, and transformations

Foraging bout activity data were converted to proportions by dividing the counts of each activity by the total number of observations for each focal individual during a daily observation session. Data were included in analyses only if an entire 15-minute

observation session had been completed on a given duck. Data on duck foraging methods (i.e., surface, subsurface, upend, and paddle) also were converted to proportions, but this was done by dividing the number of each feeding method recorded by the total number of feeding acts a focal duck employed during an observation session. Proportion data were not normally distributed so these values were arcsine square root transformed (Zar 1996); doing this improved the error residual distributions of these data but did not entirely normalize them (PROC UNIVARIATE; SAS Institute Inc., 1990). Statistical model selection was done using these transformed values, but percentages were reported in tables to allow easier and more meaningful interpretation of results. Nonparametric analyses were not used because parametric statistics are fairly robust to deviations from normality (Johnson 1995, Smith 1995, Stewart-Oaten 1995). Covariates also can be used in parametric models to obtain more precise estimates of effect sizes.

4.4.2. Model selection and parameter estimation

An information-theoretic approach was used to select the most parsimonious model from an a priori candidate set of models that best described the information contained within these data (see Burnham & Anderson 1998; Anderson et al. 2000). This approach to data analysis emphasizes the strength of evidence for a given model or effect and reduces bias in estimation of effect sizes and their precision, especially when it is combined with model averaging techniques (Burnham & Anderson 1998). Akaike's Information Criterion with correction for small sample size (AIC_c) was used to select the best model from an a priori candidate set of biologically meaningful models. Competing candidate models were ranked from lowest to highest AIC_c . Akaike differences (ΔAIC_c) were then calculated by subtracting the lowest AIC_c from every other one in the candidate

set; ΔAIC_c of zero indicates the “best” candidate model. Models with $\Delta AIC_c \leq 2.0$ were considered to have the most support for being the best model, while those with values much > 2.0 had progressively less support. Akaike or model weights ($^W AIC_c$) were calculated from ΔAIC_c and were normalized to sum to 1.0 (see Burnham & Anderson 1998). These values were considered the weight of evidence in favor of a given model being the best model in the candidate set. Whenever possible, model selection uncertainty was incorporated into estimation of treatment effects and their measures of precision (\pm SE) by reporting unconditional estimates (least-squares means \pm SE) calculated from $^W AIC_c$ in a model-averaging technique (see Burnham and Anderson 1988).

4.4.3. Specification of statistical models and effects

General Linear Models were designed using PROC MIXED (SAS Institute Inc. 1990) and model selection information criterion was obtained using the IC (METHOD = ML [maximum likelihood]) option in this procedure. Four candidate models were specified to assess variation in the percentage of time that foraging ducks spent in feed, vigilance, and locomotion activities and in the frequency in use of feeding methods employed during foraging bouts in relation to species and Tundra Swan activity and proximity. All models included class effects of year (Y) (1999 & 2000), observation location (L) (North Pond & South Pond), and continuous effect of Julian date (D); these effects were not ones of interest, but were included to account for their influence on the factors and interactions of interest and to aid in discerning the best statistical models. Further, because my main interest was in determining if duck behaviour depended on both the proximity (P) (close [≤ 3 m] & far [≥ 30 m]) and activity (A) (active/feeding & inactive/non-feeding) of

Tundra Swans, all models were constrained to include interactions between these two effects; one two-way interaction model included a duck species (S) (American Black Duck & Mallard) main effect and one did not, whereas the largest candidate model contained a species \times proximity \times activity effect. A candidate set null model, which included only effects of year, observation location, and Julian date, was included to assess the strength of evidence for models that included effects and interactions of interest. To further aid in assessing the strength of evidence for each candidate model, relevant model selection information, including R^2 (explained variation), K (number of model parameters), N (sample size), ΔAIC_c (change in AIC_c), & $^W AIC_c$ (AIC_c weight), were reported in tables.

4.5. RESULTS

4.5.1. Foraging activities

Model selection for variation in percentage of time spent feeding (i.e., feeding intensity) by American Black Ducks and Mallards showed most support ($^W AIC_c = 0.54$) for the model that contained no species effect and only the interaction between Tundra Swan proximity and activity ($\{Y, L, D, P, A, P \times A\}$) (Table 4.1). However, the second best model, $\{Y, L, D, S, P, A, P \times A\}$, also had relatively high support ($^W AIC_c = 0.40$) and it did contain the species main effect. Inspection of model averaged parameter estimates, however, showed that there was no overall species effect (American Black Duck > Mallard: $1 \pm 1\%$ difference not shown in Figure 4.1), but there was variation in the amount of time ducks spent feeding in relation to proximity and activity of Tundra Swans (Figure 4.1). First, regardless of swan activity, ducks generally spent more time feeding

Table 4.1. Model selection information for variation in percentage time spent in feed, vigilance, and locomotion activities for American Black Ducks (*Anas rubripes*) and Mallard (*Anas platyrhynchos*) during fall at Long Point, Ontario. Under Model, Y = year (1999 & 2000), L = location (Big Creek North Pond, Big Creek South Pond), D = Julian date, S = Species (American Black Duck & Mallard), P = Tundra Swan proximity (close & far), A = Tundra Swan activity (active & inactive). Model selection information includes, variation explained (R^2), number of model parameters (K), sample size (N), change in Akaike's Information Criterion corrected for small sample size (ΔAIC_c), and model weight ($^w\text{AIC}_c$).

Response	Model	R^2	K	N	ΔAIC_c	$^w\text{AIC}_c$
% Feed	{Y, L, D, P, A, P×A}	0.14	8	343	0.00	0.54
	{Y, L, D, S, P, A, P×A}	0.14	9	343	0.60	0.40
	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.15	12	343	4.20	0.07
	{Y, L, D}	0.06	5	343	22.80	0.00
% Vigilance	{Y, L, D, P, A, P×A}	0.30	8	343	0.00	0.44
	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.32	12	343	0.60	0.32
	{Y, L, D, S, P, A, P×A}	0.30	9	343	1.20	0.24
	{Y, L, D}	0.10	5	343	80.60	0.00
% Locomotion	{Y, L, D, S, P, A, P×A}	0.09	9	343	0.00	0.76
	{Y, L, D, P, A, P×A}	0.07	8	343	3.40	0.14
	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.09	12	343	4.20	0.09
	{Y, L, D}	0.03	5	343	11.90	0.00

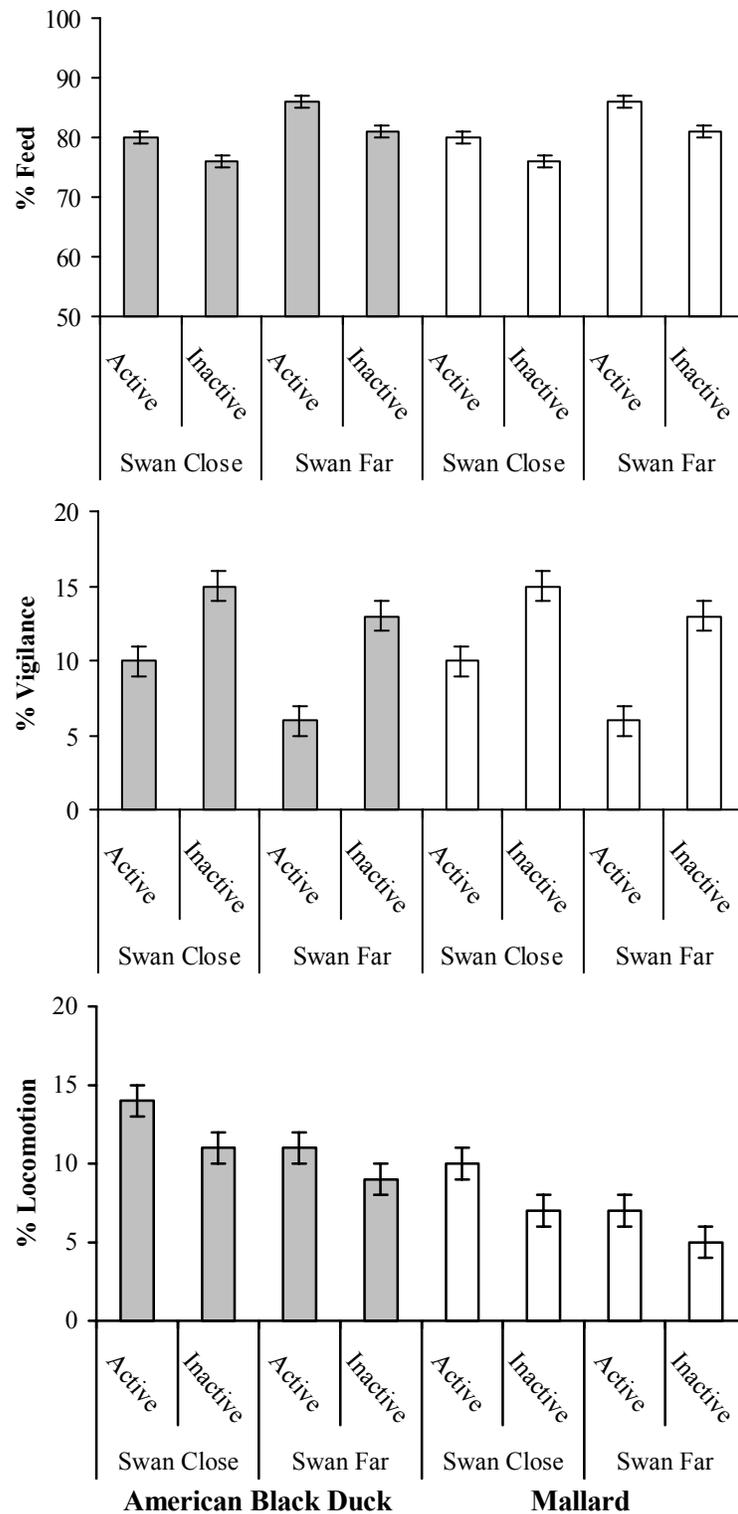


Figure 4.1. Percentage of time spent in feeding, vigilance, and locomotion activities by foraging American Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*) in relation to Tundra Swan (*Cygnus columbianus*) proximity and activity.

when they were far from, as opposed to close to, swans. Secondly, there also was an overall swan activity effect on duck feeding intensity; ducks generally spent more time feeding when Tundra Swans were active on ponds. Ducks that were far from active swans spent 6% more time feeding than did those that were close to active swans. However, because of the overall Tundra Swan proximity effect, the most appropriate assessment of the influence of Tundra Swan activity on duck feeding intensity should control for swan proximity. Thus, when ducks were close to swans their feeding intensity increased from $76 \pm 1\%$ to $80 \pm 1\%$ when swans inactive and active, respectively; this represented a 5% increase (i.e., % change = $([80\% - 76\%] / 80\%)$) in duck feeding intensity. Further, when ducks were far from swans their time spent feeding increased from $81 \pm 1\%$ to $86 \pm 1\%$, which was a 6% increase in feeding intensity.

Model selection for time ducks spent vigilant during foraging bouts resulted in the three candidate models of interest having $\Delta AIC_c < 2.0$ (Table 4.1). The best model, however, was one that included only an interaction between Tundra Swan proximity and activity ($\{Y, L, D, P, A, P \times A\}$). Likelihood of model fit for this model was about 1.4 and 1.8 times greater than that of the second and third ranked models, respectively. Model averaged estimates of time spent vigilant during foraging bouts showed the same pattern of among group differences for both species (Mallard > American Black Duck: $1 \pm 1\%$ difference not shown in Figure 4.1). Taking Tundra Swan proximity into consideration, foraging ducks were less vigilant when Tundra Swans were active and feeding. More specifically, vigilance of ducks close to swans decreased from $15 \pm 1\%$ to $10 \pm 1\%$ when swans were inactive and active, respectively; this was a 33% decrease in vigilance activity of foraging ducks. Vigilance of ducks far from feeding swans was $7 \pm 1\%$ lower

than that of individuals far from inactive Tundra Swans, which represented a 54% decrease in vigilance of foraging ducks in response to Tundra Swans feeding activity. Further, ducks foraging close to active swans spent more time ($4 \pm 1\%$) vigilant than did those that were far from feeding swans.

The model that best described variation in time spent in locomotion by foraging ducks was one that included a species main effect and an interaction between Tundra Swan proximity and activity ($^W\text{AIC}_c = 0.76$, {Y, L, D, S, P, A, P×A}) (Table 4.1). Based on this model, American Black Ducks generally spent $4 \pm 1\%$ more time in locomotion than did Mallards, but behaviour of individuals of each of these species did not differ relative to proximity and activity of Tundra Swans (Figure 4.1). Among American Black Ducks and Mallards, individuals close to active swans spent about $3 \pm 1\%$ more time in locomotion than did conspecifics that were close to inactive swans and also those that were far from Tundra Swans (Figure 4.1). This absolute difference of approximately 3% actually represented a 21% and 30% increase in locomotion for American Black Ducks and Mallards, respectively, that were foraging close to feeding Tundra Swans.

4.5.2. Feeding methods

The candidate model containing the species × proximity × activity effect was selected as the one best describing variation in frequency of surface-feeding methods employed by foraging ducks (Table 4.2). In addition, the second ranked model ({Y, L, D, S, P, A, P×A}, $^W\text{AIC}_c = 0.38$) also contained the species effect, showing that there was relatively strong evidence supporting interspecific differences in use of surface-feeding methods. Least-squares means from the best model showed American Black Ducks that were close to active or inactive Tundra Swans did not differ in their use of surface-feeding acts, but

Table 4.2. Model selection information for variation in percentage of surface, subsurface, upend, and paddle acts employed during feeding bouts by American Black Ducks (*Anas rubripes*) and Mallard (*Anas platyrhynchos*) during fall at Long Point, Ontario. Under Model, Y = year (1999 & 2000), L = location (Big Creek North Pond, Big Creek South Pond), D = Julian date, S = Species (American Black Duck & Mallard), P = Tundra Swan proximity (close & far), A = Tundra Swan activity (active & inactive). Model selection information includes, variation explained (R^2), number of model parameters (K), sample size (N), change in Akaike's Information Criterion corrected for small sample size (ΔAIC_c), and model weight ($^W AIC_c$).

Response	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$
% Surface	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.32	12	343	0.00	0.59
	{Y, L, D, S, P, A, P×A}	0.31	9	343	0.90	0.38
	{Y, L, D, P, A, P×A}	0.29	8	343	5.60	0.04
	{Y, L, D}	0.13	5	343	70.30	0.00
% Subsurface	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.21	12	343	0.00	0.97
	{Y, L, D, S, P, A, P×A}	0.17	9	343	7.80	0.02
	{Y, L, D, P, A, P×A}	0.17	8	343	8.70	0.01
	{Y, L, D}	0.07	5	343	41.70	0.00
% Upend	{Y, L, D, P, A, P×A}	0.14	8	343	0.00	0.63
	{Y, L, D, S, P, A, P×A}	0.14	9	343	1.80	0.26
	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.15	12	343	3.50	0.11
	{Y, L, D}	0.09	5	343	12.20	0.00

Table 4.2. Continued.

Response	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$
% Paddle	{Y, L, D, S, P, A, P×A}	0.21	9	343	0.00	0.53
	{Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}	0.22	12	343	1.30	0.28
	{Y, L, D, P, A, P×A}	0.20	8	343	2.00	0.19
	{Y, L, D}	0.03	5	343	60.60	0.00

American Black Ducks that were far from active, as opposed to inactive, swans showed a 63% decrease in use of surface-feeding (Figure 4.2). Mallards, however, increased surface feeding by 37% when they were foraging close to active and feeding Tundra Swans. Further, an interspecific comparison of individuals in the same proximity groups, when swans were inactive, should reflect use of surface-feeding methods employed under “normal” conditions on ponds. This comparison showed that American Black Ducks consistently used surface-feeding methods more than did Mallards when foraging close ($61 \pm 8\%$ vs. $32 \pm 8\%$, respectively) to and far ($40 \pm 5\%$ vs. $26 \pm 4\%$, respectively) from inactive swans. However, comparisons between these species, in which swan proximity was controlled, showed that there were no interspecific differences in use of surface-feeding methods.

The candidate model that contained a species \times proximity \times activity effect best described variation in the frequency of subsurface-feeding by American Black Ducks and Mallards during foraging bouts ($^W AIC_c = 0.97$, {Y, L, D, S, P, A, S \times P, S \times A, P \times A, S \times P \times A}) (Table 4.2). Both species altered their use of subsurface-feeding in relation to Tundra Swans’ activity state, but these differences also depended on the proximity of individuals of each species to swans (Figure 4.2). When American Black Ducks were close to swans, individuals used subsurface feeding at the same frequency when swans were active or inactive, but increased use of this feeding method by 35% when they were foraging far from feeding, as opposed to inactive and non-feeding, swans. Mallards, however, showed the exact opposite pattern. That being, individuals close to swans decreased subsurface-feeding by 48% in response to feeding activities of Tundra Swans,

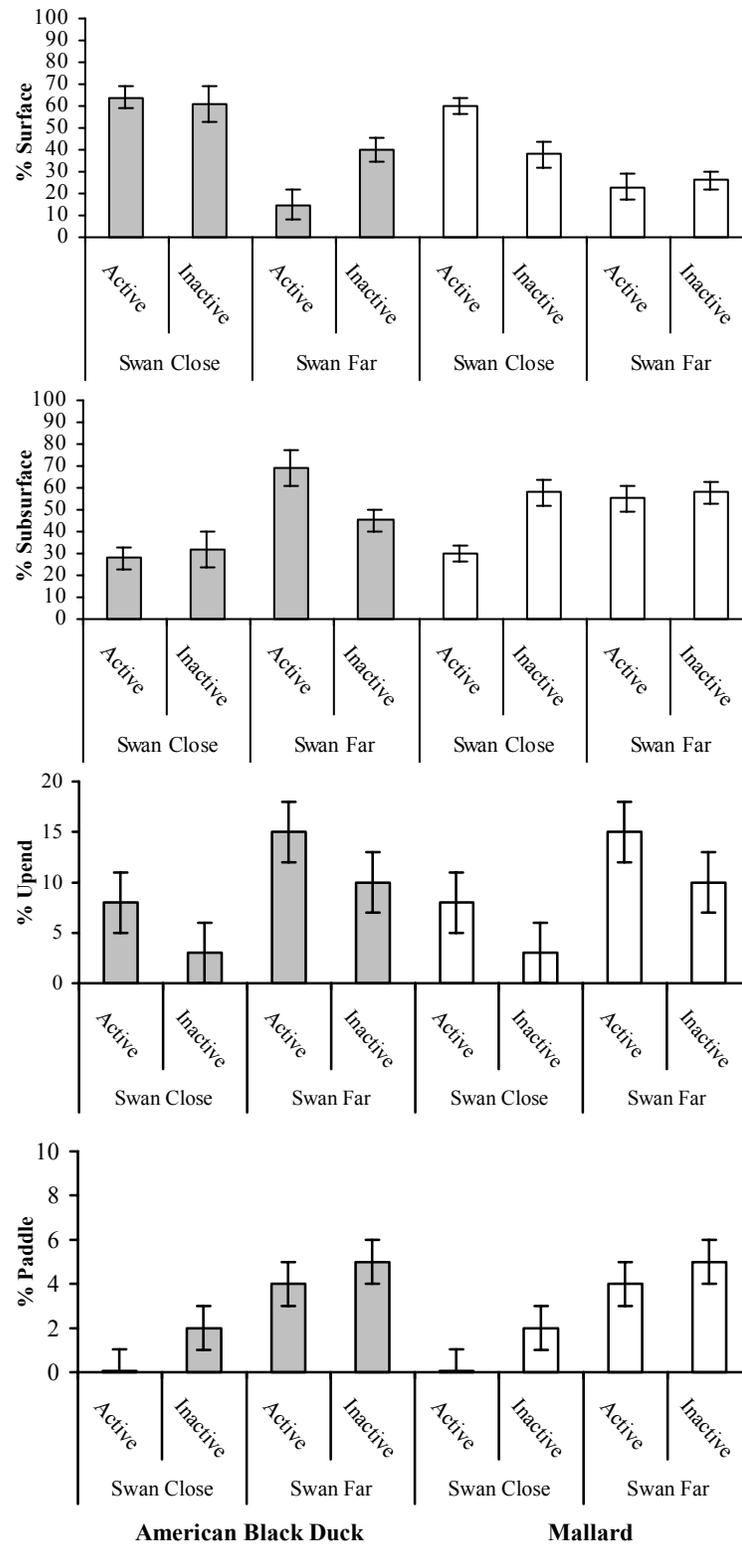


Figure 4.2. Frequency (% of feed acts) that foraging American Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*) used surface-, subsurface-, upend, and paddle feeding methods in relation to Tundra Swan (*Cygnus columbianus*) proximity and activity.

whereas Mallards that were far from swans showed no discernable change in use of this feeding method when swans were active or inactive on ponds. Contrary to the pattern observed for surface-feeding under “normal” conditions, Mallards used subsurface-feeding methods more than did American Black Ducks both when feeding close ($58 \pm 6\%$ vs. $32 \pm 8\%$, respectively) to and far ($58 \pm 5\%$ vs. $45 \pm 5\%$, respectively) from inactive swans. However, a comparison of subsurface-feeding by ducks foraging in a “swan-altered environment” showed that there were no interspecific differences when ducks were close to swans, but that use of this feeding method did differ slightly between species when they were far from swans. Specifically, American Black Ducks used subsurface-feeding acts more frequently than did Mallards ($69 \pm 8\%$ vs. $55 \pm 6\%$ of acts, respectively) when feeding far from active Tundra Swans.

Variation in frequency of upend acts used by foraging ducks was best described by $\{Y, L, D, P, A, P \times A\}$ (Table 4.2.). Likelihood of model fit for this model was 2.7 times that of the second best model, $\{Y, L, D, S, P, A, P \times A\}$; even though there was some support for an overall species effect, model averaged parameter estimates showed that it was negligible (American Black Duck > Mallard: $1 \pm 2\%$ not shown in Figure 4.2). Further, there was substantial variability about the model averaged least-squares mean estimates generated from this analysis, which precludes making strong inferences from these data concerning frequency of upending during foraging bouts. Given this, Tundra Swan activity did not appear to strongly influence duck-use of upending during foraging bouts, especially when considering only individuals that were the same distance from swans (Figure 4.2). There was, however, a general tendency for foraging ducks to upend more frequently when swans were active, as compared to when they were inactive. But,

there was more support for an overall proximity effect, suggesting that ducks upended slightly more when they were foraging far from, as opposed to close to, active or inactive Tundra Swans.

The three candidate models specified to investigate variation in use of paddling during duck foraging bouts all had $\Delta AIC_c \leq 2.0$, but the highest ranked model, {Y, L, D, S, P, A, P×A}, had 1.9 times more weight of evidence in favor of it being the best model as compared to the second ranked model, {Y, L, D, S, P, A, S×P, S×A, P×A, S×P×A}) (Table 4.2). Model averaged parameter estimates for the species main effect was negligible (Mallards > American Black Ducks: $< 1 \pm 1\%$ not shown in Figure 4.2), showing that American Black Ducks and Mallards did not differ greatly in their use of paddling during foraging bouts (Figure 4.2). Because paddling was a feeding method that was used relatively infrequently by ducks, some of the very small differences presented in Figure 4.2 warrant mention. Most noticeably, foraging ducks close to active swans were rarely observed paddling ($0.3 \pm 1\%$), whereas those close to inactive swans ($2 \pm 1\%$) and those far from active ($4 \pm 1\%$) or inactive swans ($5 \pm 1\%$) did so more frequently while foraging. Secondly, there was some indication that when swans were feeding, ducks paddled less than they did when swans were inactive on ponds; this small $2 \pm 1\%$ difference represented about a 50% decrease in use of paddling. Finally, ducks foraging close to swans tended to use paddling less frequently than did ducks that were far from active or inactive swans; again this small $4 \pm 1\%$ difference represented an 80% change in frequency of use of this feeding method.

4.6. DISCUSSION

4.6.1. Duck foraging activities

Tundra Swan feeding activity did not negatively affect foraging intensity of American Black Ducks or Mallards and both species showed similar responses to Tundra Swan foraging activity. These findings contradicted the hypothesis that Tundra Swans have a large negative effect on feeding activity of other syntopic waterfowl (Petrie et al. 2002, see Chapter 3) and further suggested that swan behaviour, at least in the short-term, had no measurable adverse effect on waterfowl (see Chapters 2 and 3, see also Pöysä and Sorjonen 2000). Notably, as previously postulated by Bailey and Batt (1974), Thomas (1982) and Pöysä and Sorjonen (2000), foraging activities of swans had a slight positive influence on duck feeding intensity (see Chapter 3). For example, foraging intensity of ducks increased by about 5% when swans were feeding, as compared to when they were not feeding. Increased feeding intensity of dabbling ducks when swans were active and feeding qualifies as evidence for interspecific feeding facilitation (see also Pöysä 1986a, Pöysä 1986b, Thompson et al. 1991, Mönkkönen et al. 1996, Elmberg et al. 1997, van der Wal et al. 2000, see Chapter 3). Facilitation of duck feeding activity could result if foraging swans increased food availability by creation of a novel feeding microhabitat (Bailey and Batt 1974, Thomas 1982, see Chapter 3).

Tundra Swans are well suited for modifying foraging behaviors and microhabitats of ducks. First, because swans are large birds with extremely long necks, they are able to feed at greater depths and dislodge foods that relatively smaller waterfowl, such as dabbling ducks, cannot normally obtain (Sherwood 1960, Thomas 1982, Pöysä and Sorjonen 2000). Swans also employ a unique feeding method called treadling in which

they excavate relatively large, deep craters in the marsh substrate to uncover and dislodge tubers of aquatic plants (Limpert and Earnst 1994, see Chapter 3). By doing so, they disturb and turn-over the marsh substrate, thereby liberating food items, such as seeds or aquatic plant parts, that previously were buried too deep for dabbling ducks to attain while foraging on their own.

It is easy to envision how feeding intensity of ducks that were close to swans could increase as a direct result of foraging activity of swans, but it is less obvious how ducks far from swans could benefit from such activities. Increased feeding intensity of these birds probably was related to ducks remaining to feed in areas disturbed by Tundra Swans long after they had departed to forage in more distant locations on observation ponds. During this study, it was common to begin observations on ducks feeding close to swans and only a few minutes later terminate the session because swans had left to forage elsewhere, leaving the ducks behind at the original feeding location. Consequently, at least some ducks that were initially selected for observation because they were far from feeding swans probably were feeding in swan-altered microhabitats. Thus, observations made when swans were feeding controlled for the swan's physical proximity, but not necessarily for the presence of the foraging microhabitat that swans created in ponds.

For ducks to increase their feeding intensity in the presence of feeding swans, they had to reduce time spent in other foraging activities. I found that, foraging ducks showed a trade-off between feeding and vigilance. Specifically, ducks feeding close to and far from foraging swans spent 33% and 54% less time vigilant, respectively, than did individuals foraging the same relative distances from inactive swans. Such reductions suggested that ducks, especially those close to swans, did not identify Tundra Swans as a

substantial physical threat, despite swans occasionally directing aggressive acts toward ducks while they were feeding (see Chapter 3). Alternatively, ducks may have reduced their vigilance when swans were active because the latter also contributed to scanning the environment for danger, but preening, loafing, and sleeping swans were less likely to do so. This situation is analogous to birds feeding in larger groups where more eyes are watching for predators, thus reducing each individual's risk of predation (Roberts 1996). Further, Tundra Swans, by their presence and large size, may even deter some predators from attempting an attack on ducks that are foraging on ponds with swans. It may also be that ducks can easily monitor vigilance of large and conspicuous swans, especially when swans vocalize upon observation of a potential threat (S. Badzinski, personal observation). This type of association between ducks and swans would be similar to one where mammals use noisy and conspicuous birds as a signal of approaching predators while foraging in mixed species assemblages (Rasa 1984).

American Black Ducks and Mallards showed an increase in locomotion when they were foraging close to feeding Tundra Swans. This effect was small and could be due to chance, but it further suggested that these ducks altered their foraging behaviour somewhat in response to swan feeding activity. This effect likely would have been larger except that locomotion and surface feeding were not always mutually exclusive events and I gave priority to recording the feeding behaviours. This behavioural modification also corroborated observations of ducks continually moving to position themselves behind swans or patrolling a perimeter around a foraging swan (beyond the reach of a swan's neck) and periodically picking floating food items off the water's surface (see also Sherwood 1960, Bailey and Batt 1974, Thomas 1982, see Chapter 3).

Interpretation of results concerning feeding intensity of waterfowl is complicated because they were based on observation of foraging ducks that fed primarily below the water's surface where it was impossible to determine their foraging success, food selection, and intake rates (Baldassarre et al. 1988). Thus, it is possible that increased feeding intensity may not reflect an increase in feeding rate, but rather an increase in time spent searching for food (Owen et al. 1992, Percival and Evans 1997). Wintering Gadwall (*Anas strepera*) and American Coot (*Fulica americana*), however, responded to lower food availability by decreasing their feeding rates (McKnight 1998). Further, American Black Ducks and Mallards generally spent most of the day preening and resting on ponds, probably because food availability was low (see: Chapters 2 and 3), but when swans began to forage the number of ducks on ponds would gradually increase and some of them would continually follow feeding swans (S. Badzinski, personal observation). Given this, I contend that the higher feeding intensity observed when ducks were foraging with swans was due to a temporary, small-scale increase in food availability on observation ponds. Future investigations of interspecific foraging associations and resource partitioning in waterfowl should strive to combine behavioural observation with determination of actual feeding rates and dietary selection of species feeding with and without feeding swans (or other potential competitors) to test the validity of my interpretations (e.g., see McKnight and Hepp 1998).

4.6.2. Duck foraging methods

Foraging activities of Tundra Swans not only influenced time ducks spent in major activities while foraging (i.e., feeding, vigilance, and locomotion), but also altered methods ducks used to obtain food. Swan feeding activity did not, however, substantially

influence use of all foraging methods nor did it affect foraging patterns used by American Black Ducks and Mallards in the same way, especially when their proximity to swans was considered. American Black Ducks foraging close to Tundra Swans, for example, did not greatly alter their use of any foraging method in response to swan activity, but this was not the case for individuals far from swans; subsurface-feeding (head/neck-under) was used more and surface-feeding (picking and dabbling) less when swans were active, as opposed to inactive. This change probably was a response to exploitation of the feeding craters swans created in the marsh substrate and subsequently abandoned (see above, see Chapter 3).

Mallards showed a slightly different response to swan feeding activity than did American Black Ducks. Individuals of this species, for instance, did not alter their mode of foraging when far from feeding swans, but, when swans were close, they used surface-feeding methods much more and subsurface feeding methods considerably less when close to feeding, as compared to inactive, Tundra Swans. Thus, Mallards close to swans shifted from a predominantly subsurface foraging pattern to a shallower one where they could pick or filter food items stirred to the water's surface by foraging activities of swans. This change in use of feeding methods also agreed well with increased locomotion observed when Mallards foraged close to feeding swans. Other researchers have noted that ducks appear to spend considerable time surface-feeding near swans, presumably capitalizing on foods that had floated to the water's surface after being dislodged by feeding swans (Sherwood 1960, Bailey and Batt 1974, Thomas 1982). To my knowledge, however, this is the first study to actually show a measurable increase in this mode of feeding as a direct result of swan foraging activities. As I have previously

shown, Tundra Swans occasionally attacked American Black Ducks and Mallards when foraging in mixed species flocks (see Chapter 3). So, it also was possible that ducks close to Tundra Swans used a feeding method where they could continually monitor their surroundings and distance from swans because their eyes were constantly above the water's surface, thereby reducing their risk of being attacked or injured by Tundra Swans (see Chapter 3) or being killed by predators (Pöysä 1987, Guillemain et al. 2000).

4.6.3. Interspecific differences in duck foraging methods

American Black Ducks and Mallards show little genetic and morphological differences (Ankney et al. 1986, Avise et al. 1990, Hanson and Ankney 1994,). Based on this evidence, and as previously proposed by Ankney et al. (1986), American Black Ducks might simply be “Black Mallards”. If so, it is likely that both species would show identical foraging patterns (i.e., spend the same time in major activities during foraging bouts and use same frequency of surface-feeding, subsurface-feeding, upending, and paddling acts) regardless of swan activity on ponds, but especially when swans were inactive as their behaviour under these conditions is not confounded by swan feeding activity effects and most approximates a “normal”, or at least a swan-free, environment.

My results showed that in a “normal” or “swan-free” environment there were sizeable and consistent interspecific deviations in use of feeding methods, whereas, when swans were “present”, active, and feeding, foraging patterns of American Black Ducks and Mallards were virtually identical. These findings were not entirely consistent with those of Eadie et al. (1979) because they found that American Black Ducks and Mallards, in a largely “swan-free” environment at Long Point, Ontario, were identical in all aspects of foraging behaviour studied (but none of which included frequency in use of different

feeding methods). The divergent patterns of foraging methods displayed by these species under “swan-free” conditions further suggest they may partition food on these heavily used ponds by feeding at slightly different depths (Pöysä 1983a, Pöysä 1986b, Pöysä et al. 1994, Elmberg et al. 1997, Green 1998, McKnight and Hepp 1998, Pöysä and Sorjonen 2000) and thus must be competitors. If this is true, it may be that, as I have previously suggested (see Chapter 3), swan foraging activities on ponds increased duck food availability, which caused American Black Ducks and Mallards to converge on virtually identical foraging patterns in a swan-altered environment. This hypothesized foraging niche shift could be explored in a future comprehensive study of foraging niche dynamics involving all three of these waterfowl species. At any rate, my results suggest that, although American Black Ducks and Mallards are genetically and morphologically identical, they are, at least under some conditions, behaviourally different while foraging.

If Tundra Swan populations continue to increase there will be more opportunity to study how these large birds influence smaller-scale, foraging interactions and larger-scale, community dynamics among waterfowl (see also Pöysä and Sorjonen 2000). This study showed that these large birds may have short-term, positive influences on foraging waterfowl by facilitating their feeding activities or by providing information about or protection from potential predators. Further, evidence suggested that swan foraging activities could alter the feeding methods some species of waterfowl use to obtain food in mixed species foraging assemblages. Thus, I conclude that Tundra Swans can influence foraging behaviour of American Black Ducks and Mallards. I further suggest that Tundra Swans also likely will have effects on small scale foraging behaviour, food choice, and habitat use of other co-occurring waterfowl species, as well as, on the composition and

dynamics of mixed species foraging assemblages or possibly entire communities.

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CHAPTER 5. GENERAL DISCUSSION

5.1. DISCUSSION

This study was done to determine if of Tundra Swans (*Cygnus columbianus columbianus*) at Long Point, Ontario were negatively influencing other staging waterfowl (Petrie 1998, Petrie et al. 2002). Tundra Swans could affect other waterfowl directly by aggressively excluding them from food resources, which in turn could cause ducks to alter their distribution or reduce time that they spend feeding. They also may indirectly influence distribution, abundance, and feeding activity of staging waterfowl by reducing seasonal abundance of aquatic foods preferred by those species. Results presented in this dissertation generally showed that Tundra Swans did not have negative effects on either within-season abundance of aquatic vegetation or on abundance, distribution or diurnal foraging activities of other staging waterfowl. Rather, evidence suggested that foraging activities of Tundra Swans positively influenced several other waterfowl species through facilitation of their feeding activities.

There were several potential reasons why strong negative effects of Tundra Swans on aquatic plant and waterfowl communities were not observed in this study. In the paragraphs that follow, I discuss the disturbance regime that Tundra Swans encounter at Long Point, potential differences in food habits between swans and other waterfowl, and staging population size of Tundra Swans at Long Point and how these factors may have contributed to the results of this study.

The waters and marshes of Long Point are well known for their fall waterfowl hunting, fishing, and other water-related activities. Consequently, this study was

conducted in an environment that generally had high levels of diurnal human disturbance (Knapton et al. 2000). Consistent daily disturbance by boats caused Tundra Swans and other waterfowl to congregate on ponds in National Wildlife Areas or other “refuge” areas that were free of human disturbance (Knapton et al. 2000, S. Badzinski, unpublished data). Such areas have low rates of disturbance, but high waterfowl use throughout the fall resulted in rapid depletion of aquatic foods (see Chapter 2). Low availability of preferred foods explained why Tundra Swans generally spent little time feeding during the day on these ponds (see Chapter 3). Low levels of feeding and activity limited the potential for Tundra Swans to interact with other species. At night, however, Tundra Swans and other waterfowl species left these undisturbed areas and congregated in areas with high diurnal, but low nocturnal, disturbance (e.g., Inner Long Point Bay and private and public hunting areas) to feed on preferred aquatic plants (S. Badzinski, unpublished data). I collected data on nocturnal abundance, distribution, and behaviour of Tundra Swans, but could not do so for other waterfowl because of their darker color and smaller size. Tundra Swan activity and feeding intensity were much higher at night, than during the day (S. Badzinski, unpublished data), thereby greatly increasing the potential for them to influence abundance, distribution, and behaviour of other waterfowl. Because all waterfowl data presented in this dissertation were collected during the day and in areas of low disturbance and relatively low feeding activity, my results may underestimate the influence that Tundra Swans have on the abundance, distribution, and feeding activity of other waterfowl. Thus, it would be informative to compare my results with a similar study done at a staging or wintering area with lower levels of diurnal disturbance and higher swan feeding activity in order to determine the

generality of swan-waterfowl relationships observed at Long Point.

There are no quantitative data on food habits of Tundra Swans using aquatic habitats at Long Point. Studies done elsewhere found that staging Tundra Swans fed primarily on tubers of *Potamogeton pectinatus* and *Vallisineria americana* (Beekman et al. 1991, Dirksen et al. 1991, Earnst 1994, Limpert and Earnst 1994, Nolet and Drent 1998, Froelich 2001). These two plants are very common and known to be important waterfowl foods at Long Point (Petrie 1998). Thus, I assumed that Tundra Swans at Long Point would also feed heavily on the relatively small tubers of these plants. However, after spending many hours watching Tundra Swans and documenting their preferred feeding locations, I found that they foraged mostly on aquatic plants that produce relatively large tubers and rhizomes, including *Sagittaria* spp, *Scirpus* spp, and *Nuphar* spp. Thus, Tundra Swan exploitation of tubers that are too large for ducks to consume likely reduced competition between Tundra Swans and herbivorous diving ducks (*Aythya* spp) and dabbling ducks (*Anas* spp).

Potential for competition between Tundra Swans and ducks depends on large- and small-scale habitat use and specific food habits. However, in general, widespread competition is unlikely between Tundra Swans and herbivorous diving ducks at Long Point because they are somewhat ecologically separated by general feeding methodology (upending versus diving) and large-scale habitat preferences (shallow, emergent marsh habitat versus deep, open water habitat). Potential for competition between Tundra Swans and *Aythya* spp is much greater at relatively smaller geographic scales, especially on large, shallow ponds that are dominated by *Vallisineria Americana*, such as in the marshes of the Long Point Company and in several other private hunting clubs at Long

Point (see also Froelich 2001).

Dabbling ducks and Tundra Swans overlap considerably in their large-scale habitat preferences (shallow, emergent marsh habitat) and foraging depths (see also Pöysä and Sorjonen 2000). Data from hunter-shot birds at Long Point suggest that dabbling ducks primarily consumed seeds and agricultural grains but also ate some subterranean and vegetative plant parts (Petrie 1998, Petrie and Knapton 1999). Thus, there is potential for widespread, food resource based competition between Tundra Swans and dabbling ducks. So, Tundra Swans consumption of aquatic plant tubers, especially those of relatively large size, indicates some degree of food resource partitioning because dabbling ducks primarily consumed seeds and relatively smaller tubers of aquatic plants. This hypothesis of foraging niche separation was supported by the increased feeding activity and extremely low rates of interspecific aggression that I observed when dabbling ducks were foraging with active and feeding Tundra Swans. However, more data are needed to properly evaluate these hypotheses about potential competition and resource partitioning between Tundra Swans and both diving and dabbling ducks at Long Point.

Negative effects of increasing populations of waterfowl become much easier to detect as populations begin to approach the carrying capacity of their critical habitats (Cooke et al. 1995, Batt 1997). Tundra Swan numbers have increased substantially since the early 1970's at Long Point (Petrie et al. 2002). However, my results suggested that their numbers have not yet become high enough for density dependent factors, such as overexploitation of aquatic food resources, aggressive resource defense and exclusion, and habitat/spatial limitations, to cause large, adverse effects on large-scale abundance of other staging waterfowl at Long Point (see also Pöysä 1983, Pöysä and Sorjonen 2000).

Even at much smaller spatial scales (i.e., individual ponds), Tundra Swan numbers on ponds were not consistently high enough to cause measurable negative influences on abundance, distribution, or behaviour of other staging waterfowl. If Tundra Swan numbers continue to increase, however, density dependent effects may begin to adversely affect Tundra Swans and other staging waterfowl, but I predict that such effects will initially be greatest on the aquatic plant community. Thus, it is important to continue to monitor waterfowl populations and their large- and small scale distributions at key staging areas. Such information would be most useful if coupled with a vegetation-monitoring program designed to detect long-term changes in aquatic plant species composition, abundance, and distribution at different spatial scales.

One of the most interesting findings of my research was the positive influence that Tundra Swans had on feeding activity of other waterfowl. Several other researchers have hypothesized that, based on their morphology and feeding activities, swans might have such an influence on waterfowl (Sherwood 1960, Bailey and Batt 1974, Thomas 1982). However, to my knowledge, this study provides the first quantitative evidence supporting swan facilitation of waterfowl feeding activities (see Badzinski 2003: Chapter 3 & 4). Tundra Swans excavate large, deep craters in the marsh substrate while foraging for tubers of aquatic plants (Limpert and Earnst 1994, S. Badzinski, unpublished data). Tundra Swans also disturb large areas of the marsh substrate and likely increased availability of aquatic plant seeds and tubers that smaller waterfowl species normally could not obtain because they were buried too deep. However, it is unknown how increased feeding activities of smaller waterfowl in swan-disturbed habitats may influence the structure of the aquatic plant community in subsequent seasons. Possibly,

the short-term benefit ducks receive by feeding with Tundra Swans may have longer-term, indirect negative effects on the seed and tuber bank in shallow ponds. Reduction in the seed and tuber bank could affect composition, abundance, distribution and quality of aquatic plants in areas used by these groups of waterfowl (Cronk and Fennessy 2001). These potential indirect effects would be intensified if Tundra Swan use of feeding habitats increases and ducks deplete increasingly greater amounts of the seed and tuber bank. Additional enclosure experiments and longer-term monitoring of aquatic vegetation and the seed and tuber banks in wetlands would enable evaluation of this potentially important swan-facilitated herbivory effect.

5.2. FUTURE RESEARCH

This study has elucidated several other broad avenues of research and specific studies that could be undertaken to better assess the role that increasing numbers of Tundra Swans could have on influencing aquatic plant and staging waterfowl. Because waterfowl abundance and distributions are largely related to abundance and distribution of their preferred aquatic foods (Lodge et al. 1998), it is imperative that a spatially well-replicated study of aquatic vegetation (and the associated seed and tuber bank in marshes) be undertaken to assess natural and herbivore induced changes in aquatic macrophyte abundance, distribution, and composition over the longer-term (i.e., several years, decades, etc.). Such a study holds most promise for assessing the cumulative and more complex, indirect impacts that large herbivores, such as Tundra Swans, have on other waterfowl and on the aquatic vegetation community (e.g., Hamilton 2000).

Quantitative information is needed on food habits of Tundra Swans at Long Point. Actively foraging swans could be collected from major feeding areas at Long Point at

different times throughout both fall and spring. Aquatic vegetation samples also could be collected simultaneously in the immediate vicinity so that food availability and dietary preference can be determined. This sampling methodology would ensure that diet samples are representative of aquatic foods that Tundra Swans were eating and selecting at Long Point. These data would help to determine whether Tundra Swans had seasonal preferences for certain foods or if they showed within season changes in their food preferences. These data would also aid in determining which aquatic plant species were most susceptible to Tundra Swan herbivory and which species of waterfowl were most likely to be influenced by feeding activities of Tundra Swans.

Finally, investigations into dietary overlap between Tundra Swans and other waterfowl could be combined with the food habits study described above to better understand the potential competitive effects and resource partitioning among these waterfowl species (e.g., McKnight 1998, McKnight and Hepp 1998). It would be most informative to collect Tundra Swans and ducks foraging together on ponds. Another sample of ducks also could be collected at times when swans were not feeding on ponds. Dietary samples of the two groups of ducks (swan active and swan inactive) could be compared to each other and to those of Tundra Swans to determine the extent of dietary overlap and if ducks altered their choice of foods when Tundra Swans were feeding. Foraging and intake rates also could be directly determined to test my hypothesis that feeding activity of Tundra Swans increases the amount of food available to ducks. It also would be interesting to determine if dietary overlap increased, remained the same, or decreased over time within seasons and if there were large seasonal differences in resource overlap.

5.3. OVERALL SUMMARY AND CONCLUSION

In conclusion, results presented in this dissertation did not support my overall hypothesis that Tundra Swans would have large, negative effects on aquatic plants or other staging waterfowl. In fact, some evidence suggested that foraging activities of Tundra Swans positively influenced several other waterfowl species through facilitation of their feeding activities. Thus, I conclude that Tundra Swans, during the short time frame of this study, had little effect on aquatic plants and other staging waterfowl at Long Point. However, future longer term studies should be conducted to further advance our knowledge regarding interactions between Tundra Swans and other staging waterfowl and their preferred aquatic food plants. Further research concerning how Tundra Swans may influence aquatic plant and waterfowl communities is important because populations of these large birds may increase and the information that is amassed now will enable biologists to make much more informed decisions regarding future management of waterfowl populations, particularly Tundra Swans, in North America.

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**APPENDIX 1. MEAN WATER DEPTHS AT VEGETATION SAMPLING LOCATIONS DURING
FALL 1998 AND 1999 AT LONG POINT, ONTARIO**

Table A1.1. Water depths at bird exclosures, swan exclosures, and open exclosures (reference plots) during the early (late September – early October) and late (early December) sampling periods during fall 1998 and 1999 at Long Point, Ontario.

		Water depth (Mean [cm] \pm SD)					
		Bird		Swan		Open	
Year	Location	Early	Late	Early	Late	Early	Late
1998	BCNP	66.0	34.1	63.9	28.0	65.8	32.0
		(5.9)	(7.1)	(7.4)	(9.4)	(6.0)	(11.1)
	BK	71.6	38.6	59.1	32.2	67.4	37.8
		(16.8)	(19.3)	(6.2)	(15.8)	(15.9)	(21.4)
	TP	65.7	27.1	61.8	23.6	66.7	25.5
		(5.7)	(3.6)	(9.1)	(3.4)	(8.7)	(2.7)
1999	BCNP	27.4	18.7	32.4	11.6	32.0	11.0
		(4.8)	(6.9)	(12.0)	(10.8)	(7.1)	(5.9)
	BK	38.1	26.7	45.9	32.7	49.7	36.9
		(2.6)	(5.9)	(8.8)	(12.8)	(4.6)	(5.8)
	IB	68.0	52.0	69.9	58.3	71.4	56.6
		(6.0)	(5.4)	(7.3)	(6.5)	(9.2)	(8.4)

APPENDIX 2. ESTIMATING DRY MASS OF AQUATIC PLANTS FROM THEIR WETMASS

Table A2.1. Relationships between the dry and wet masses of above-ground parts of common aquatic plants at Long Point, Ontario. These equations were developed from a sub-sample of aquatic plants from data collected during fall 1998 with known wet and dry masses, which were subsequently used to estimate the dry mass of all above-ground biomass samples in the 1998 and 1999 aquatic vegetation data sets.

Species dry mass (Y) =	Intercept (SE)	$b_{\text{wet mass}}$ (SE)	N	r^2	P
<i>Ceratophyllum demersum</i>	0.10 (0.09)	0.17 (0.01)	23	0.98	0.0001
<i>Chara spp</i>	6.07 (1.43)	0.19 (0.02)	57	0.74	0.0001
<i>Elodea canadensis</i>	-0.03 (0.10)	0.20 (0.01)	36	0.98	0.0001
<i>Myriophyllum spicatum</i>	0.07 (0.05)	0.19 (0.01)	44	0.97	0.0001
<i>Najas flexilis/gaudalupensis</i>	0.12 (0.13)	0.18 (0.01)	12	0.97	0.0001
<i>Nuphar variegatum</i>	-1.75 (2.47)	0.16 (0.01)	41	0.77	0.0001
<i>Pontedaria cordata</i>	-1.29 (0.61)	0.12 (0.01)	52	0.86	0.0001
<i>Potamogeton spp</i>	-8.00 (6.10)	0.57 (0.11)	12	0.73	0.0001
<i>Potamogeton natans</i>	-0.15 (0.14)	0.17 (0.01)	26	0.98	0.0001
<i>Potamogeton pectinatus</i>	0.04 (0.13)	0.18 (0.01)	30	0.95	0.0001
<i>Potamogeton pusillus</i>	0.07 (0.05)	0.13 (0.01)	47	0.90	0.0001
<i>Potamogeton richardsonii</i>	0.28 (0.10)	0.13 (0.01)	38	0.95	0.0001
<i>Ranunculus longirostris</i>	0.02 (0.12)	0.16 (0.01)	18	0.97	0.0001
<i>Sagittaria spp</i>	-0.16 (0.19)	0.11 (0.01)	23	0.97	0.0001

Table A2.1. Continued.

Species dry mass (Y) =	Intercept (SE)	$b_{\text{wet mass}}$ (SE)	N	r^2	P
<i>Utricularia spp</i>	-0.10 (0.17)	0.18 (0.01)	29	0.97	0.0001
<i>Vallisneria americana</i>	-0.05 (0.13)	0.15 (0.01)	51	0.94	0.0001
<i>Zizania palustris</i>	0.02 (0.17)	0.16 (0.01)	44	0.95	0.0001

APPENDIX 3. POND-LEVEL DISTRIBUTIONS OF SEVERAL WATERFOWL SPECIES IN RELATION TO THEIR PROXIMITY TO TUNDRA SWANS

Table A3.1. Percentage of individuals of each waterfowl species (see methods for abbreviations) that were less than 3 m, between 3 m and 30 m, and more than 30 m from Tundra Swans (*Cygnus columbianus*) on observation ponds at Long Point, Ontario, during fall and spring. Under Model, S = waterfowl species and Null = intercept model ($Y =$). Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^w AIC_c$).

Site	Response (%)	Distance	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	Mean (\pm SE) percentage (%) of individuals in distance categories							
									ABDU	AMWI	CAGO	GADW	GWTE	MALL	NOPI	RNDU
BCNI	Individuals	< 3 m	{Null}	0.00	2	37	0.00	1.00								
			{S}	0.19	9	37	12.40	0.00	34 (10)	5 (13)	29 (10)	0 (25)	0 (15)	21 (10)	27 (10)	33 (15)
	Individuals	3-30 m	{Null}	0.00	2	37	0.00	1.00								
			{S}	0.06	9	37	18.00	0.00	35 (13)	46 (16)	46 (13)	73 (32)	52 (18)	49 (12)	35 (12)	63 (18)
	Individuals	> 30 m	{Null}	0.00	2	37	0.00	1.00								
			{S}	0.12	9	37	15.50	0.00	31 (12)	49 (15)	26 (12)	27 (29)	48 (17)	30 (11)	37 (11)	4 (17)

Table A31. Continued.

Site	Response (%)	Distance	Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Mean (\pm SE) percentage (%) of individuals in distance categories							
									ABDU	AMWI	CAGO	GADW	GWTE	MALL	NOPI	RNDU
BCNP	Individuals	< 3 m	{S}	0.37	8	86	0.00	1.00	22 (5)	12 (5)	36 (5)	2 (5)	10 (5)	18 (5)	0 (11)	—
			{Null}	0.00	2	86	26.50	0.00								
	Individuals	3-30 m	{S}	0.31	8	86	0.00	1.00	50 (7)	64 (8)	28 (8)	83 (7)	78 (7)	45 (7)	50 (16)	—
			{Null}	0.00	2	86	18.00	0.00								
	Individuals	> 30 m	{S}	0.22	8	86	0.00	0.98	28 (5)	24 (6)	35 (6)	15 (6)	12 (6)	38 (5)	50 (12)	—
			{Null}	0.00	2	86	7.50	0.02								
BIO	Individuals	< 3 m	{Null}	0.00	2	25	0.00	0.86								
			{S}	0.39	7	25	3.70	0.14	71 (12)	53 (18)	25 (22)	—	1 (15)	60 (12)	37 (18)	—
	Individuals	3-30 m	{Null}	0.00	2	25	0.00	1.00								
			{S}	0.12	7	25	12.80	0.00	8 (15)	33 (21)	25 (25)	—	51 (18)	25 (13)	33 (21)	—
	Individuals	> 30 m	{Null}	0.00	2	25	0.00	1.00								
			{S}	0.16	7	25	11.80	0.00	22 (12)	13 (17)	50 (21)	—	48 (15)	15 (11)	30 (17)	—

Table A3.1. Continued.

Site	Response (%)	Distance	Model	R^2	K	N	ΔAIC_c	$^w AIC_c$	Mean (\pm SE) percentage (%) of individuals in distance categories								
									ABDU	AMWI	CAGO	GADW	GWTE	MALL	NOPI	RNDU	
BK	Individuals	< 3 m	{S}	0.33	9	52	0.00	0.78	13 (2)	4 (3)	0 (6)	2 (2)	6 (2)	8 (2)	3 (2)	10 (2)	
			{Null}	0.00	2	52	2.50	0.22									
	Individuals	3-30 m	{Null}	0.00	2	52	0.00	0.99									
			{S}	0.17	9	52	8.50	0.01	49 (8)	73 (10)	100 (24)	78 (9)	62 (8)	76 (8)	74 (9)	73 (9)	
	Individuals	> 30 m	{Null}	0.00	2	52	0.00	0.99									
			{S}	0.15	9	52	9.30	0.01	38 (8)	23 (9)	0 (22)	20 (8)	33 (8)	16 (8)	34 (8)	17 (8)	
LRB	Individuals	< 3 m	{S}	0.36	8	79	0.00	1.00	18 (6)	9 (7)	68 (6)	33 (12)	28 (6)	17 (6)	40 (6)	—	
			{Null}	0.00	2	79	21.80	0.00									
	Individuals	3-30 m	{S}	0.50	8	79	0.00	1.00	19 (5)	29 (5)	1 (5)	0 (10)	23 (5)	29 (5)	0 (5)	—	
			{Null}	0.00	2	79	40.40	0.00									
	Individuals	> 30 m	{Null}	0.00	2	79	0.00	0.62									
			{S}	0.15	8	79	1.00	0.38	64 (6)	63 (7)	31 (7)	67 (14)	49 (6)	54 (6)	59 (7)	—	

**APPENDIX 4. AVERAGE DISTANCE OF ACTIVE AND INACTIVE WATERFOWL FROM
ACTIVE AND INACTIVE TUNDRA SWANS**

Table A4.1. Average minimum distance (meters) of active and inactive waterfowl from active and inactive Tundra Swans (*Cygnus columbianus*) over all observation ponds during fall at Long Point, Ontario. Under Model, S = swan activity, W = Waterfowl activity, and S×W = the interaction between swan activity and waterfowl activity. Shown for each candidate model are the proportion of variance explained (R^2), number of model parameters (K), sample size (N), Akaike Information Criterion (AIC) difference with correction for small sample size (ΔAIC_c), and model weight ($^W AIC_c$).

Species Model	R^2	K	N	ΔAIC_c	$^W AIC_c$	Waterfowl active		Waterfowl inactive	
						Average distance (meters \pm SE) to swan			
						Swan	Swan	Swan	Swan
						active	inactive	active	inactive
ABDU {S, W, S×W}	0.01	5	1763	0.0	1.0	5.0 (0.4)	6.3 (0.3)	7.5 (0.7)	5.8 (0.2)
{Null}	0.00	2	1763	9.4	0.0				
AMWI {S, W, S×W}	0.00	2	373	0.0	0.9	3.9 (0.3)	4.2 (0.3)	3.4 (0.5)	3.9 (0.2)
{Null}	0.01	5	373	4.0	0.1				
CAGO {S, W, S×W}	0.03	5	844	0.0	1.0	7.7 (0.7)	6.6 (0.5)	5.6 (0.6)	4.7 (0.2)
{Null}	0.00	2	844	20.1	0.0				
GADW {S, W, S×W}	0.06	5	317	0.0	1.0	8.0 (1.1)	12.0 (0.7)	7.6 (1.8)	8.2 (0.6)
{Null}	0.00	2	317	13.1	0.0				

Table A4.1. Continued.

Species Model	R^2	K	N	ΔAIC_c	$W AIC_c$	Waterfowl active		Waterfowl inactive	
						Average distance (meters \pm SE) to swan			
						Swan	Swan	Swan	Swan
						active	inactive	active	inactive
GWTE {S, W, S \times W}	0.02	5	653	0.0	1.0	3.4 (0.4)	3.5 (0.2)	5.3 (0.7)	4.6 (0.4)
{Null}	0.00	2	653	7.3	0.0				
MALL {S, W, S \times W}	0.01	5	2163	0.0	1.0	4.9 (0.3)	6.1 (0.2)	5.3 (0.5)	6.0 (0.2)
{Null}	0.00	2	2163	10.7	0.0				
NOPI {S, W, S \times W}	0.13	5	469	0.0	1.0	2.9 (0.4)	3.7 (0.2)	3.6 (1.3)	7.4 (0.4)
{Null}	0.00	2	469	60.2	0.0				
RNDU {S, W, S \times W}	0.17	5	345	0.0	1.0	1.7 (0.1)	4.6 (0.4)	2.2 (0.2)	2.6 (0.3)
{Null}	0.00	2	345	58.0	0.0				

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PEER REVIEWED SCIENTIFIC PUBLICATIONS, DISSERTATIONS, AND THESES:

Badzinski, S. S. 2003. Dominance relations and agonistic behaviour of Tundra
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- Badzinski, S. S. 2003. Influence of Tundra Swans (*Cygnus columbianus columbianus*) on aquatic vegetation and staging waterfowl at Long Point, Ontario. Unpublished Ph.D. dissertation. University of Western Ontario, London.
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- Petrie, S. A., S. S. Badzinski, and K. L. Wilcox. 2002. Population trends and habitat use of Tundra Swans staging at Long Point, Lake Erie. Pages 143-149 in Proceedings of the Fourth International Swan Symposium, 2001 (E. C. Rees, S. L. Earnst, and J. C. Coulson, Eds.). Waterbirds 25, Special Publication 1.
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SCIENTIFIC PUBLICATIONS IN REVIEW AND IN PREPARATION:

Badzinski, S. S. Social influences on diurnal and foraging activities of Tundra Swans during fall and spring migration. In preparation.

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Badzinski, S. S., C. D. Ankney, and S. A. Petrie. 2001. Aquatic feeding activity of Tundra Swans during spring and fall migration at Long Point, Ontario. Fourth International Swan Symposium, Warrington, Virginia.

Badzinski, S. S., C. D. Ankney, and S. A. Petrie. 2001. Diurnal activities of Tundra Swans in relation to social status, family size, and flock size during fall and spring migration. Fifth Biennial Institute for Wetland and Waterfowl Research Student and Staff Symposium, Winnipeg, Manitoba.

Badzinski, S. S., C. D. Ankney, J. O. Leafloor, and K. F. Abraham. 2001. Egg size as a predictor of nutrient composition of eggs and neonates of Canada Geese and Lesser Snow Geese. Tenth North American Arctic Goose Conference, Quebec City, Quebec.

Petrie, S. A., S. S. Badzinski, and K. L. Wilcox. 2001. Population trends and habitat use of Tundra Swans staging at Long Point, Lake Erie. Fourth International Swan Symposium, Warrington, Virginia.

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Badzinski, S. S., C. D. Ankney, J. O. Leafloor, and K. F. Abraham. 1998. Comparative growth and development of external morphology, digestive organs, and skeletal muscles of Canada and Lesser Snow Geese of Akimiski Island, Northwest Territories. Ninth North American Arctic Goose Conference, Victoria, British Columbia.

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