

**Dietary intake of Mute Swans, *Cygnus olor*, in relation to
reproduction on the lower Great Lakes**

Submitted to Dr. R. Podesta, Dr. R.J. Scott, and Dr. L. Zanette

April 7, 2003

Investigator: M.L. Bailey, Honors student
Department of Zoology, University of Western Ontario
Email: meganbailey@orionsoftware.ca

Supervisor: Dr. S.A. Petrie, Research Director
Long Point Waterfowl and Wetlands Research Fund
Email: spetrie@bsc-eoc.org

Co-supervisor: Dr. J.S. Millar, Professor, Departmental Chair
Department of Zoology, University of Western Ontario
Email: jsmillar@uwo.ca

ABSTRACT

Populations of exotic Mute Swans, *Cygnus olor*, have been increasing on the lower Great Lakes for the past 30 years. Because Mute Swans are aggressive and have high consumptive requirements, concern has been raised among scientists and resource managers about their impact on native waterfowl and their habitats. Ninety-four Mute Swans were collected from lower Great Lakes coastal wetlands and during the 2001 and 2002 breeding seasons to study dietary intake in relation to sex, age, and stage of reproduction. Collectively, diets consisted primarily of the vegetative structures of Common Waterweed (*Elodea Canadensis*), Muskgrass (*Chara vulgaris*), Coontail (*Ceratophyllum demersum*) and pondweed species (*Potamogeton spp.*), as well as tubers. Although most differences were non-significant, there was a trend for males to consume large quantities of *Chara vulgaris* (62% aggregate dry mass) and *Ceratophyllum demersum* (32%) during the pre-laying/laying period, followed by large quantities of sagittaria tubers (68%) during incubation. Females primarily consumed *Ceratophyllum demersum* (35%) and *Elodea Canadensis* (16%) during pre-laying/laying, *potamogeton spp.* (35%) and *Ceratophyllum demersum* (22%) during incubation, followed by tubers (60%) during brood rearing. Consumption of *Ceratophyllum demersum* during early reproductive stages may be a function of the high relative availability of this plant in early spring. Increased tuber consumption during late reproduction may be a strategy to replenish depleted lipid stores. Cygnets consumed large quantities of Flat-stemmed Pondweed (*Potamogeton zosteriformis*)(69%); the delicate stems and leaves of this plant may provide an easily digestible food source for cygnets. With exception of

Ceratophyllum demersum, there is considerable dietary overlap between exotic Mute Swans and native waterfowl species that stage on lower Great Lakes coastal wetlands.

INTRODUCTION

Coastal wetlands serve several ecological roles, including the provision of habitat for fish and wildlife; they are also centers of biodiversity and primary productivity (Chow-Fraser 1998, Gottgens et al. 1998, Mitsch and Bouchard 1998). Perhaps their value is best realized when considering the extensive habitat coastal wetlands provide for migratory waterfowl (Smith et al. 1991). Lower Great Lakes (LGL) wetlands support hundreds of thousands of waterfowl during spring and fall migration (Dennis et al. 1984). These birds depend on the diverse and plentiful flora of the LGL to build up energy reserves for migration and reproduction (Dennis and Chandler 1974). Unfortunately, the integrity of these wetlands has been compromised substantially by human development and drainage (Jessen et al. 1983, Smith et al. 1991). Less than 5% of western Lake Erie's wetlands remain (Herndendorf 1987). Consequently, the importance of the remaining LGL wetlands as staging grounds for migratory waterfowl is evident.

A further concern on LGL coastal wetlands is the introduction of exotic species (Gottgens 1998, Ricciardi and MacIsaac 2000, Hall and Mills 2000). The LGL have been invaded by at least 145 alien species since the early 1800's, (Hall and Mills 2000). Potential issues of introduced species include competition, predation, habitat alteration, disease and parasite introductions, as well as genetic effects (Hall and Mills 2000). Exotic waterfowl can have substantial ecological impacts on native species and their

habitats (Weller 1969, Sondergaard et al. 1996, Hughes et al.1999). This is particularly true for aggressive species, and those that may compete for food or habitat (Weller 1969).

The Mute Swan, *Cygnus olor*, is an exotic bird to North America that may compete with native waterfowl (Willey and Halla 1972). Mute Swans were brought to North America from Europe and Asia during the late 19th and early 20th centuries for esthetic reasons (Allin et al. 1987). Following their escape and introduction to the wild in the 1940's and 1950's, Mute Swan populations expanded rapidly. In 1954, the US Fish and Wildlife Service first recorded Mute Swans in their annual mid-winter waterfowl survey of the Atlantic Flyway (Allin et al. 1987). Populations have since grown exponentially; current estimates report the Atlantic Flyway population at nearly 15,000 Mute Swans (Allin 2003).

Mute Swans are a relatively recent arrival to the LGL, with the first established populations dating to the 1960's and 1970's (Knapton 1993). Petrie and Francis (2003) estimated that the present LGL population is approximately 2000 birds and that the population has been increasing at 10 to 20 % annually over the past 20 years. Petrie and Francis (2003) attributed this rapid growth rate to three factors. First, the LGL region is climatically similar to the Mute Swan's Eurasian range (Ciaranca et al. 1997). Second, there are few natural predators for Mute Swans on the LGL (Ciaranca et al. 1997). Third, protection provided under the Migratory Birds Act since 1974, has allowed the population to grow unchecked. Unless management plans are implemented, the most conservative estimate of a 10% growth rate per annum will theoretically result in a doubling of the population in 7 years (Petrie and Francis 2003).

This rapid population growth is potentially problematic as Mute Swans have high consumptive requirements and disruptive foraging behaviours (Allin et al. 1987; Ciaranca et al. 1997). Consequently, Mute Swan foraging can be destructive to macrophyte growth and availability (Gillham 1956, Mathiasson 1973, and Ciaranca et al. 1997). Mute Swans are present throughout the year on the LGL, and therefore forage continuously on SAV. These combined factors suggest that Mute Swans have the potential to substantially impact the wetland ecosystem. As the LGL coastal wetlands provide submerged aquatic vegetation, SAV, for migratory waterfowl, Mute Swan presence on the LGL may compromise the availability of this food resource for native birds.

OBJECTIVES AND PREDICTIONS

The primary objective of this research was to identify which species of SAV are being consumed by Mute Swans. Mute Swans are herbivorous, with some invertebrates being consumed incidentally during foraging (Perry, unpubl data). Previous studies concluded that the diet of Mute Swans in England consisted of roots, shoots, and grains (Owen and Cadbury 1975). A study conducted in the Chesapeake Bay area of Maryland identified Eelgrass (*Zostera marina*), and Widgeon grass (*Ruppia Maritima*), as the primary dietary items consumed by Mute Swans (Perry, unpubl data). Although a similar study has never been conducted on the LGL, I predicted that there is dietary overlap between Mute Swans and native waterfowl. Species identified as important for waterfowl on the LGL include Muskgrass, *Chara vulgaris*, Common Waterweed, *Elodea canadensis*, various Pondweeds, *Potamogeton spp.*, Wild Rice, *Zizania palustris*, various Arrowhead tubers, *Sagittaria spp.*, and Wild Celery, *Vallisneria americana* (Martin and

Uhler 1939, Pauls and Knapton 1993, Petrie 1998, Knapton and Petrie 1999). If this prediction is true, Mute Swans may in fact be competing inter-specifically with native waterfowl. This study will also compare dietary intake between sexes and ages over the reproductive period. I further predicted that the diet of female Mute Swans changes throughout reproduction due to changes in nutritional requirements. Furthermore, I predicted that Mute Swan cygnets consume similar items as adults because adults dislodge food items for cygnets. Because this is the first study investigating Mute Swan dietary intake on the LGL, results will be instrumental in informing researchers and government officials of the potential impacts of Mute Swans on this ecosystem. This information will also assist these individuals in making informed management decisions with respect to this rapidly expanding population, and lay the foundation for future research.

STUDY AREA

Mute Swans were collected from various coastal wetlands associated with the LGL (Figure 1). The primary collection sites were the marshes at Long Point, Lake Erie, as well as the marshes on the Canadian side of Lake St. Clair, and the Detroit River. Long Point is a 35 Km sandspit extending into the eastern basin of Lake Erie and encompassing 24,000 hectares of marsh habitat (Petrie 1998). Among coastal wetlands on the LGL, Long Point's Inner Bay has the highest waterfowl use, providing staging habitat for hundreds of thousands of migratory waterfowl (Petrie 1998); Long Point was designated as a Ramsar site based on this. Knapton and Petrie (1999) suggest the high waterfowl use is at least partially due to the amount of SAV present in Long Point's Inner

Bay: over 95% of the Bay is covered by SAV. There are approximately 18,880 hectares of wetlands along Lake St. Clair and the Detroit River that are used extensively by several species of waterfowl (Petrie and Francis 2003, Prince et al. 1992). Wetlands along the southeastern shore of Lake St. Clair have been designated as a National Wildlife Area because of the importance of the area for staging waterfowl.

METHODS

Collection and Dissection

Mute Swans were collected from various coastal LGL wetlands during 2001 and 2002 ($n = 202$). Birds were collected opportunistically throughout the pre-breeding and breeding period (4 Apr - 25 May, 2001 and 26 Jan – 24, June 2002) by shotgun and rifle. Approximately 50 ml of 80% ethanol was injected into the esophagus of birds shortly after collection to preserve dietary contents. Birds were tagged for identification and returned to the laboratory where they were frozen. After thawing, birds were dissected and the esophagus and proventriculus contents were removed. Diet samples were sorted to genus or species level (Martin and Uhler 1939, Martin 1954, Hotchkiss 1972, Newmaster et al. 1997). Unknown plant parts were grouped as leaves, stems, tubers, seeds, or decaying/digested. Samples were dried at 60°C for 48 hours and weighed to 0.0001g. Birds containing less than 5 identifiable dietary items, or less than 0.01g (dry) were excluded from the analysis. Of the 202 Mute Swans collected, 94 had sufficient diet samples for statistical analysis.

Birds were sexed by internal examination of ovaries/testes. Female Mute Swans and their mates were assigned to the following reproductive stages:

1/ Pre-laying/Laying - birds in early rapid follicular growth, rapid follicular growth, and

birds with post ovulatory follicles which also had an ova in the oviduct or developing follicles ($n = 10$ females, 18 males)

2/ Incubating - post-ovulating birds, possessing a brood patch (vascularization of breast region), with regressed ovary and oviduct. Many of these birds were collected on or near nests with eggs ($n = 18$ females, 13 males).

3/ Brood rearing - with a brood of cygnets ($n = 5$ females, 2 males).

4/ Non-breeders/failed Breeders - Subadult birds possessing obvious signs of a bursa of fabricius and no internal or external signs of having reproduced. Adult females with burst and regressed follicles but no sign of a brood patch, flocked birds with no obvious internal or external signs of having reproduced ($n = 5$ females, 7 males).

All males collected during peak incubation that were alone and persistently defending territories were placed into the incubating category. Cygnets ($n = 16$) were also collected for dietary analysis.

Data Analysis

Kruskal-Wallis rank sums multiple comparisons tests were used to test for between chronological stage (within-sex) and within chronological stage (between-sex) differences in dietary intake (Zar 1999). Comparisons were conducted for the primary food items consumed, and those that have been identified as important foods for native waterfowl. Composite male (all chronological stages combined), composite female, and cygnet diets were compared in the same manner. Non-parametric multiple comparison post-hoc tests were applied when significance from the Kruskal-Wallis test was determined (Zar 1999). A significance level of $\alpha = 0.05$ was used, with the

Bonferonni correction being applied for the number of tests being run on each data set (Zar 1999). As multiple tests are run on one data set, power is compromised, and it was necessary to reduce alpha to combat this problem. Dietary data are presented as mean aggregate dry mass and percent frequency of occurrence (Swanson et al. 1974). Where vegetative species contributed less than 5% by mass to all categories, they were grouped and summed as “other identified” for tables.

RESULTS

Male Mute Swan diets were primarily composed of Muskgrass (*Chara vulgaris*), and Coontail (*Ceratophyllum demersum*) vegetation, and Arrowhead (*Sagittaria spp.*) tubers (Table 1, Table 2). Slender Naiad (*Najas flexilis*), Common Waterweed (*Elodea Canadensis*), several Pondweed species (*Potamogeton spp.*), and various invertebrates were frequently present in the diet but did not contribute greatly by mass (Table 1, Table 2). Consumption of Muskgrass ($\chi^2=2.5351$, $df=2,36$, $p=0.400$), Coontail ($\chi^2=5.056$, $df=2,36$, $p=0.080$), and Arrowhead tubers ($\chi^2=4.442$, $df=2,36$, $p=0.110$) did not vary significantly by reproductive stage. This analysis was conducted having removed brood-rearing males ($n = 2$) because of the small sample size in this group. Although not statistically significant, males appear to consume a greater proportion of Coontail during the Pre-Laying/Laying period (32 % aggregate % dry mass) than during Incubation (3.4%) and non/failed breeding (5.6%).

Female Mute Swan diets consisted primarily of Coontail, Common Waterweed, and *Potamogeton spp.*, with Muskgrass constituting the majority of the diet of non/failed breeders (Table 3). Invertebrates were probably incidentally ingested as they were

consumed frequently by females, but never contributed substantially to overall dietary mass (Table 3, Table 4). As was observed with males, females frequently consumed Slender Naiad, several species of Pondweed, and Wild Rice (*Zizannia palustris*), however these food items were never consumed in high proportions. Pre-laying/laying females ate higher proportions of Coontail than non/failed breeders ($Q=2.834$); Coontail was consumed by 90% of the Pre-Lay/Lay individuals and 0% on non/failed breeders (Table 4). Although not statistically different ($0.441 \leq Q \leq 2.611$), Coontail consumption by females appears to decrease throughout reproduction. There were no significant differences throughout female reproduction for Muskgrass ($\chi^2=2.949$, $df=3,33$, $p=0.400$), or Common Waterweed ($\chi^2=1.003$, $df=3,33$, $p=0.801$).

Males and females in the pre-laying/laying category consumed similar proportions of Common Waterweed ($\chi^2=0.181$, $df=1,25$, $p=0.671$), Muskgrass ($\chi^2=1.184$, $df=1,25$, $p=0.277$) and Coontail ($\chi^2=0.001$, $df=1,25$, $p=0.981$). Incubating males and females also consumed similar proportions of the same respective species ($\chi^2=4.124$, $df=1,28$, $p=0.042$), ($\chi^2=1.940$, $df=1,28$, $p=0.164$), ($\chi^2=0.037$, $df=1,28$, $p=0.847$). Although the Bonferonni correction removes significance from the Waterweed comparison, this trend suggests that perhaps incubating males are consuming more Common Waterweed than are incubating females. Waterweed was present in 62% of incubating male (Table 2) and 28% of incubating females (Table 4).

Mute Swan cygnet diets were primarily composed of Common Waterweed and Flat-stemmed Pondweed, *Potamogeton zosteriformis* (Table 5). Although invertebrates were identified in greater than 12% of cygnet diets, they represented less than 0.04g to overall dietary mass (Table 5, Table 6). Cygnets consumed significantly more Flat-

stemmed Pondweed than adult males ($Q = 3.63$); differences were not significantly different from adult females ($Q = 2.515$). Flat-stemmed Pondweed was present in the diets of 69% of cygnet, 52% of adult males and 49% of adult females. Cygnets and adults consumed similar proportions of Muskgrass ($\chi^2=4.700$, $df=2,90$, $p=0.095$), Common Waterweed ($\chi^2=3.430$, $df=2,90$, $p=0.180$) and Coontail ($\chi^2=7.998$, $df=2,90$, $p=0.018$), although the latter comparison was noted as a trend. Cygnets appear to consume less Coontail than either male or female Mute Swans.

DISCUSSION

Dietary Consumption

Breeding and non-breeding Mute Swans primarily consumed the vegetative structures, such as leaves and stems, of SAV on the lower Great Lakes. This agrees with previous studies of Mute Swan dietary habits on Chesapeake Bay (Ciaranca et al. 1997, Perry, unpub data). Incubating males and brood-rearing females foraged on high proportions of Arrowhead tubers. Although Sago, (*Potomageton pectinatus*), and Wild Celery (*Valisneria americana*) tubers contributed to female consumption in the incubating category, the large tuber mass in the Brood-Rearing group was solely due to the presence of Arrowhead. Martin and Uhler (1939) reported that Arrowhead tubers have excellent nutritional value for waterfowl. The large quantities of tubers consumed by Incubating males and Brood-Rearing females may be influenced by the large amounts of body fat lost by both sexes during these stages (Petrie, unpub data), as tubers have high quantities of carbohydrates.

Both males and females consumed large quantities of Coontail during the early stages of reproduction and subsequently reduced their consumption of this plant as reproduction progressed (non-significant for males). Coontail can over-winter as above ground biomass and individual plants bud off tips, which begin growth in late winter or early spring (Martin and Uhler 1939). The availability of this plant in early spring could be the primary determinant of why it is foraged on so heavily by male and female Mute Swans during the early stages of reproduction. Reznicek and Catling (1989) report Coontail as a widespread and dominant member of the Long Point flora, yet it is generally not an important food for waterfowl (Low and Bellrose Jr. 1944, Bartonek and Hickey 1969, Pauls and Knapton 1993). Willey and Halla (1972) also reported the presence of Coontail in the diets of Mute Swans in Rhode Island.

Cygnets diets contained a substantially higher proportion of Flat-stemmed Pondweed when compared to composite male and female diets. Perhaps this plant is more easily digested than bulkier vegetation. Birkhead and Perrins (1986) suggest that Mute Swan cygnets prefer green or yellow vegetation. Although cygnets can dabble on their own by 10 days of age, they continue to eat food dislodged by their parents (Ciaranca et al. 1997). Although adults may dislodge Flat-stemmed Pondweed for cygnets, males are not consuming it in similar proportions. Despite the fact that Martin and Uhler (1939) suggest that Flat-stemmed Pondweed has only fair nutritive value for waterfowl, its delicate leaves and stems may represent an ideal food source for cygnets.

Dietary Overlap

The SAV present on coastal wetlands serves as a vital food resource for the tens of thousands of waterfowl migrating through the LGL during the spring and fall. Four major food sources for native waterfowl also appear to be important in the diet of Mute Swans: Muskgrass, Common Waterweed, Arrowhead species and Pondweed species. Although Coontail is an important Mute Swan dietary item, it does not seem to be an important plant for most native waterfowl (Petrie 1998).

Muskgrass, a perennial algae, comprised the largest proportion of SAV in the Inner Bay at Long Point in 1992 (Knapton and Petrie 1999). In their assessment of waterfowl diets at Long Point, Pauls and Knapton (1993) calculated Muskgrass to be the third most consumed waterfowl food by weight. Only corn and oats, which are not aquatic vegetation, were consumed in greater proportions. Its abundance and nutrient content make Muskgrass an important component in the diets of native waterfowl migrating through the LGL; Martin and Uhler (1939) identified it as a nutritive food source sought after by diving ducks. Pauls and Knapton (1993) reported Coontail in all 9 species of waterfowl they studied.

Common Waterweed also constituted a substantial proportion of foods consumed by Mute Swans. While Reznicek and Catling (1989) observed widespread distribution of Common Waterweed, Pauls and Knapton (1993) reported that it represented less than 0.8% of the total plant composition in the Inner Bay in 1992. Although Martin and Uhler (1939) reported its value as low for waterfowl, Common Waterweed ranked as the fourth most important aquatic waterfowl food (Pauls and Knapton 1993). The leaves of the plant are an important food source for waterfowl, specifically in the diets of American

Wigeon (*Anas americanus*) and American Black Ducks (*Anas rubripes*) (Pauls and Knapton, 1993).

The seeds and vegetative portions of various *Potamogeton* species are consumed by several waterfowl, namely American Wigeon, Canvasbacks (*Aythya valisineria*), American Black Ducks, Redheads (*Aythya americana*), and Ruddy Ducks (*Oxyura jamaicensis*) (Pauls and Knapton 1993). Several *Potamogeton* species were also consumed by the Mute Swans in this study, including *P. zosteriformis*, *P. richardsonii*, *P. pusillus*, and *P. pectinatus*. However, other than the high proportion of Flat-stemmed Pondweed in cygnet diets, no single species was heavily foraged on.

The high consumption of Arrowhead tubers by incubating males and brood-rearing female Mute Swans may have ecological consequences. Because of their high caloric value, tubers are a food resource which is sought after by a number of native waterfowl species (Martin and Uhler 1939). Mute Swan dietary consumption of Arrowhead may decrease this energy-rich resource for other waterfowl. Jonzen et al. (2002) point out that consumption of tubers usually involves ingestion of the entire structure. Thus consumption of these food items could compromise the future growth of the plant (Jonzen et al. 2002).

As Arrowhead and Muskgrass vegetation are important foods for migrating Tundra Swans at Long Point (S.A. Petrie, unpubl. data), exotic Mute Swans may compete inter-specifically with this native species. Up to 30,000 Tundra Swans pass through Long Point during spring migration (Petrie 1998).

Potential Implications

Where it has been demonstrated that Mute Swans share similar diets with native waterfowl, inter-specific competition is possible. Native Tundra Swans (*Cygnus columbianus*) stage on the LGL for short periods during spring and fall migrations. In contrast, Mute Swans are generally non-migratory and consume SAV on the LGL throughout the annual cycle. It has been suggested that Mute Swans increase their dietary intake prior to reproduction in the late winter and early spring (Mathiasson 1973). This increased foraging may be problematic because the American Bird Conservatory has identified this time period as vital for maintaining the integrity of SAV (Fenwick and Winegrad 2001). Consequently, less vegetation may be available for waterfowl in the subsequent breeding and staging season (Idestam-Almquist 1998).

To add to this potential problem, Mute Swans tend to overgraze areas, causing localized decreases in vegetative productivity (Ciaranca et al. 1997). Sondergaard et al. (1996) and Idestam-Almquist (1998) noted that even small populations of waterfowl can overgraze areas, significantly suppressing macrophyte growth. Mathiasson (1973) concluded that Mute Swans were responsible for the removal of widespread beds of sea lettuce, *Ulva lactuca*. Mathiasson (1973) reported that 45 Mute Swans effectively removed 8,635 kg of the vegetation. Recent studies report Maryland's population of 4,500 Mute Swans consumes upwards of nine million pounds of submerged aquatic vegetation per year (Hindman, unpubl data).

Mute Swans forage using a variety of feeding strategies, however upending and paddling are perhaps the most destructive to macrophyte growth. In both methods, the Swans dig at the substrate, thus destroying both above and below ground biomass (Ciaranca et al. 1997). Consequently, many submerged aquatic plants are destroyed and

the integrity of the remaining plant is severely compromised. Although Mute Swans uproot 20 lbs of wet vegetation daily, only approximately 8 lbs are consumed (Mathiasson 1973, Fenwick 1983).

The coastal wetlands of the LGL provide important habitat for many wetland dependent wildlife (Mitsch and Gosselink 1993, Petrie 1998). It is therefore necessary that the integrity of remaining LGL coastal wetlands be maintained (Petrie 1998). Sondergaard et al. (1996) suggest that adequate densities of submerged aquatic vegetation are necessary to maintain clear water conditions in shallow lakes. Reese (1975) also notes that a decrease in SAV provides less cover for fish and insects, and Reid et al. (1996) have reported the importance of LGL wetlands to various insects, amphibians and reptiles. The damaging foraging behaviours of Mute Swans have the capacity to severely limit the productivity of the LGL coastal areas. Furthermore, results of this study suggest that Mute Swans are consuming SAV that is important to native waterfowl, therefore the potential for inter-specific competition is a concern.

The LGL are an important staging area for 25 native waterfowl species (Petrie 2002). During the migratory period these birds depend on increasing their food reserves to ensure energy for migration and subsequent reproduction. The rapidly expanding Mute Swan population foraging on species of SAV consumed by native waterfowl could reduce the carrying capacity of the LGL ecosystem for these birds.

Future Studies

The ability to quantify scientific phenomena is vital in the field of ecology. Although this study suggests Mute Swans and native waterfowl consume similar

vegetation on the LGL, we still cannot ascertain if Mute Swans are adversely impacting SAV or lowering the carrying capacity of the LGL for native waterfowl. Mute Swan exclusion plots and control plots should be placed in areas where Mute Swan dietary items are found. Exclusion experiments could offer quantifiable results as changes in vegetative composition could be observed over time. It is important to note that, because Mute Swans have presumably not come close to reaching their carrying capacity on the LGL (Petrie and Francis 2003), it may be difficult to ascertain if Mute Swans are presently impacting SAV abundance or species composition. However if these experiments are done on a local level, where high numbers of Mute Swans are known to congregate, impacts might be quantifiable. Sondergaard et al. (1996) found significantly higher macrophyte biomass in exclosure plots versus areas where waterfowl were permitted to graze. Recolonization events within control plots should be observed to determine the length of time necessary for SAV biomass to return to pre-grazed levels.

Given the present population growth rate of LGL Mute Swans, research should continue in order to establish the role of Mute Swans in the LGL ecosystem. Specifically, ways that Mute Swans are affecting growth and biomass of SAV should be identified.

ACKNOWLEDGEMENTS

I would like to take this opportunity to express my gratitude to those individuals involved in the completion of this endeavor. I would like to thank my supervisor, Dr. S. Petrie, for extending me the opportunity to complete a thesis project, and for his support and suggestions along the way. I also wish to thank Dr. J. Millar for agreeing to co-supervise the project as an on-campus contact. I would like to thank my advisors, Drs.

R.J. Scott and L. Zanette for agreeing to serve on my committee, and for their input and assistance throughout. I further wish to thank K. Wilcox and S. Meyer for their assistance in identifying species, and for providing reference materials; E. Craggie and J. Anthonypillai for assistance in sorting diets; A. Flowers and C.D. Ankney for the use of their laboratory space; and S. Meyer for reviewing and commenting on my paper. Finally I would like to thank the Long Point Waterfowl and Wetlands Research Fund for funding.

REFERENCES

- Allin, C.C. 2003. Atlantic Flyway Mute Swan Management Plan. Report Prepared for the Snow Goose, Brant, and Swan Committee: Atlantic Flyway Technical Section. Atlantic Flyway Council.
- Allin, C.C., G.G. Chasko, and T.P. Husband. 1987. Mute Swans in the Atlantic flyway: A review of the history, population growth, and management needs. *Transactions of the Northeast Fish and Wildlife Conference* 44:32-47.
- Bartonek, J.C., and J.J. Hickey. 1969. Food habits of Canvasbacks, Redheads, and Lesser Scaup in Manitoba. *The Condor*. 71:280-290.
- Birkhead, M., and C. Perrins. 1986. *The Mute Swan*. Croom Helm, London.
- Chow-Fraser, P. 1998. A conceptual ecological model to aid restoration of Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario, Canada. *Wetlands Ecology and Management*. 6(1): 43-57.
- Ciaranca, M. A., C. C. Allin, and G. S. Jones. 1997. Mute Swan (*Cygnus olor*). *In The Birds of North America*, No. 273, A. Poole and F. Gill, eds. The academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- Dennis, D.G., and R.E. Chandler. 1974. Waterfowl use of the Ontario shorelines of the southern Great Lakes during migration. *In Waterfowl studies in eastern Canada*, H. Boyd, ed. Canadian Wildlife Service Report Series 29.
- Dennis, D.G., G.B. McCullough, N.R. North, and R.K. Ross. 1984. An updated assessment of migrant waterfowl use of Ontario shorelines of the southern Great Lakes. Pages 37-42 in *Waterfowl Studies in Ontario*, S.G. Curtis, D.G. Dennis, and H. Boyd, eds. Canadian Wildlife Service Occasional Paper No. 54.

- Fenwick, G.H. 1983. Feeding behavior of waterfowl in relation to changing food resources in the Chesapeake Bay. Dissertation, Johns Hopkins University, Baltimore, Maryland, USA.
- Fenwick G.H., and G.W. Winegrad. 2001. Letter sent on behalf of the American Bird Conservancy to the Mute Swan Management Plan of Maryland Department of Natural Resources.
- Gillham, M.E. 1956. Feeding habits and seasonal movements of mute swans on two south Devon estuaries. *Bird Study*. 3(3):205-212.
- Gottgens, J.F., B.P. Swartz, R.W. Kroll, and M. Eboch. 1998. Long-term GIS-based records of habitat changes in a Lake Erie coastal marsh. *Wetlands Ecology and Management*. 6(1):5-17.
- Hall, S.R., and E.L. Mills. 2000. Exotic species in large lakes of the world. *Aquatic Ecosystem Health and Management*. 3(1):105-135.
- Herdendorf, C.E. 1987. The ecology of the coastal marshes of western Lake Erie: A community profile. Rept. 85 (7a.) National Wetlands Research Center, Fish and Wildlife Service, US Department of the Interior, Washington, D.C.
- Hotchkiss, N. 1972. Common March, Underwater and Floating-leaved Plants of the United States and Canada. Dover Publications, Inc., New York.
- Hughes, B., J. Kirby, and J. M. Rowcliffe. 1999. Waterbird conflicts in Britain and Ireland: Ruddy Ducks *Oxyura jamaicensis*, Canada Geese *Branta canadensis*, and Cormorants *Phalacrocorax carbo*. *Wildfowl* 50:77-99.
- Idestam-Almquist, J. 1998. Waterfowl herbivory on *Potamogeton pectinatus* in the Baltic Sea. *OIKOS* 81:323-328.
- Jessen, S., J.C. Day, and J.G. Nelson. 1983. Assessing land-use regulation in coastal wetlands: the case of the Long Point Area, Lake Erie, Ontario. *Coastal Zone Management Journal*. 11:91-115.
- Jonzen, N., B.A. Nolet, L. Santamaria, and M.G.E. Svensson. 2002. Seasonal herbivory and mortality compensation in a swan-pondweed system. *Ecological Modelling*. 147(3):209-219.
- Knapton, R.W. 1993. Population Status and Reproductive Biology of the Mute Swan, *Cygnus olor*, at Long Point, Lake Erie, Ontario. *The Canadian Field-Naturalist* 107:354-356.

- Knapton, R.W., and S.A. Petrie. 1999. Changes in distribution and abundance of submerged macrophytes in Long Point's Inner Bay, Lake Erie: implications for foraging waterfowl. *Journal of Great Lakes Research* 25:783-798.
- Low, J.B., and F.C. Bellrose Jr. 1944. The seed and vegetative yield of waterfowl food plants in the Illinois River Valley. *Journal of Wildlife Management* 8(1): 7-22.
- Martin, A.C. 1954. Identifying pondweed seeds eaten by ducks. *Journal of Wildlife Management* 18:514-520.
- Martin, A.C., and F.M. Uhler. 1939. Food of Game Ducks in the United States and Canada. United States Department of Agriculture Technical Bulletin No. 634, Washington, D.C.
- Mathiasson, S. 1973. A moulting population of non-breeding Mute Swans with special reference to flight-feather moults, feeding ecology and habitat selection. *Wildfowl* 24: 43-53.
- Mitsch, W.J., and J.G. Gosselink. 1993. *Wetlands* 2nd Edition. Van Nostrand Reinhold, NY, USA.
- Mitsch, W.J., and V. Bouchard. 1998. Enhancing the roles of coastal wetlands of the North American Great Lakes. *Wetlands Ecology and Management*. 6(1):1-3.
- Newmaster, S.G., A.G. Harris, and L.J. Kershaw. 1997. *Wetland Plants of Ontario*. Lone Pine Publishing, Edmonton, Canada.
- Owen, M, and C.J. Cadbury. 1975. The ecology and mortality of swans at the Oaks Washes, England. *Wildfowl*. 25:31-42.
- Pauls, K., and R. Knapton. 1993. Submerged macrophytes of Long Point's Inner Bay: Their distribution and value for waterfowl. Long Point Environmental Folio Publication Series, Technical Paper 1, J.G. Nelson and P.L. Lawrence, editors. Heritage Resource Center, University of Waterloo, Ontario.
- Petrie, S.A. 2002. Mute Swans make noise: lower Great Lakes population scrutinized. *Birding* 34:642-644.
- Petrie, S.A. 1998. Waterfowl and Wetlands of long Point Bay and Old Norfolk County: Present Conditions and Future Options for Conservation. Report prepared for the Norfolk Land Stewardship Council.
- Petrie, S.A. and C.M. Francis. 2003. Rapid increase in the lower Great Lakes population of feral mute Swans: A review and a recommendation. Submitted: *Wildlife Society Bulletin*.

- Prince, H.H., P.I. Padding, and R.W. Knapton. 1992. Waterfowl use of the Laurentian Great Lakes. *Journal of Great Lakes Research* 18:673-699.
- Reese, J. G. 1975. Productivity and management of feral Mute Swans in Chesapeake Bay. *Journal of Wildlife Management*. 39:280-286.
- Reid, R., R. Symmes, and D. van Hemessen. 1996. Towards a Conservation Strategy for Carolinian Canada. Report prepared for the Carolinian Canada Steering Committee. 59pp.
- Reznicek, A.A., and P.M. Catling. 1989. Flora of Long Point, Regional municipality of Haldimand-Norfolk, Ontario. *The Michigan Botanist*. 28:99-174.
- Ricciardi, A. And H.J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology and Evolution*. 15(2):62-65.
- Smith, P.G.R., V. Glooschenko, and D.A. Hagan. 1991. Coastal wetlands of three Canadian Great Lakes: inventory, current conservation initiatives, and patterns of variation. *Canadian Journal of Fisheries and Aquatic Science*. 48:1581-1594.
- Sondergaard, M., L. Bruun, T. Lauridsen, E. Jeppesen, and T.V. Madsen. 1996. The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. *Aquatic Botany* 53:73-84.
- Swanson, G.A., G.L. Krapu, J.C. Bartonek, J.R. Serie, and D.H. Johnson. 1974. Advantages in mathematically weighting waterfowl food habits data. *Journal of Wildlife Management* 38:302-307.
- Weller, M. W. 1969. Potential dangers of exotic waterfowl introductions. *Wildfowl* 20:55-58.
- Willey, C.H., and B.F. Halla. 1972. Mute Swans of Rhode Island. Rhode Island Dept. Nat. Res., Div. Fish and Wildl., Wildl. Pamphlet, no.8.
- Zar, J.H. 1999. *Biostatistical Analysis*. Prentice-Hall, Inc., New Jersey.

Table 1. Aggregate percent dry mass of the esophageal and proventriculus contents of breeding and non-breeding male Mute Swans, *Cygnus olor*, collected from coastal lower Great Lakes wetlands during the 2001 and 2002 breeding seasons

Food Item	Pre-Laying/Laying n = 18	Incubating n = 13	Brood-Rearing n = 2	Non/Failed Breeder n = 7
<i>Elodea canadensis</i>	3.0	7.2		28.1
<i>Chara vulgaris</i>	61.5	13.0		12.2
<i>Ceratophyllum demersum</i>	32.3	3.4		5.6
<i>Najas flexilis</i>	0.2	1.9		1.8
<i>Potamogeton spp.</i>	1.1	3.3	99.7	4.4
<i>Zizania palustris</i>	0.4	0.4	0.3	3.5
Other identified	0.5	0.2		2.0
<i>Sagittaria</i> Tubers		67.5		10.7
Seeds	0.3	tr*		
Algae		0.1		
Invertebrates	0.2	1.4		12.2
Unknown	0.6	1.6		19.5

* = trace < 0.04 g

Table 2. Percent occurrence of the esophageal and proventriculus contents of breeding and non-breeding male Mute Swans, *Cygnus olor*, collected from coastal lower Great Lakes wetlands during the 2001 and 2002 breeding seasons

Food Item	Pre-Laying/Laying n = 18	Incubating n = 13	Brood-Rearing n = 2	Non/Failed Breeder n = 7
<i>Elodea canadensis</i>	42.1	61.5		42.9
<i>Chara vulgaris</i>	42.1	30.8		14.3
<i>Ceratophyllum demersum</i>	57.9	38.5		28.6
<i>Najas flexilis</i>	26.3	38.5		28.6
<i>Potamogeton spp.</i>	33.3	47.1	100.0	36.4
<i>Zizania palustris</i>	5.3	15.4	50.0	42.9
Other identified	23.8	17.6		42.9
<i>Sagittaria</i> Tubers		23.1		14.3
Seeds	1.9	5.9		
Algae		7.7		
Invertebrates	47.4	30.8		28.6
Unknown	47.6	52.9		54.5

Table 3. Aggregate percent dry mass of the esophageal and proventriculus contents of breeding and non-breeding female Mute Swans, *Cygnus olor*, collected from coastal lower Great Lakes wetlands during the 2001 and 2002 breeding seasons

Food Item	Pre-Laying/Laying n = 10	Incubating n = 18	Brood-Rearing n = 5	Non/Failed Breeder n = 5
<i>Elodea canadensis</i>	16.1	4.7	16.6	0.2
<i>Chara vulgaris</i>	4.6	1.4		78.4
<i>Ceratophyllum demersum</i>	34.5	21.6	4.2	
<i>Najas flexilis</i>	0.4	8.3		
<i>Potamogeton spp.</i>	0.5	34.6	5.6	1.2
<i>Zizania palustris</i>	3.5	8.3	1.2	18.5
Other identified	1.2	7.0	0.2	
Tubers		0.9	59.9	
Seeds	0.9	tr*		0.2
Algae		4.4		
Invertebrates	3.9		0.6	tr
Unknown	34.4	8.7	11.8	1.3

* = trace < 0.04 g

Table 4. Percent occurrence of esophageal and proventriculus contents of breeding and non-breeding female Mute Swans, *Cygnus olor*, collected from coastal lower Great Lakes wetlands during the 2001 and 2002 breeding seasons

Food Item	Pre-Laying/Laying n = 10	Incubating n = 18	Brood-Rearing n = 5	Non/Failed Breeder n = 5
<i>Elodea canadensis</i>	40.0	27.8	20.0	20.0
<i>Chara vulgaris</i>	30.0	11.1		40.0
<i>Ceratophyllum demersum</i>	90.0	27.8	20.0	
<i>Najas flexilis</i>	30.0	22.2		
<i>Potamogeton spp.</i>	16.7	40.9	20.0	33.3
<i>Zizania palustris</i>	10.0	27.8	40.0	20.0
Other identified	25.0	22.7	20.0	40.0
Tubers		4.5	40.0	
Seeds	16.7	22.7		
Algae		13.6		20.0
Invertebrates	30.0		40.0	
Unknown	58.3	54.5	60.0	44.4

Table 5. Aggregate percent dry mass of the esophageal and proventriculus contents of composite adult male, adult female and cygnet Mute Swans, *Cygnus olor*, collected from coastal lower Great Lakes wetlands during the 2001 and 2002 breeding seasons

Food Item	Males n = 40	Females n = 38	Cygnets n = 16
<i>Elodea canadensis</i>	6.1	9.5	49.8
<i>Chara vulgaris</i>	38.9	15.6	0.1
<i>Ceratophyllum demersum</i>	19.0	20.4	0.2
<i>Najas flexilis</i>	1.0	3.0	
<i>Potamogeton spp.</i>	3.5	13.0	42.1
<i>P. zosteriformis</i>	1.2	9.0	35.9
<i>Zizania palustris</i>	0.6	7.4	0.3
Other identified	0.5	2.6	4.3
Tubers	26.8	7.8	1.0
Seeds	0.1	0.1	0.8
Algae	tr	1.5	
Invertebrates	1.4	1.5	tr
Unkown	2.1	17.1	1.4

* = trace < 0.04 g

Table 6. Percent occurrence of the esophageal and proventriculus contents of composite adult male, adult female and cygnet Mute Swans, *Cygnus olor*, collected from coastal lower Great Lakes wetlands during the 2001 and 2002 breeding seasons

Food Item	Males n = 40	Females n = 38	Cygnets n = 16
<i>Elodea canadensis</i>	43.2	28.2	18.8
<i>Chara vulgaris</i>	29.5	17.9	6.3
<i>Ceratophyllum demersum</i>	40.9	38.5	6.3
<i>Najas flexilis</i>	27.3	17.9	
<i>Potamogeton spp.</i>	52.3	48.7	68.8
<i>P. zosteriformis</i>	17.5	38.5	68.8
<i>Zizania palustris</i>	15.9	25.6	12.5
Other identified	29.5	30.8	6.3
Tubers	9.1	7.7	6.3
Seeds	18.2	17.9	25.0
Algae	2.3	7.7	
Invertebrates	34.1	15.4	12.5
Unknown	72.7	82.1	56.3

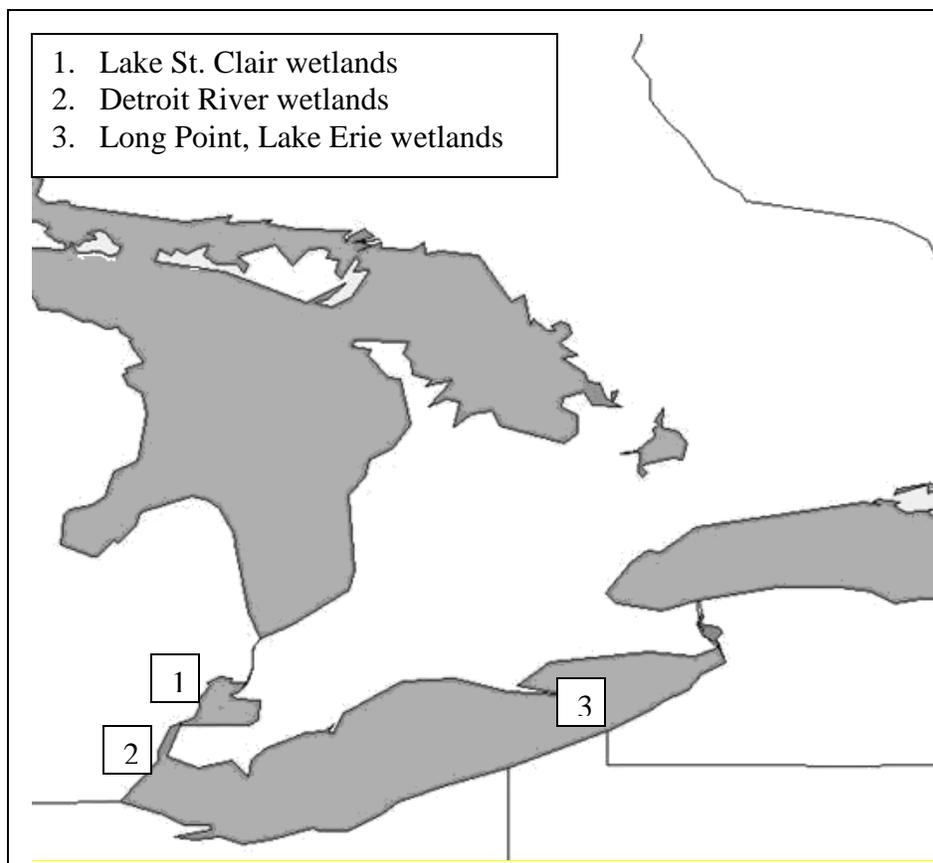


Figure 1. Geographic location of Mute Swan collection sites on the lower Great Lakes, 2001 and 2002