THE UNIVERSITY OF CALGARY

Use of Migratory Stopover Areas by Trumpeter Swans in Southern Alberta

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

AUGUST, 2000

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ABSTRACT

Migratory stopover areas for waterfowl provide energy reserves that are critical to success in breeding and rearing young. Trumpeter Swans (*Cygnus buccinator*) are considered 'at-risk' in Alberta, yet little is known of what constitutes suitable spring migratory habitat. Spring pond use was investigated near Calgary and in the Cardston-Mountain View area of southern Alberta. Trumpeter Swan time-budgets were measured using focal-animal techniques. Biotic and abiotic properties of ponds were assessed to determine habitat selection. I measured swan impact on macrophyte communities using exclosures to compare tuber and summer macrophyte densities in the excluded versus used areas of ponds. Trumpeter Swans spent the majority of their time feeding, and tuber and rhizome biomass and salinity were factors that influenced pond choice. Swans decreased macrophyte densities, but biomass was not significantly affected. Areas >1m deep that support macrophyte growth may help recolonize impacted zones, thus maintaining the food of Trumpeter Swans.

ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge the support given to me by my supervisors, Lee Jackson and Robert Barclay. Thank you both for giving me the opportunity to undertake this project and for your encouragement and advice during my studies. To my committee members: Elizabeth Crone, C.C. Chinnappa, and Cormack Gates, your input has been greatly appreciated, and thanks to Elizabeth for taking the time to discuss statistics. I learned a great deal from all of you.

Thanks to Claire Solohub, Abbie Dennis, and Cynthia Friedrich for their help observing swans and with many other tasks. Laura McCreanor, Colleen Rosenegger, Trecia Nussbaumer, and Lilly Cesh were great volunteers helping me to conduct winter fieldwork, and Janine Gano assisted in the lab. Don Iredale and Graham Lawson, your help was invaluable. Thanks to Judy Buchanan-Mappin for GPS assistance, and Elsie Pelletier, Karen Barron, and Norma Klein for their support. I would also like to thank all my lab-mates, Marianne Meding, Robyn Irvine, and the members of the Bat-lab; Krista Patriquin, Cori Wright and Lydia Hollis, for their support and providing the occasional distraction.

Gerry Beyersbergen (CWS- Edmonton), Darcy Brown (Alberta Environmental Protection- Cardston), Len Hills, and Vicki Romeril, provided information about pond locations and historical use. I would also like to thank Mr. D. Copithorne, Mr. R. Goodwin, Mr. G. Ibbotson, Mr. A. Kinsey, Mr. L. Marshall, N. and V. Romeril, Mr. W. Sibbald, Mr. J. Walburger, and Mr. W. Wolsey for allowing me access to the ponds, without whose cooperation this project would not have been possible. I would also like to add a special thanks to D. Lybbert for helping me "out" on more than one occasion.

And of course, I thank my parents for all of their support, no wonder why I've been in school so long!

E. Crone and the Cardston office of Alberta Environmental Protection also provided logistical support. This study was supported by the Challenge Grants in Biodiversity Program, a University of Calgary Thesis Research Grant, an Ellis Bird farm Graduate Scholarship, and Natural Sciences and Engineering Research Council of Canada awards to Robert Barclay and Lee Jackson.

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CHAPTER I

INTRODUCTION

The Trumpeter Swan (*Cygnus buccinator*) is the largest of the eight swan species and the largest species of waterfowl in North America (Mitchell 1994). It historically bred throughout North America, from Alaska to Ontario and south into Florida and New Mexico, but as European settlements moved west, Trumpeter Swan populations decreased (Banko 1960). Trumpeter Swans were hunted by native North Americans and early settlers for food, but a market for Trumpeter Swan feathers, down, and skin led to their near extinction. Hudson's Bay Company records show that the number of Trumpeter Swan skins taken into trading districts totalled 71 329 from 1821 to 1841 (Houston et al. 1997). Hunting was so great that in 1913 ornithologists thought the Trumpeter Swan would soon be extinct (Coale 1915). By the 1930's only 77 Trumpeter Swans were known in Canada and 69 in the United States, as the existence of an Alaskan breeding population was not verified until the 1950's (Banko 1960, Mackay 1978). Trumpeter Swans were classified as an "endangered species" in Canada until 1978 when their status was upgraded to "vulnerable". In 1996 they were listed as "not at risk" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) when the worldwide population of Trumpeter Swans approached 20 000 (Alvo 1996).

Recovery of the Trumpeter Swan began with the Migratory Bird Treaty Act of 1916 which led to a ban on hunting Trumpeter Swans, and the designation of Red Rock Lakes National Wildlife Refuge in Montana in 1935 (Banko 1960). Although Trumpeter Swans were removed from the endangered species list in Canada in 1978, they are presently considered blue-listed (threatened) in Alberta (Anonymous 1996).

Three Trumpeter Swan populations (Pacific Coast (PCP), Rocky Mountain (RMP) and Interior (IP)) are managed based on their geographical distribution (Figure 1.1) (Gillette and Shea 1995). The PCP consists of approximately 16 300 birds that breed in Alaska and winter in areas along the pacific coast from British Columbia to Southern California (Caithamer 1996). The RMP, which consists of approximately 2900 swans, contains the resident Tri-state and the migratory "Canadian" subpopulation (Subcommittee on Rocky Mountain Trumpeter Swans 1998). The Tri-state population resides year-round in the Greater-Yellowstone area of Wyoming, Montana and Idaho, and is estimated at approximately 400 individuals. The Canadian population is composed of an estimated 2500 swans that winter in the Tri-state area and migrate approximately 1400 km north along the east side of the Rocky Mountains to breeding sites primarily in Grande Prairie, Alberta (Mackay 1978), but also to some Yukon sites. Breeding Trumpeter Swans have also been reported in Southwestern Saskatchewan and Southern Alberta (Burgess 1997). The IP is made up of many small populations in Ontario and the upper mid-western United States and all 900 Trumpeter Swans present in 1995 were the result of reintroduction programs. Estimates of the historical population size of the IP exceed 100 000 birds (Gillette and Shea 1995).

Although Trumpeter Swan behaviour and habitat selection in breeding and wintering areas has been studied in the U.S. and Canada, especially for the Rocky Mountain Population (Shea 1979, Hampton 1981, Holton 1982, Maj 1983, Squires 1991), little is known of Trumpeter Swan habitat requirements during migration. In wintering and breeding areas, Trumpeter Swans appear to be selective in their habitat choice (Squires et al. 1992). Trumpeter Swans wintering in the Yellowstone area concentrate

Figure 1.1: Distribution of Trumpeter Swan populations. The breeding range of the Pacific Coast Population is shown in light shading and wintering range in dark shading. Winter and summer ranges overlap for both the Rocky Mountain and Interior Populations (from Gillette and Shea 1995).

in only a few areas where macrophytes are present, and tubers appear to be an important food (Shea 1979). It is suspected that poor quality wintering areas restrict growth of the RMP (Mitchell 1994, Subcommittee on Rocky Mountain Trumpeter Swans 1998). In Grande Prairie, Alberta, adults and cygnets use areas of lakes where submerged macrophyte biomass is high (Holton 1982). Significantly more total vegetation was located in lakes used for breeding than historically used or unused lakes, in Idaho and Wyoming, although there was no significant difference in the abundance of either emergent or submergent vegetation between lake-use classes (Maj 1983). Swans wintering in Idaho and Wyoming selected slow moving rivers that contained a greater tuber and macrophyte biomass compared to random sites, and tubers comprised a small percentage of available food, but represented 25% of the diet of Trumpeter Swans (Squires 1991). Tubers are high in energy and were consumed more in spring than in winter. Trumpeter Swans significantly increase their feeding time, and decrease the amount of time spent sleeping from winter to spring. However, little is known regarding habitat selection by Trumpeter Swans during migration and the use of sites by the Canadian migrating population.

It is suspected that during spring migration, waterfowl species gather energy required for reproduction (Gammonley and Heitmeyer 1990). Thus, it is important to identify habitat requirements and habitat-use strategies in migratory stopover areas between wintering and breeding grounds. During spring migration, Trumpeter Swans move in stages with documented stopover areas where individual neck-banded birds have been observed yearly (G. Beyersbergen, pers. comm.). Within stopover areas many ponds occur, but not all are used by Trumpeter Swans. Differential use of ponds by

swans suggests that particular physical and/or biological characteristics may be favoured and that these differ between frequently used and unused ponds. Another important aspect in examining Trumpeter Swan biology is to quantify the time-budgets of individuals in migratory stopover areas to determine the role that these areas play in preparing Trumpeter Swans for breeding.

Consumption of macrophyte overwintering structures by swans that use ponds each year may influence macrophyte abundance and community composition, and ultimately affect the sustainability of habitat use in stopover areas. The timing of herbivory with respect to the growing season, tissue consumption, selective feeding, and nutrient cycling, each affect macrophyte dynamics. Potential impacts of herbivory on macrophyte communities range from a shift in community composition and a reduction in the favoured macrophyte species, to an increase in phytoplankton associated with lowered macrophyte biomass, and increased nutrient inputs to the water (Mitchell and Perrow 1998). Macrophytes can cover the entire sediment surface if the water is shallow and transparent (Horne and Goldman 1994). Dense macrophytes can inhibit phytoplankton growth, but in areas of high nutrient loading, algal production may increase water turbidity and decrease macrophyte abundance by shading (Faafeng and Mjelde 1998). Early spring feeding by Trumpeter Swans may depress macrophyte numbers, although most likely not to the point of eliminating macrophytes in the short term. However, repeated feeding by swans may eventually cause a shift from a macrophyte-dominated to an algal-dominated state (Scheffer et al. 1993), and the habitat would no longer be useful to migrating Trumpeter Swans.

In my research I investigated three aspects of the migratory behaviour and ecology of Trumpeter Swans: 1) time-budgets in spring migratory stopover areas, 2) habitat selection for ponds within stopover areas, and 3) Trumpeter Swan energetic requirements and foraging, and the impact of Trumpeter Swans on macrophyte resources. No published research has been carried out in migratory areas in Canada and the information gained through my research can be applied to ensure the presence of adequate migratory habitat for reintroduced birds and also to identify and preserve current migratory habitat.

The chapters in my thesis address these issues, and my objectives for each chapter are to:

Chapter II: 1) Determine the dominant activity of adults and cygnets in stopover areas, 2) Determine if the proportion of time allocated to behaviours is affected by age-class (adult or cygnet) or site (year and area) effects, 3) Determine whether adults and cygnets have different foraging strategies, 4) Relate adult and cygnet behaviours to time of day, and 5) Determine if behaviours are correlated with ambient temperature.

Chapter III: 1) Document the movement of Trumpeter Swans through migratory stopover areas, 2) Determine abiotic and biotic properties of ponds that differentiate consistently used, variably used and unused ponds.

Chapter IV: 1) Calculate energetic requirements of Trumpeter Swans, 2) Determine quantity of forage removed, 3) Estimate foraging efficiency, and 4) Determine Trumpeter Swan impacts on the macrophyte community, and discuss habitat sustainability.

Chapter V: Summarize my research.

CHAPTER II

BEHAVIOUR OF TRUMPETER SWANS IN MIGRATORY STOPOVER AREAS OF SOUTHERN ALBERTA

INTRODUCTION

Analyses of activity time-budgets have been widely used to determine the needs of a variety of organisms. Determining time-budgets, in addition to determining the distribution of individuals, helps to identify important habitats, determine species' requirements, assess current and future habitat needs, and predict responses to expected habitat change (Van Horne 1983, Baldassarre et al. 1988, Paulus 1988, Hobbs and Hanley 1990, Earnst 1994). For example, time-budget data show that foraging is the dominant activity in migratory stopover areas of Lesser Scaup (*Aythya affinis*) (Gammonley and Heitmeyer 1990), and it is also known that during migration, Mallards (*Anas platyrhynchos*) accumulate lipid reserves (LaGrange and Dinsmore 1988), that are later used for reproduction (Krapu 1981). Body condition is a critical factor in determining reproductive success, and is often influenced by migratory conditions such as the quality of migratory stopover sites (Ankney and MacInnes 1978, Raveling 1979, Krapu 1981, Gammonley and Heitmeyer 1990, Dunn 2000). However, the role of these migratory habitats has been largely overlooked for some waterfowl species, because most research occurs in overwintering and breeding areas.

Time-budgets of Trumpeter Swans *(Cygnus buccinator)* during migration are poorly understood. It is suspected that at migratory stopover areas, Trumpeter Swans, like other waterfowl species, obtain nutrient, lipid, and protein reserves that are required for continued migration and subsequent reproduction (Mitchell 1994). Most Trumpeter

Swans in the Rocky Mountain Population migrate 1400 km in spring from overwintering areas in the Tri-state region of Montana, Idaho and Wyoming, to breeding grounds in Grande Prairie, Alberta, or continue north to the Yukon (Mackay 1978). During spring migration, Trumpeter Swans move north through Southern Alberta in a series of stages with documented stopover areas where individual neck-banded birds have been observed yearly (G. Beyersbergen, pers. comm.). Trumpeter Swans typically arrive at breeding lakes two to three weeks prior to thaw (Shandruk 1991), and nesting occurs as soon as nesting sites become ice-free (Pinel et al. 1991). Therefore, individuals must arrive at breeding areas with energy reserves. If Trumpeter Swans are using stopover areas to gain energy reserves for breeding, then an examination of Trumpeter Swan time-budgets may help demonstrate the role of migratory stopover ponds, and foraging should be the dominant activity.

Most Trumpeter Swans pair by their third winter and the average age of first reproduction is five years (Brechtel 1982), therefore individuals identified as cygnets (first-year swans) will not breed for several years, and need not allocate energy to breeding reserves. Therefore, I also predicted that if Trumpeter Swans use stopover areas to collect energy reserves required for breeding, adults would allocate more time to foraging compared to cygnets. No distinction between Trumpeter Swan sexes can be made at a distance, therefore I did not incorporate differences between sex into my study. I collected data on adult and cygnet behaviours during spring migration in two stopover areas of Southern Alberta to calculate time-budgets, determine if differences in activities exist between stopover sites, and investigate the influence of age-class (adult vs. cygnet) and external factors (ambient temperature, time of day) on time-budget allocation.

METHODS

Study area.- I studied Trumpeter Swan behaviour in two areas of Southern Alberta: i) approximately 50km west of Calgary (51°05'N, 114°30'W to 51°09'N, 114°42'W), and ii) in the Cardston-Mountain View area (49°02'N, 113°08'W, and 49°18'N, 113°32'W to 113°36'W). Both sites were located in foothill areas with numerous ponds and ranching was the main land-use practice. West of Calgary I studied thirteen ponds with a varied history of Trumpeter Swan use (G. Beyersbergen, pers. comm.; conversations with landowners), while in the Cardston-Mountain View area I focused on six ponds that had been used consistently by Trumpeter Swans for many years (D. Brown, pers. comm.; conversations with landowners).

Habitat use and time-budgets.- I made daily counts and observations of Trumpeter Swans in the Calgary study area from 7 April to 21 May 1999 (referred to as Calgary-1999) and from 12 April to 11 May 2000 (Calgary-2000). In the Cardston-Mountain View study area, I made weekly counts from 4 March to 27 March 2000 and daily from 29 March to April 11, 2000 (Cardston-Mountain View-2000). I used focal-animal techniques to quantify behaviours (Martin and Bateson 1986) each day on ten randomly selected individuals from each pond, if Trumpeter Swans were present. If fewer than ten swans were present, I observed all swans. I did not discriminate between adults and cygnets while randomly selecting individuals, but I did record the age-class (adult or cygnet) of each observation. Each observation period lasted for 10 minutes and I assumed that all observations were independent. If an individual disappeared from view during an observation, I discarded that observation, as observations that were not a full ten minutes in length might skew the data (Baldassarre et al. 1988). I sampled during

all daylight hours.

I made Trumpeter Swan observations from a vehicle at distances varying from 20 to 750 m. The closest observations were made with either the naked eye or with binoculars. For greater distances, I used a spotting scope with a 15-45x zoom. I checked all study ponds for the presence of Trumpeter Swans and conducted observations each day for the entire duration of swan presence for Calgary in 1999 and for Cardston-Mountain View ponds in 2000. In 2000, observations in the Calgary area began approximately 5 days after the first Trumpeter Swans arrived, as I was conducting observations in the Cardston-Mountain View area.

I recorded the total duration of activities from 10 minute focal-animal observations into one of six behaviour categories: swimming, flying/walking, sleeping (head curled onto back or tucked under wing), resting (head up, either alert or relaxed), preening, and foraging (with numbers of tip-ups and rocks recorded). Rocking was defined as the side-to-side motion associated with paddling feet to expose food, occurring during foraging on subsurface vegetation (Grant et al. 1997). I also recorded the time (Mountain Daylight Time) that each observation session began, and ambient temperature.

To assess adult versus cygnet foraging behaviour in more detail, I examined foraging bouts for 40 individuals (27 adults, 13 cygnets). I recorded the total duration of foraging to a maximum of 15 tip-ups and the duration of submergence during each tip-up of the foraging bout.

Statistical analysis.- To analyse behaviours, I combined resting and sleeping into a single category ("rest2"), and flying/walking and swimming were combined into "locomotion". In correlations I used sleeping as a variable in the analysis. I conducted

multivariate analysis of variance (MANOVA) on ln-ratio transformed behaviour data to determine variables that significantly influence Trumpeter Swan behaviour, with age-class (adult or cygnet), site (Calgary-1999, Cardston-Mountain View-2000, Calgary-2000), and the interaction of age-class and site as independent variables, and the ln-ratio transformed behaviours as dependent variables. I conducted univariate tests when the MANOVA returned a significant result and I completed multiple comparison tests on significant univariate tests.

Prior to multivariate analysis, I replaced values of 0 with 0.001 and then ln-ratio transformed the raw behavioural data, a standard procedure following compositional data analysis (Aitchison 1986, Aebischer et al. 1993). I ln-ratio transformed the raw data as there are inherent problems in analysing proportional data, such as the lack of independence of dependent variables within a single observation, which violates assumptions of most statistical tests (Aebischer et al. 1993). This violation occurs in my data because the proportion of time an individual allocates to one behaviour is linked to that of the other behaviours. Conducting a ln-ratio transformation of the data makes the ln-ratio variables independent, and statistical tests can then be applied to the ln-ratio variables (Aitchison 1986). Positive ln-ratio values indicate that the value of the numerator is greater than the denominator, while negative values are the opposite. The data did not follow a normal distribution (Klomoglorov-Smirnov, $P<0.05$) and this could not be rectified with the arcsine transformation that is typically applied to behavioural data (Zar 1984). However, multivariate tests are robust against the assumption of normality if the sample size is large, and I used Pillai's trace as it is the most robust against violations of assumptions (Olson 1974, Lindman 1992). It may be of interest to

note that the other, less robust, MANOVA measures (i.e. Wilks' lamda) returned the same results as Pillai's trace.

I compared the foraging behaviour of adults and cygnets with Mann-Whitney U-tests. I compared the rate of tip-ups and the rate of rocks during foraging, and the average proportion of foraging time submerged during tip-ups, between the two age classes. I used Spearman rank-correlation to determine the influence of ambient temperature on the proportion of time allocated to foraging and sleeping. I did not differentiate between age-class or site for correlation analysis. I calculated an average value for foraging and sleeping at each temperature and conducted the correlation on the average values, to reduce the sample size and decrease the chance of receiving a significant result simply due to a large sample size. I also compared the average daily minimum temperature during the time that swans were present in April 1999 and 2000 for the Calgary area, with data obtained from the Climatological Station at the Barrier Lake Field Station (Environment Canada 2000), to assess whether conditions differed between these years. I used untransformed behavioural data to examine time of day effects on proportions of time allocated to different activities. I used five time-intervals: early morning (0600-0859), late morning (0900-1159), early afternoon (1200-1459), late afternoon (1500-1759) and evening (1800-2059). I combined all sites for this analysis, although I conducted separate analyses for adults and cygnets using a Kruskal-Wallis test for each behaviour. I conducted nonparametric pairwise comparisons on significant results (Siegel and Castellan 1988). Means and standard errors are reported throughout, and I used a 0.05 probability level to determine significance. I used SYSTAT (Version 7.0) to conduct all statistical analyses.

RESULTS

During the course of this study I conducted 1338 behavioural observations, for a total of 223.0 hours. In the Calgary-1999 study area I conducted 542 10-minute observations (409 adults and 133 cygnets), from the total 1300 Trumpeter Swan-days counted (where one swan-day represents a single swan present on a pond for a single day). In Calgary-2000, I counted 2002 Trumpeter Swan-days and observed 431 adults and 174 cygnets, for a total of 605 observations. In Cardston-Mountain View-2000, I completed 191 observations, including 158 adults and 33 cygnets, from the total 667 Trumpeter Swan-days counted on study ponds.

At all sites, swans spent more time foraging than any other activity, with flying/walking being the least common activity (Table 2.1). The proportion of time spent foraging in 1999 was 53% and 58% for adults and cygnets, respectively. This decreased in 2000 to 42-46% for adults and cygnets in Cardston-Mountain View-2000 and Calgary-2000, while the proportion of time sleeping/resting increased over 1999 levels. Flying/walking was more common in 2000 compared to 1999. The overall activity budgets of both adults and cygnets in Cardston-Mountain View-2000 and Calgary-2000 were similar, with the exception that cygnets in Cardston-Mountain View-2000 preened approximately twice as much as cygnets in Calgary-2000.

The proportion of time allocated to ln-ratio behaviours differed significantly with age (MANOVA, Pillai's trace=0.061, df=12 and 2656, $P<0.001$), site (MANOVA, Pillai's trace=0.011, df=12 and 2656, $P<0.05$), and age x site (MANOVA, Pillai's trace=0.018, df=12 and 2656, $P<0.05$). Age explained a significant component of the variation in ln(preen/rest2) (Tables 2.2 and 2.3), as cygnets in Cardston-Mountain

Table 2.1: Mean proportions (SE) of time spent in activities by adult and cygnet Trumpeter Swans in Calgary-1999, Cardston Mountain View-2000, and Calgary-2000. Sample sizes are the number of 10-min observations completed.

	Calgary-1999		Cardston-Mountain View-2000		Calgary-2000	
Activity	**Adult (n=409)**	**Cygnet (n=133)**	**Adult (n=158)**	**Cygnet (n=33)**	**Adult (n=431)**	**Cygnet (n=174)**
Forage	0.531 (0.021)	0.581 (0.035)	0.465 (0.033)	0.420 (0.073)	0.445 (0.021)	0.436 (0.032)
Preen	0.129 (0.012)	0.161 (0.023)	0.109 (0.016)	0.237 (0.057)	0.109 (0.011)	0.127 (0.020)
Rest[1]	0.027 (0.004)	0.019 (0.007)	0.037 (0.005)	0.012 (0.005)	0.036 (0.005)	0.035 (0.007)
Sleep[1]	0.173 (0.017)	0.079 (0.020)	0.256 (0.031)	0.196 (0.059)	0.259 (0.019)	0.219 (0.029)
Fly/walk[2]	0.001 (0.001)	0.000 (0.000)	0.014 (0.006)	0.012 (0.010)	0.007 (0.002)	0.006 (0.002)
Swim[2]	0.138 (0.010)	0.161 (0.021)	0.119 (0.014)	0.123 (0.031)	0.143 (0.011)	0.177 (0.020)

[1]-combined into a single category for data analysis

[2]-combined into a single category for data analysis

Table 2.2: Univariate test statistics for ln-ratio behaviours included in MANOVA.

Ln-Ratio behaviour	df	Age effect		Site effect		Age x site effect	
		F	P	F	P	F	P
Forage/preen	2, 1332	0.910	0.340	3.762	0.023	2.170	0.115
Forage/rest2	2, 1332	2.010	0.153	16.649	<0.001	0.416	0.660
Forage/locomotion	2, 1332	0.004	0.949	15.156	<0.001	2.989	0.051
Locomotion/preen	2, 1332	1.828	0.177	6.625	0.001	4.179	0.016
Locomotion/rest2	2, 1332	2.354	0.122	5.183	0.005	0.443	0.642
Preen/rest2	2, 1332	11.575	0.001	19.069	<0.001	1.460	0.233

Table 2.3: Tukey post-hoc comparisons of ln-ratio behaviour means (SE) included in the MANOVA, following significant univariate tests. Same letters across site and stage were statistically similar ($P>0.05$).

	ADULTS			CYGNETS		
Ln-Ratio behaviour	**Calgary1999**	**Cardston2000**	**Calgary2000**	**Calgary1999**	**Cardston2000**	**Calgary2000**
Forage/preen	3.24 (0.47)a	2.66 (0.74)b	2.57 (0.45)b	4.17 (0.81)a	-0.65 (1.91)b	2.84 (0.73)b
Forage/rest2	4.96 (0.56)a	1.47 (0.90)b	1.31 (0.56)b	7.20 (0.81)a	1.79 (2.02)b	2.53 (0.87)b
Forage/locomotion	2.61 (0.37)a	1.40 (0.52)b	1.15 (0.34)b	3.92 (0.67)a	1.24 (0.87)b	0.11 (0.51)b
Locomotion/preen	0.64 (0.37)ab	1.26 (0.58)ab	1.33 (0.36)ab	0.25 (0.62)ab	-1.89 (1.57)a	2.52 (0.55)b
Locomotion/rest2	2.34 (0.45)a	0.07 (0.73)b	0.11 (0.47)b	3.28 (0.69)a	0.55 (1.74)b	2.05 (0.74)b
Preen/rest2	1.71(0.37)a	-1.19 (0.54)b	-1.21 (0.38)b	3.03 (0.59)a	2.44 (1.09)ab	-0.23 (0.57)b

View preened significantly more, and rested significantly less than adults (Table 2.1). There was no significant difference between adults and cygnets for any ln-ratio behaviour that included foraging (Table 2.2). There was a site effect for all ln-ratio behaviours (Table 2.2). Generally, behaviours at Cardston-Mountain View-2000 and Calgary-2000 were not significantly different, while Calgary-1999 behaviours were significantly different from the 2000 data (Table 2.3). However, for ln(forage/preen), no significant differences were detected with pairwise comparisons. Both site and age x site explained variation in ln-ratio locomotion/preen, with cygnets in Cardston-Mountain View-2000 preening significantly more, and conducting significantly less locomotion activities than cygnets in Calgary-2000 (Tables 2.2 and 2.3).

As no significant difference was detected in the time allocated to foraging by adults versus cygnets, I examined foraging behaviour in more detail to determine if there were differences in the way adults and cygnets forage. There was not a significant difference in the tip-up rates of adults (3.41 ± 0.04 tip-ups·min^{-1}) compared to cygnets (3.35 ± 0.07 tip-ups·min^{-1}; Mann-Whitney U, U=77389, n=638 and 233, P>0.05) during foraging, nor in the average time submerged during a tip-up (adults 12.61 ± 0.34 s, cygnets 11.88 ± 0.46 s; Mann-Whitney U, U=26590.5, n=323 and 156, P>0.005). The proportion of foraging time submerged was also not significantly different between adults (0.70 ± 0.03) and cygnets (0.73 ± 0.03; Mann-Whitney U,U=149, n=27 and 13, P>0.05). However, adults had a significantly higher rate of rocks (0.86 ± 0.03 rocks·min^{-1}) compared to that of cygnets (0.68 ± 0.05 rocks·min^{-1}; Mann-Whitney U, U=84451, n=638 and 233, P<0.005). This difference was also evident in the proportion of time that rocking occurred before a tip-up. Adults rocked 0.266 ± 0.011 of the time before a tip-up

while cygnets rocked 0.215 ± 0.016 of the time before tipping (Mann-Whitney U, U=83792, n=638 and 233, P<0.005).

Ambient temperature had a significant effect on the proportion of time that Trumpeter Swans allocated to foraging (Spearman, r=0.268, n=30, P<0.05) and sleeping (Spearman, r=-0.331, n=30, P<0.05), the two major activities. Trumpeter Swans restricted their activities at lower temperatures (< -4° C), at which point sleeping was the dominant activity and foraging levels decreased (Figure 2.1). At temperatures > -4° C, Trumpeter Swans allocated an average of approximately 55% of their time to foraging, while the proportion of time allocated to sleeping declined rapidly and remained low (0-20%) with further increases in temperature. The average daily minimum temperatures in April 1999 and 2000 were significantly different (Paired sample t-test, t=1.69, df=23, P=0.05). It was on average two degrees colder in 2000 (-3.9 ± 1.1° C) compared to 1999 (-1.8 ± 1.0° C). In addition, in 1999 the coldest daily minimum temperature was -13° C, while in 2000 the coldest day was -17° C.

Time of day significantly affected the proportion of time adults allocated to preening (Kruskal-Wallis, T=20.26, n=999, P<0.001) and locomotion (Kruskal-Wallis, T=20.85, n=999, P<0.001), but not to foraging (Kruskal-Wallis, T=8.34, n=999, P>0.05) or rest2 (Kruskal-Wallis, T=7.59, n=999, P>0.05). Foraging remained high throughout the day, while rest2 was highest from early morning to early afternoon, and decreased consistently into the evening (Figure 2.2). Preening was least common in the early and late morning, with higher levels occurring during late afternoon. The proportion of time adults spent in locomotion was almost uniform throughout the day, but increased into the evening, although no significant difference was detected with pairwise comparisons.

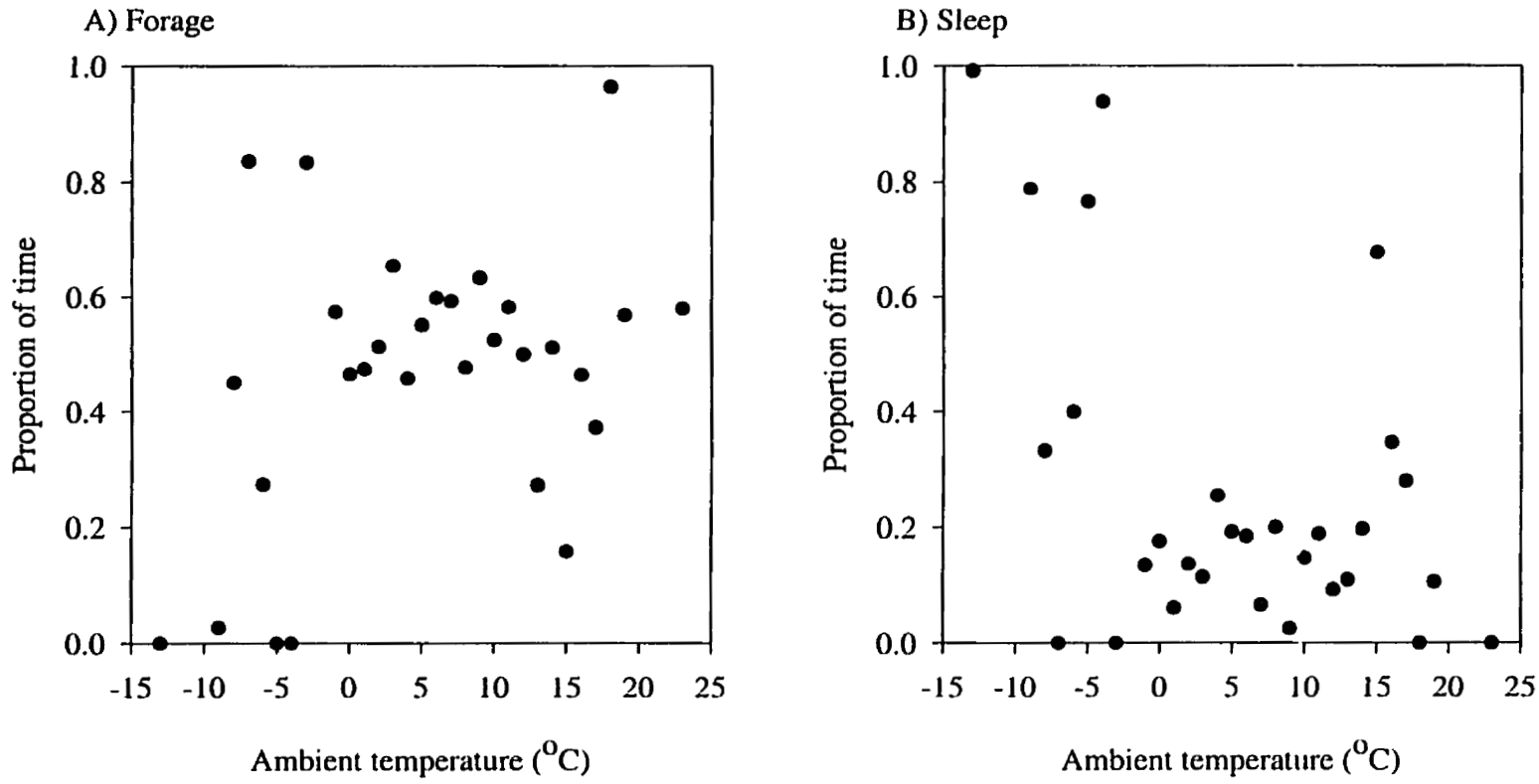

Figure 2.1: The influence of ambient temperature on the proportion of time Trumpeter Swans A) Forage and B) Sleep. Each point represents the average proportion of time the activity was performed at each given temperature.

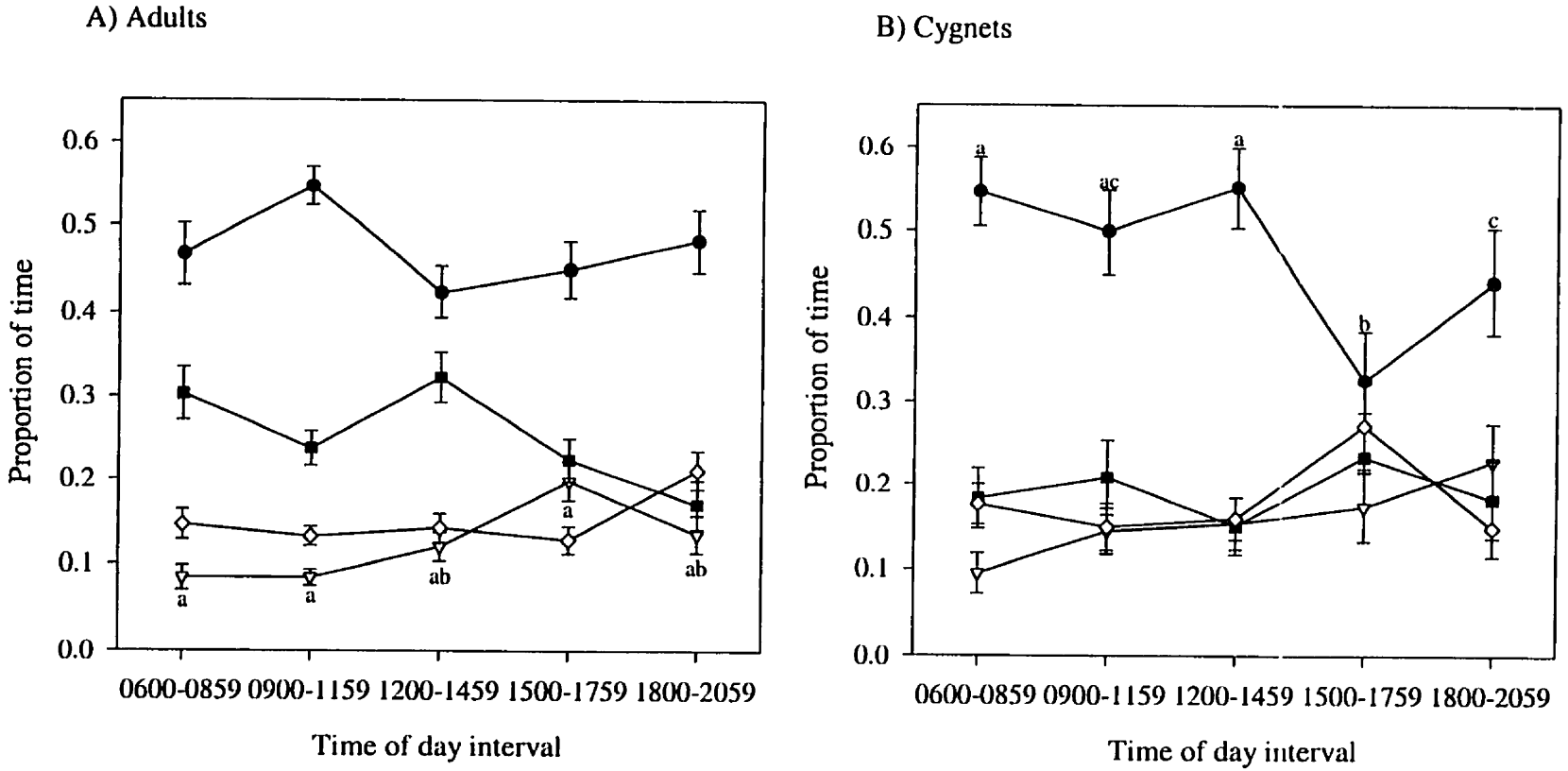

Figure 2.2: Mean (± SE) proportion of time allocated by A) Adults and B) Cygnets to: —●— foraging, —▽— preening, —■—rest2, and—◇— locomotion, according to time of day. Values with the same letter indicate no significant difference between proportion of time allocated to a behaviour within time of day intervals, from multiple comparison test.

The proportion of time that cygnets foraged was their only behaviour significantly affected by time of day (Kruskal-Wallis, T=10.35, n=339, P<0.05). Cygnets fed the most from early morning to early afternoon. In the late afternoon cygnets foraged significantly less compared to all other times of the day, but increased again in the evening (Figure 2.2). Although not significant, the proportion of time allocated to preening gradually rose from early morning (0.095) to evening (0.227; Kruskal-Wallis, T=8.31, n=339, P>0.05). The proportion of time allocated by cygnets to rest2 was somewhat variable throughout the day, fluctuating around an average of 0.191, lower than the adult average of 0.291 from early morning to early afternoon (Kruskal-Wallis, T=0.34, n=339, P>0.05). Finally, cygnets performed locomotion activities at almost constant levels from early morning to early afternoon, and in the evening, with a peak during late afternoon, although this was not significant (Kruskal-Wallis, T=4.02, n=339, P>0.05).

Discussion

Migrating Trumpeter Swans allocated the greatest proportion of their time to foraging while at stopover areas. This was similar to the behaviour of other species of migrating waterfowl (Paulus 1988). The average proportion of time spent foraging (0.486 ± 0.012) was much higher than has been reported in wintering areas (0.296 ± 0.027, Squires and Anderson 1997), but similar to the spring proportion (0.445 ± 0.021) recorded in the nonmigratory Tri-state subpopulation of the Rocky Mountain Population of Trumpeter Swans (Squires and Anderson 1997). The proportion of time allocated to the other primary behaviours (swimming, preening, sleeping) was also similar for this

migratory subpopulation compared to the spring data for the nonmigratory subpopulation (Squires and Anderson 1997). The overall average proportions that I recorded, and those for the springtime studies of nonmigratory swans were; swimming (0.145 ± 0.006 vs. 0.133 ± 0.013), preening (0.126 ± 0.007 vs. 0.115 ± 0.009), and sleeping (0.207 ± 0.010 vs. 0.166 ± 0.019).

The dominance of foraging in the spring time-budgets of both migratory and nonmigratory Trumpeter Swans suggests that swans have to build up energy reserves before breeding. Trumpeter Swans in the Canadian subpopulation take up to two months to complete their relatively short migration of 1400 km, which allows considerable time for foraging (Mackay 1978, Mitchell 1994), and suggests either that stopover sites are rich in food (Shea 1979) and worth remaining at, and (or) that they must stay longer to recoup energy reserves lost in each stage of migration. Individuals in the Tri-state population, although considered nonmigratory, move up to 80km from wintering to breeding areas (Shea 1979). Trumpeter Swans arrive at breeding lakes prior to ice-out to reclaim previous territories (Holton 1982, Shandruk 1991, Mitchell 1994) and breeding activities begin as soon as nesting sites become ice-free, in late April or early May (Pinel et al. 1991, Squires 1991). Therefore little opportunity exists for individuals to gather the reserves at breeding areas that are required for laying four to seven 300g eggs (Holton 1982, Maj 1983). During incubation (32-34 days), females spend 95-96% of their day on the nest (Cooper 1979, Holton 1982), and incubation constancy positively influences reproductive success (Shea 1979, Squires 1991). Since female swans essentially fast during the incubation period, they must rely heavily on endogenous energy reserves for survival (Bacon and Anderson-Harild 1989). The high spring foraging effort I observed

suggests that spring stopover areas are important for gaining those reserves, as observed in species of arctic nesting geese (Ankney and MacInnis 1978, Raveling 1979, McLandress and Raveling 1981). Female Lesser Snow Geese (*Chen caerulescens caerulescens*) with insufficient reserves to complete incubation either abandon the nest or starve (Ankney and MacInnes 1978). Although males do not incubate the eggs (Holton 1982), they defend the territory and maintain the nest (Shea 1979, Henson and Cooper 1992), and foraging levels of females and males increase after eggs hatch (Squires 1991).

The proportion of time allocated to foraging did not differ significantly between adults and cygnets, contrary to my prediction that adults would forage more than cygnets. This similarity was also found in winter and spring for Tri-state Trumpeter Swans (Squires 1991). Cygnet overwinter mortality is much higher than that of adults (R. Shea, pers.comm.) therefore it is likely that cygnets depart wintering areas in a poorer condition compared to adults, and consequently cygnets allocate a large proportion of their time to foraging at spring migration stopover areas. Additionally, since Trumpeter Swans typically begin breeding at five years of age (Brechtel 1982), and gain white feathers after their second summer (Mitchell 1994), nonbreeding sub-adults were included in the adult group, and may have contributed to the insignifincant difference in the behaviours of breeding adults and cygnets. Nonetheless, adults had a greater rate of rocking compared to cygnets, although there was no significant difference in the rate of tip-ups, the time spent underwater during a tip-up, or the proportion of foraging time spent underwater. Because adults rocked before tipping a greater proportion of the time compared to cygnets, and the foot action associated with rocking results in exposing and dislodging food items from the sediment (Hampton 1981), adults may collect more food

per tip-up than cygnets, and therefore gain greater energy reserves that are allocated for breeding. Therefore, although foraging times were similar, my results show that adults may be more efficient foragers compared to cygnets due to their experience, and hence have a higher net gain of energy (Woodrey and Moore 1997). I occasionally observed cygnets tipping-up in close proximity to an adult, and they may have been attempting to parasitize the foraging effort of adults. In all cases the cygnets were chased off and the adult resumed foraging.

The only significant difference in time-budget allocation between adults and cygnets was the amount of time individuals spent preening compared to resting and sleeping. This effect stemmed from cygnets in Cardston-Mountain View preening more than adults. This group of cygnets also preened more than both cygnets and adults in the Calgary area in both 1999 and 2000. The relatively smaller sample size of cygnet observations in Cardston-Mountain View (n=33), may have contributed to this significant effect as there is no obvious biological reason for the difference.

The amount of time individuals allocated to locomotion compared to preening was the only case that was significantly affected by the age by site interaction, because cygnets in Calgary-2000 were involved with locomotion activities more, and preened less than cygnets in Cardston-Mountain View-2000. Site was also a significant factor, as Calgary-1999 and Calgary-2000 were significantly different. For all other behaviour ratios, there was no significant effect of study area but there was a year effect, with Calgary-1999 significantly different from Calgary-2000 and Cardston-Mountain View-2000. In other words, Trumpeter Swans behaved differently in the two years of study.

In 2000, there was no effect of stopover site on the behaviour of migrating

Trumpeter Swans. I suggest that the year effect on Trumpeter Swan behaviour in Calgary was primarily due to spring 1999 being warmer than spring 2000. The average minimum daily April temperature in Calgary in 2000 was significantly colder than in 1999. In 1999 most ponds had open water when Trumpeter Swans arrived in Calgary, while in 2000. Trumpeter Swans arrived in the Cardston-Mountain View area when most ponds were still ice-covered. Swans sat on shallow flooded fields and did not forage (pers. observ.). Some ponds in the Cardston-Mountain View area were not used in 2000 because they became ice-free after the swans had moved north. Even though I began counts and observations a few days after the initial influx of swans to the Calgary area in 2000, there was still ice present on the study ponds, and one pond that was heavily used early in 1999 remained frozen until approximately two weeks after the first swans arrived. In Calgary-2000, there was also a period one week after Trumpeter Swans arrived that was particularly cold, and most study ponds refroze.

Reduced foraging by Trumpeter Swans in 2000 was consistent with colder conditions compared to 1999. Although decreased foraging in 2000 may have been influenced by the decreased availability of foraging areas due to ice-cover, decreased foraging and increased sleeping, with decreasing temperature has been found in other studies (Squires and Anderson 1997), and air temperature is a dominant weather variable affecting Trumpeter Swan behaviour (Squires 1991). As temperatures decrease to 0° C, foraging activity of other waterfowl species typically increases (Paulus 1988), but at lower temperatures, energetic costs may exceed benefits gained from foraging (Brodsky and Weatherhead 1984, Paulus 1988), and sleeping becomes the dominant activity (Squires 1991). In this study, foraging by Trumpeter Swans decreased sharply at

temperatures < -4° C, which was close to the average daily minimum temperature of -3.9° C in 2000, and corresponds with decreased foraging compared to 1999. At temperatures above -4° C, the allocation of time to foraging was not related to temperature and sleeping was uncommon. At higher temperatures, energetic constraints would be less, and swan behaviour not restricted.

Timing of activities and movement of waterfowl are typically cued by dawn and dusk (Paulus 1988). Although there was some variation in Trumpeter Swan behaviour during the day, overall time-budgets were not strongly influenced by time of day. In spring, time allocated to different activities by nonmigratory Trumpeter Swans also did not vary with time of day (Squires and Anderson 1997). Other studies have found Trumpeter Swans to be active throughout the night, with little variation in their time-budget compared to daytime activity (Squires and Anderson 1997).

Migratory stopover areas appear to be important habitats for the accumulation of reserves for Trumpeter Swans prior to breeding. My results demonstrate that Trumpeter Swans allocate the majority of their time to foraging and use energy-conserving strategies in adverse weather conditions. While there was no significant difference in the duration of foraging by adults and cygnets, there were indications that adults may be more efficient foragers compared to cygnets. Additionally, since Trumpeter Swans begin nesting shortly after their arrival at breeding grounds, the availability and quality of migration habitats may be important influences on Trumpeter Swan breeding success.

CHAPTER III

HABITAT PREFERENCES OF TRUMPETER SWANS IN MIGRATORY STOPOVER AREAS OF SOUTHERN ALBERTA

INTRODUCTION

Differential habitat use is central to studies of animal ecology and conservation biology. Most habitats occur as patches and organisms choose how to allocate their time among these patches. Habitat selection theory predicts that the use of an area should be non-random, with more time spent in habitats that provide the greatest reward, and less time in less rewarding areas (Rosenzweig 1985). Johnson (1980) proposed that habitat selection occurs at four levels. First-order habitat selection involves the geographic range of a species. Within the geographic range, second-order habitat selection deals with the use or non-use of the environment. The use of specific sites within a home range is considered third-order habitat selection, and the differential use of resources at sites within the home range is fourth-order habitat selection. Habitat preferences are then used as indicators of species' requirements.

Although Trumpeter Swan *(Cygnus buccinator)* habitat preferences have been investigated in wintering and breeding areas, (Shea 1979, Hampton 1981, Holton 1982, Maj 1983, Squires 1991) little is known about habitat preferences in migratory stopover areas. The majority of Trumpeter Swans in the Rocky Mountain Population (RMP) migrate approximately 1400 km in spring from overwintering areas in the Tri-state region of Montana, Idaho and Wyoming, to Grande Prairie, Alberta to breed, or continue migrating to the Yukon (first-order selection) (Mackay 1978). During spring migration, Trumpeter Swans move through Southern Alberta in a series of stages with documented

stopover areas where individual neck-banded birds have been observed yearly (second-order selection) (G. Beyersbergen, pers. comm.). Within stopover areas many ponds occur, but not all are used by Trumpeter Swans (third-order selection). The differential use of ponds suggests that particular physical and/or biological characteristics may be favoured by Trumpeter Swans and differ between ponds that are consistently used during spring migration and ponds that have variable use between years or are unused.

It is suspected that at migratory stopover areas Trumpeter Swans, like other waterfowl species, gather nutrients, lipid and protein reserves required for continued migration and reproduction (Mitchell 1994). Condition of habitats along migration routes influences the reproductive potential of Lesser Snow Geese (*Chen caerulescens*; Ankney and MacInnes 1978, Davies and Cooke 1983), Canada Geese (*Branta canadensis*; (Raveling 1979), Mallards (*Anas platyrhynchos*; Krapu 1981), Buffleheads (*Bucephala albeola*) and Lesser Scaups (*Aythya affinis*; Gammonley and Heitmeyer 1990). Trumpeter swans in the RMP depend solely on aquatic habitats for their feeding requirements (Mitchell 1994) and limnological features such as pond area, trophic status and pH, act as indirect measures of pond suitability for some aquatic bird species (Heglund et al. 1994).

My goal was to evaluate physical, chemical and biological characteristics of ponds in relation to third-order habitat selection by Trumpeter Swans. The primary activity of Trumpeter Swans in spring migratory stopover areas is foraging (Chapter II). If stopover areas are used for gaining energy to continue migration and initiate breeding, I expected that Trumpeter Swans should prefer ponds with higher food availability, specifically the overwintering structures of macrophytes (tubers and rhizomes), compared

to ponds that have variable use or are unused.

METHODS

Study area.- Trumpeter Swans were studied in two areas of Southern Alberta: i) approximately 50km west of Calgary (51°05'N, 114°30'W to 51°09'N, 114°42'W), and ii) in the Cardston-Mountain View area (49°02'N, 113°08'W and 49°18'N, 113°32'W to 113°36'W). These field sites are located in the foothills of the Rocky Mountains and contain numerous ponds. Ranching is the main land-use practise. In the Calgary area, I studied thirteen ponds with a varied history of Trumpeter Swan use, including ponds that are reported to be used consistently every year and ponds that never appear to be used (G. Beyersbergen, pers. comm.; conversations with landowners). In the Cardston-Mountain View area I focused on six ponds used consistently by Trumpeter Swans (D. Brown, pers. comm.; conversations with landowners). Here I report movements of Trumpeter Swans through both study sites, but I limit the habitat preference portion to the Calgary area as I have two years of Trumpeter Swan counts with which to evaluate pond use (See Appendix A for Cardston-Mountain View data). In identifying study ponds, I assigned each a name, as there were no prior names assigned.

Trumpeter Swan use.- Daily, I counted Trumpeter Swans in the Calgary area from 7 April to 21 May 1999 and 10 April to 11 May 2000. In the Cardston-Mountain View area, I made weekly counts from 4 March to 27 March 2000 with daily counts from 29 March to 11 April 2000. The presence of Tundra Swans (*Cygnus columbianus*) had been noted in both study areas and I used a spotting scope to distinguish Trumpeter Swans from Tundra Swans. Tundra Swans typically possess a yellow lore that is absent in

Trumpeter Swans, but is also lacking in some Tundra Swans (Jordan 1988). Additional indicators used to differentiate Trumpeter Swans from Tundra Swans were vocalisations and size. Trumpeter Swans have a trumpet-like call and adults weigh 11.5 kg on average whereas Tundra Swans produce a higher pitched whistling sound and are noticeably smaller at 5.8 kg (Bellrose 1976).

Pond Morphometry.- I measured open water area and shoreline length of ponds using a GPS and walking the perimeter when the ponds were iced over. Open water is the area of the pond without emergent vegetation (i.e. sedges, rushes). I measured pond length by determining the longest part of each pond between two points on opposite shores that followed a straight line, and pond width as the widest part of the pond approximately perpendicular to the length. I determined pond depths by drilling between 8 to 19 holes through the ice at multiple, approximately evenly-spaced sites across the pond surface. At each site I measured pond depth with a meter stick or an echo-sounder, and the position of each site was recorded using GPS. I used a depth contour of 0.8 m to delineate the pond area available to swans for foraging. This accounted for water level increases due to snow melt and runoff, and the reach of an upending Trumpeter Swan (approximately 1 m; Scott 1972, Holton 1982). A 0.8 m contour also accounts for some foraging in sediments. I used a digitizer to approximate the pond area in which Trumpeter Swans could forage, and I indicate this as the area <1 m deep.

Water Chemistry.- I collected water samples from study ponds in July and August 1999. I used a Hydrolab probe (Hydrolab Inc., Austin, Texas) to measure salinity, specific conductivity, and pH. I used salinity and specific conductivity to estimate the concentration of all ionic constituents present (Hutchinson 1957). I determined

chlorophyll a by filtering 25-50 ml of water through a 25 μm Whatman glass microfibre filter (GF/C), and froze the sample until analysis, following standard acetone extraction techniques (Watson et al. 1992). I measured Total Phosphorus (TP) using the molybdate blue method following persulfate oxidation (American Public Health Association 1981). I assessed chlorophyll a and TP as measures of pond trophic status (Forsberg and Ryding 1980).

Biotic Properties.- I determined percent macrophyte cover based on aerial photographs taken 04 August 1999, when macrophytes were at or near maximum biomass (Godin and Joyner 1981). I photographed each pond from a Cessna 182 aircraft when the plane was banking, using a 35-mm camera equipped with a polarizing filter and slide film (Kirby 1976). I projected the images onto white paper, outlined areas of macrophyte coverage, and used a digitizer to determine percent macrophyte cover.

To determine rhizome and tuber densities, rhizome and tuber dry mass, and nontuber/nonrhizome dry mass, I collected six Eckman samples (each 15cm x 15cm x 15cm) from each of five 0.6 m^2 quadrats in each pond after the swans had left in spring 1999. For the four ponds that had been reported as consistently used by Trumpeter Swans, I used one of two methods to determine rhizome and tuber densities and dry mass available for consumption. First, in two ponds (Sibbald and Sibbald East), I set out five 60cm x 60cm rebar and mesh exclosures prior to the arrival of Trumpeter Swans and Eckman-sampled from the excluded area, as described above, after the swans left. Second, in the two ponds (Beaver and Jumping Pound) where this was not possible due to logistical constraints, I sampled the ponds the following fall (1999) to get an indication of densities and dry mass that would be available to Trumpeter Swans the following spring.

For the fall samples I adjusted the value of tuber and rhizome biomass to account for decomposition. I did this by also sampling Sibbald and Sibbald East in the fall and I compared the fall biomass to spring samples. Spring samples had 33% less biomass than fall samples, so the biomass of Jumping Pound and Beaver samples from fall 1999 were also reduced by this amount.

I identified macrophyte species from five rake-samples (a rake with a 15 m rope on the end thrown out into the pond) taken from each pond in July 1999. Each macrophyte species in each pond was classified as either dominant or 'other' depending on its prevalence, which was a qualitative estimate based on the amount of the macrophyte species present in rake samples and observed in ponds during sampling. Ponds that had <20 % macrophyte coverage from aerial photographs were determined to have no dominant macrophyte species.

Statistical analysis.- I divided study ponds into three groups based on Trumpeter Swan use during 1999 and 2000: 1) consistent use between years, 2) variable use between years, and 3) unused ponds. I defined consistently used ponds as those that had a total of at least 100 Trumpeter Swan-days (where one swan-day is equal to a single swan being present for a single day) in each of 1999 and 2000. I classified ponds as unused if in either 1999 or 2000 there were no Trumpeter Swans observed on the pond, *or* the total number of swan-days in 1999 and 2000 combined was <10. I classified the remainder of the ponds as variably used.

I conducted forward-stepping discriminant analysis to determine which pond characteristics, if any, separated the ponds into the predefined groups described above (Engelman 1997) (See Appendix B for individual pond characteristics). I obtained values

for canonical correlation variables in conjunction with discriminant analysis. The first canonical variable is the linear combination of the variables that best discriminates among the groups, and the second canonical variable is orthogonal to the first and is the next best combination of variables (Engelman 1997). For this analysis I used the mean values for water chemistry and biotic properties for each pond, including: open water area, area <1 m deep, shoreline length, pond length, pond width, pH, salinity, conductivity, chlorophyll a, TP, percent macrophyte coverage, rhizome density, rhizome + tuber density, rhizome + tuber dry mass·m^{-2}, and nonrhizome/nontuber dry mass·m^{-2}. I log transformed open water area, shoreline length, and pond length to conform to normality assumptions. I conducted separate ANOVA tests to determine if pond properties differed among groups. Multivariate comparisons using Tukey tests were conducted for significant ANOVA results. A Kruskal-Wallis test was conducted on tuber density, as the data were not normally distributed. I used SYSTAT (Version 7.0) with a probability level of 0.05 to determine significance for all statistical tests.

RESULTS

Trumpeter Swan counts.- In the Calgary area in 1999, Trumpeter Swans were first observed on 7 April, reached a peak of 165 on 14 April, and were last seen on 21 May 1999 (Figure 3.1A). I counted a total of 1300 Trumpeter Swan-days on study ponds in the Calgary area in 1999. In the Cardston-Mountain View area, I counted 667 Trumpeter Swan-days from 4 March 2000 to 11 April 2000. Few Trumpeter Swans were counted between 4 March and 27 March. The peak number was 133 on 7 April and decreased rapidly, with only 5 Trumpeter Swans counted on 9 April (Figure 3.1B). Counts in the

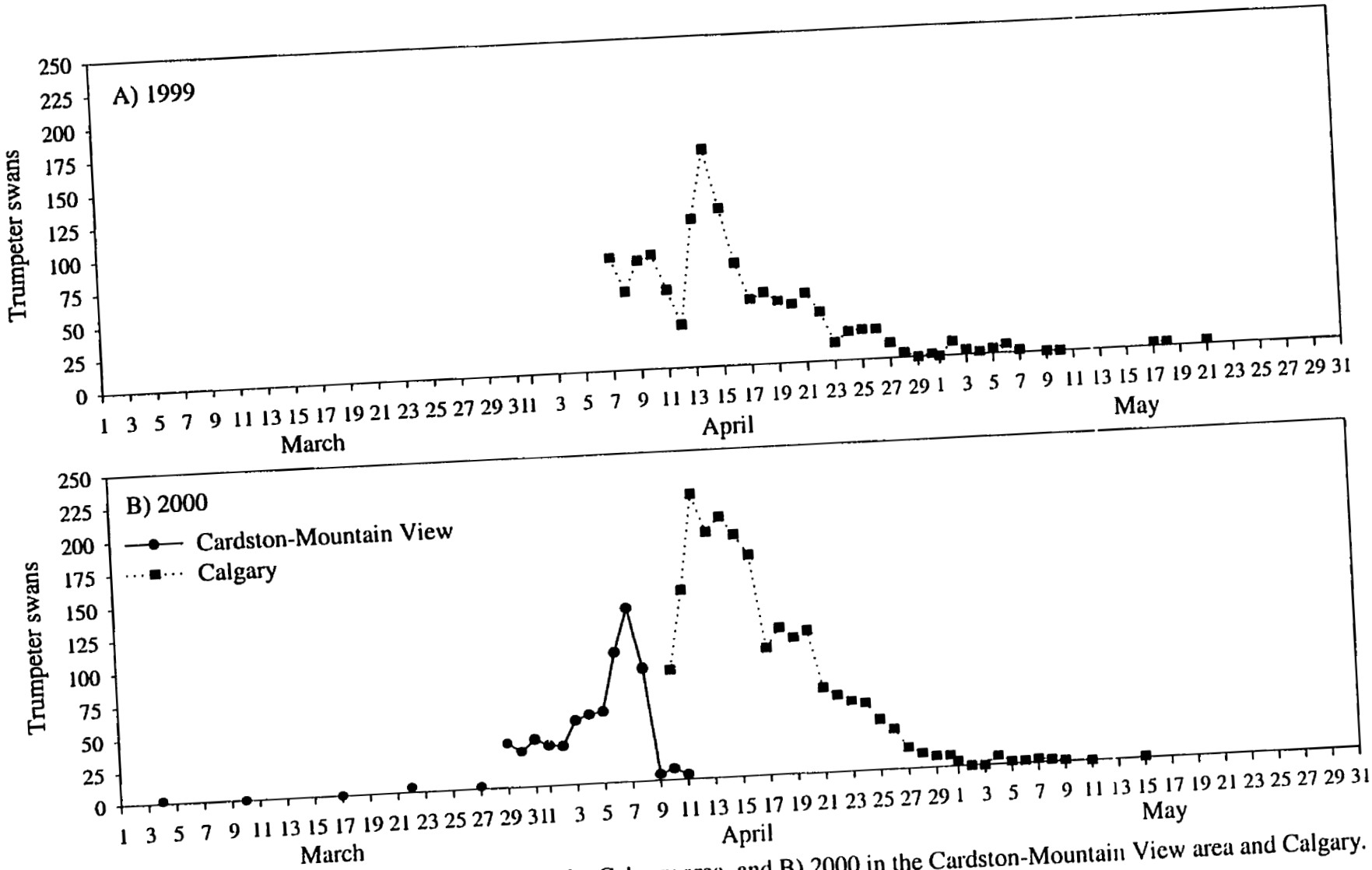

Figure 3.1: Trumpeter Swan counts for A) 1999 in the Calgary area, and B) 2000 in the Cardston-Mountain View area and Calgary.

Calgary area in 2000 began on 10 April, a few days after the arrival of Trumpeter Swans into the area (N. Copithorne, pers. comm.). From 10 April to 11 May I counted 2002 Trumpeter Swan-days. The peak number was 219 on 12 April 2000 (Figure 3.1B). This peak was five days after the peak in the Cardston-Mountain View area, and was similar to 1999 when peak Trumpeter Swan numbers in the Calgary area occurred on 14 April. Trumpeter Swan counts in Calgary-2000 reached a higher peak and remained at relatively high numbers over several days, rather than declining rapidly as was the case in Cardston-Mountain View and Calgary-1999.

Habitat preference and pond characteristics.- In the Calgary area, there were differences in the use of some of the 13 study ponds in 1999 and 2000 (Table 3.1). The ponds identified as consistently used between years included Jumping Pound, Beaver, Sibbald and Sibbald East. Both Jumping Pound and Sibbald East had similar total swan-days in 1999 and 2000, whereas the use of Beaver and Sibbald decreased in 2000. However, Trumpeter Swans were present on Sibbald prior to my counts beginning in 2000 (B. Anderson, pers.comm.), so I placed it into the consistently used group, although my counts totalled 95 swan-days. The number of calendar days that consistently used ponds were used differed between 1999 and 2000. Jumping Pound had a similar total number of swan-days in 1999 and 2000, but swans were present for almost twice as many calendar days in 2000 compared to 1999. Trumpeter Swans were present for half as many calendar days in 2000 on Beaver, Sibbald and Sibbald East. Parks, Pile-O-Bones, Ridge, and Monster were classified as variably used, with increased total swan-days in 2000. Even though Ridge and Monster had increased use in 2000 over 1999, Trumpeter Swans were only present on these two ponds for three calendar days in 2000.

Table 3.1: Total swan-days, swan-days per ha <1m deep, and number of calendar days used, for ponds west of Calgary in 1999 and 2000.

Pond	pond area <1m deep (ha)	1999 total swan-days	1999 swan-days per area <1m deep (ha^{-1})	1999 total calendar days used	2000 total swan-days	2000 swan-days per area <1m deep (ha^{-1})	2000 total calendar days used
Consistent use[1]							
Jumping Pound[2]	3.543	411	116.00	13	441	124.47	25
Beaver	2.850	320	112.28	18	243	85.26	9
Sibbald[2]	1.399	223	159.40	20	95	67.91	9
Sibbald East	1.548	196	126.63	14	197	127.28	7
Variable use[3]							
Parks[2]	1.634	51	31.21	9	792	484.67	17
Pile-O-Bones	1.678	31	18.47	3	113	67.34	20
Ridge	1.239	12	9.69	4	42	33.90	3
Monster	4.119	2	0.49	1	42	10.20	3
Unused[4]							
Horseshoe	1.392	3	2.16	1	6	4.31	2
Jumping Pound East	1.828	32	17.51	5	0	0	0
CL	2.943	19	6.46	3	0	0	0
Bend	0.633	0	0	0	0	0	0
Goodwin	0.361	0	0	0	0	0	0

[1]- ponds with > 100 swan-days in both 1999 and 2000

[2]- swan numbers underestimated in 2000

[3]- includes ponds not classified as consistently used or unused

[4]- ponds with 0 swan-days in either 1999 or 2000, or < 10 swan-days in total (1999 + 2000)

Horseshoe, Jumping Pound East, CL, Bend, and Goodwin were classified as unused. In 2000, all but Horseshoe were completely unused, while Bend and Goodwin were completely unused in 1999. However, Trumpeter Swan counts on all these ponds were low (≤ 32 swan-days). In 1999, Jumping Pound East had 32 Trumpeter Swan-days distributed over five days. All swans present were cygnets, and no swans were observed on it in 2000. Horseshoe was similar, as the majority of swans there were cygnets.

Factors influencing Trumpeter Swan pond selection were rhizome + tuber biomass, and salinity (MANOVA, Wilk's lamda =0.158, df=4,18, $P<0.005$). Conductivity had a low (0.0001) value for tolerance, indicating that it was highly correlated to either rhizome + tuber biomass or salinity. Discriminant analysis correctly classified 85% of the ponds. The first canonical variable (0.889 salinity + 0.901 (tuber + rhizome dry mass·m^{-2})) explained 93.2% of the variation between the groups, and the second canonical variable (0.611 salinity – 0.594 (tuber + rhizome dry mass·m^{-2})) contrasted variable use and unused ponds (Figure 3.2). Consistently used ponds had relatively high salinity and tuber + rhizome dry mass (Table 3.2) and are thus located at the right side of the figure. Unused ponds had high salinity and low tuber + rhizome biomass and are centrally located, while variably used ponds had both low salinity and low tuber + rhizome biomass and are located at the left side of the figure. The two misclassified ponds I had assigned to the unused category. Bend was misclassified as consistently used and Goodwin was misclassified as variably used.

Study-pond groups were not grossly different based on pond morphometry, and only some water chemistry values differed. There was no significant difference in open water area (ANOVA, $F=1.87$, df=2 and 10, $P>0.05$) or area <1 m deep (ANOVA,

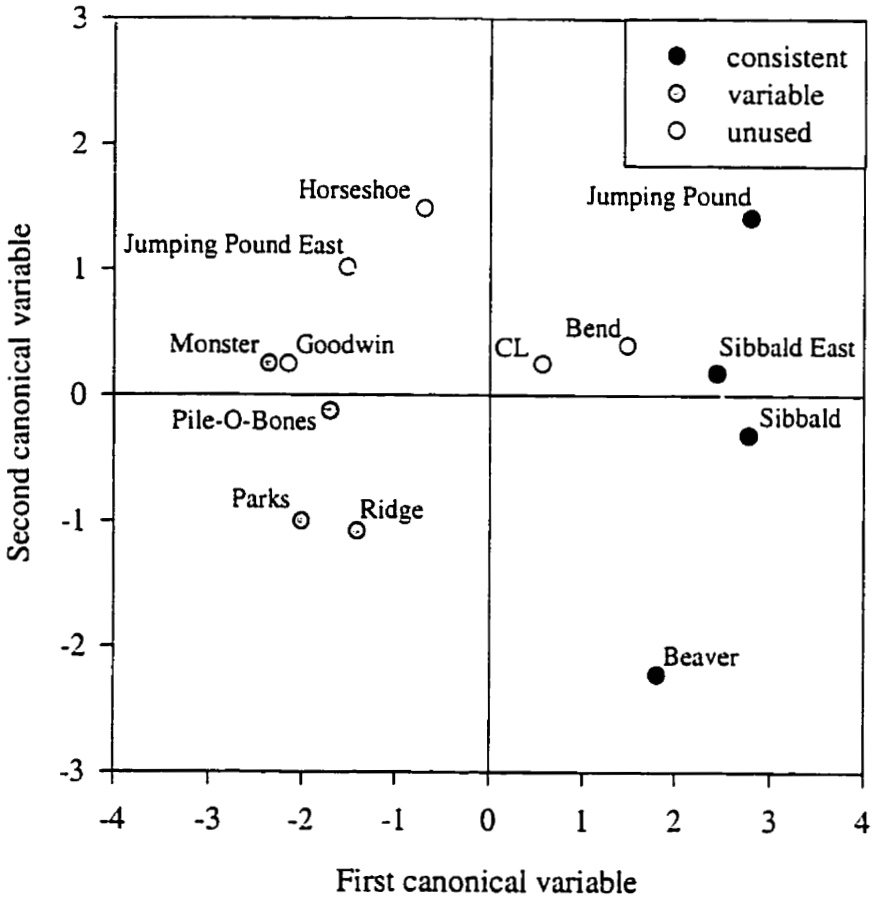

Figure 3.2: Plot of loadings of Trumpeter Swan use of ponds onto the two canonical variables. Data are from 13 study ponds west of Calgary.

Table 3.2: Mean (SE) characteristics of ponds with differential use by Trumpeter Swans during spring migration west of Calgary. Pond characteristics with a * indicate significant ANOVA tests ($P<0.05$). Pond-use categories with like letters are not significantly different.

	Pond use by Trumpeter Swans		
Pond Characteristic	**Consistent**	**Variable**	**Unused**
n	4	4	5
open water area (ha)	4.078 (1.784)	3.999 (1.727)	1.685 (0.566)
area <1 m deep (ha)	2.335 (0.518)	2.168 (0.658)	1.431 (0.460)
shoreline length (m)	859.8 (154.7)	1054.8 (234.5)	715.7 (161.9)
pond length (m)	314.8 (64.0)	411.3 (112.7)	233.8 (26.2)
pond width (m)	171.8 (33.7)	152.5 (27.2)	111.9 (34.9)
pH	8.90 (0.24)	8.75 (0.33)	8.68 (0.28)
salinity (ppt)*	0.84 (0.13)a	0.39 (0.04)b	0.68 (0.06)ab
conductivity ($\mu S \cdot cm^{-1}$)*	1574.0 (233.9)a	756.2 (70.2)b	1282.2 (118.5)ab
chorophyll a ($\mu g \cdot L^{-1}$)	2.79 (0.88)	2.85 (0.77)	1.52 (0.68)
TP ($\mu g \cdot L^{-1}$)	51.43 (14.34)	41.72 (8.42)	48.29 (11.00)
macrophyte coverage (%)	60.20 (6.93)	61.60 (8.49)	25.20 (8.36)
rhizome density (m^{-2})*	97.42 (14.62)a	24.98 (8.67)b	29.91 (17.42)b
tuber density (m^{-2})	6.31 (6.31)	4.44 (3.96)	11.24 (9.87)
rhizome + tuber density (m^{-2})	103.69 (20.58)	29.42 (10.36)	41.20 (26.62)
rhizome + tuber dry mass ($g \cdot m^{-2}$)*	3.96 (0.62)a	1.24 (0.44)b	1.16 (0.62)b
nonrhizome/nontuber dry mass ($g \cdot m^{-2}$)	183.29 (36.67)	237.64 (63.69)	228.09 (20.13)

F=0.84, df=2 and 10, P>0.05) among pond groups. Open water area ranged from a mean of 1.685 ha in unused ponds to 4.078 ha in consistently used ponds while the area <1 m deep ranged from 1.431 ha to 2.335 ha, respectively (Table 3.2). There was no significant difference in shoreline length (ANOVA, F=1.26, df=2 and 10, P>0.05), pond length (ANOVA, F=1.95, df=2 and 10, P>0.05), or pond width (ANOVA, F=0.91, df=2 and 10, P>0.05). The average pH of all pond groups was slightly alkaline, ranging between 8.68 and 8.90 (ANOVA, F=0.15, df=2 and 10, P>0.05). Salinity values were significantly lower in variable use ponds than in consistently or unused ponds (ANOVA, F=6.93, df=2 and 10, P<0.05). Values for conductivity showed the same pattern, with significantly lower values in variable use ponds (ANOVA, F=6.92, df=2 and 10, P<0.05). Chlorophyll a levels were not significantly different and ranged between 1.52 $\mu g \cdot L^{-1}$ in unused ponds to 2.85 $\mu g \cdot L^{-1}$ in variable use ponds (ANOVA, F=1.01, df=2 and 10, P>0.05). Total Phosphorus ranged from 41.72 $\mu g \cdot L^{-1}$ in variable use ponds to 51.43 $\mu g \cdot L^{-1}$ in consistently used ponds, with no significant difference (ANOVA, F=0.17, df=2 and 10, P>0.05). Macrophyte coverage did not differ significantly among pond groups (ANOVA, F=0.28, df=2 and 10, P>0.05), although unused ponds had less percent cover than consistently and variably used ponds. Rhizome density in consistently used ponds was significantly higher than in variably used and unused ponds (Table 3.2; ANOVA, F=7.07, df=2 and 10, P<0.05). There was no significant difference in the density of tubers between pond categories (Kruskal-Wallis, T=0.19, n=13, P>0.05). Rhizome densities were higher than tuber density in all pond-use categories. Rhizome + tuber density was not significantly different among pond groups even though average density was higher in consistently used ponds (ANOVA, F=3.17, df=2 and 10, P>0.05).

However, rhizome + tuber dry mass·m^{-2} was significantly lower in variable and unused ponds compared to consistently used ponds (ANOVA, F=7.21, df=2 and 10, P<0.05). The dry mass of nonrhizome/nontuber material·m^{-2} collected in Eckman samples did not differ significantly among pond-use categories (ANOVA, F=0.47, df=2 and 10, P>0.05).

All consistently used ponds were dominated by *Potamogeton pectinatus*, while *Myriophyllum exalbescens* and *P. richardsonii* were present in some of these ponds, although in lesser amounts (Table 3.3). Ponds with variable use did not all have a common dominant macrophyte species. *M. exalbescens* was dominant in two of the four ponds in this use category. *P. pectinatus* was present in all variable use ponds, although it was not always dominant. *P. zosteriformis* and *P. richarsonii* were also present in these ponds. *Chara* spp. was present in most of the unused ponds, while *P. pectinatus* was much less common. *Utricularia vulgaris* was present in unused ponds, but not in variably or consistently used ponds. In two unused ponds (Horseshoe, Jumping Pound East) there were no dominant macrophyte species, as macrophyte coverage was <20% in these ponds, other species present included *Chara* spp., *P. zosteriformis*, and *U. vulgaris*.

Discussion

Trumpeter Swans moved though migratory stopover areas in Calgary and Cardston-Mountain View in a single wave, in contrast to the Whooper Swan (*Cygnus cygnus*) migration through Finland that occurs in two waves (Haapanen and Hautala 1991). The first wave of Whooper Swans is postulated to be breeders and the second non-breeders. Breeders move up to 350 km per day in order to reclaim territories, arriving in the breeding grounds up to six weeks before ponds thaw, while non-breeders

Table 3.3: Dominant macrophyte species and other macrophyte species present in study ponds west of Calgary in July 1999. See methods for separation of ponds into use categories.

Pond	Dominant macrophyte species[a]	Other macrophyte species present[a]
Consistent use		
Jumping Pound	*P. pectinatus*	-
Beaver	*P. pectinatus*	*M. exalbescens*
Sibbald	*P. pectinatus*	*M. exalbescens, P. richarsonii*
Sibbald East	*P. pectinatus*	*Chara* spp., *M. exalbescens, P. richarsonii, P. zosteriformis*
Varible use		
Parks	*M. exalbescens*	*P. richarsonii, P. pectinatus*
Pile-O-Bones	*P. pectinatus, P. zosteriformis*	*Chara* spp.
Ridge	*P. richarsonii, P. pectinatus*	*P. zosteriformis*
Monster	*M. exalbescens*	*P. pectinatus, Chara* spp., *P. zosteriformis*
Unused		
Horseshoe	-	*Chara* spp., *P. zosteriformis*
Jumping Pound East	-	*U. vulgaris*
CL	*M. exalbescens*	*Chara* spp., *P. pectinatus*
Bend	*Chara* spp.	-
Goodwin	*P. pectinatus*	*M. exalbescens, U. vulgaris, Chara* spp.

[a] *P.- Potamogeton, M.- Myriophyllum, U.- Utricularia*

move in stages of 20-50 km per day. The adaptive values of this bimodal migration is that breeding birds will occupy the best nesting and feeding sites, while non-breeders can use the good food sources available during migration (Haapanen and Hautala 1991). The migration of Trumpeter Swans though my study areas was unimodal, perhaps because breeding habitat in Grande Prairie is not limiting (Holton 1982), or not limiting to the extent that breeding pairs have to arrive so early to reclaim territories at the current population size.

Trumpeter Swans began to move through the Calgary area and reached peak numbers at approximately the same time in 1999 and 2000. In 2000 the exodus of Trumpeter Swans after the peak was slower than in 1999, and was most likely due to cold temperatures from 13 April to 15 April, when daytime highs reached -8° C and lows were -17° C (Environment Canada 2000). During this period the dominant activity was sleeping (Chapter II). This delay in continuing migration out of Calgary in 2000 most likely contributed to the higher total number of swan-days in 2000 (2002) compared to 1999 (1300).

I believe that the use of individual ponds was modified by weather conditions between years. The average minimum ambient temperature was lower in 2000 compared to 1999 during the time that Trumpeter Swans were present in the Calgary area (Chapter II). The lower temperatures in 2000 meant that Beaver, which had a total of 320 Trumpeter Swan days in 1999 starting on 7 April, was frozen until 22 April 2000. As a result, Trumpeter Swans were present in higher numbers on Parks in 2000, a variable-use pond located only 200 m away. During the cold period in 2000, the only open water available in the study area was in Parks and Monster ponds. Trumpeter Swans converged

on these ponds, which is reflected in the higher use of these ponds in 2000. In wintering areas, Trumpeter Swans seek out open water and congregate in dense aggregations when little open water is available (Shea 1979). In 1999, pond selection did not appear to be limited by external factors, such as ice cover, as was the case in 2000. In 1999, Parks had a total of 51 swan-days but over 15 times that (792 swan-days) in 2000. As Beaver began to thaw, Trumpeter Swan numbers increased on Beaver and decreased on Parks, and I observed Trumpeter Swans flying from Parks to Beaver.

To eludicate why Trumpeter Swans used particular ponds over others in migratory stopover areas, I correlated their use to abiotic and biotic pond properties. Dry mass of rhizomes + tubers·m^{-2}, along with salinity, were the factors that separated pond groups according to their use by migrating Trumpeter Swans. I expected that Trumpeter Swans would prefer ponds with higher food availability, and although availability estimated as area <1 m deep was not important, rhizome + tuber dry mass·m^{-2} was. Mitchell (1994) hypothesised that Trumpeter Swans use migratory stopover areas to gather energy for migration and breeding. Trumpeter Swans in Cardston-Mountain View and Calgary allocated approximately 50% of their time to foraging (Chapter II). Therefore it is not surprising that Trumpeter Swans preferred ponds with higher dry mass of tubers and rhizomes. Trumpeter Swans consume the tubers, rhizomes, stems, and leaves of *P. pectinatus* (Banko 1960) and rake samples showed that consistently used ponds were dominated by *P. pectinatus*. *P. pectinatus* is a desired food source for Trumpeter Swans in summer areas, and *P. pectinatus* tubers are a primary food source in wintering areas (Squires and Anderson, 1995). Tubers are high in energy and are easily digested by Trumpeter Swans (Squires 1991). Few studies have reported rhizomes as

being an important food for Trumpeter Swans, but rhizomes may have been included in references to tubers. Rhizomes contain slightly less metabolizable energy per gram compared to tubers, but they are higher in protein and fat (Chapter IV).

Salinity was the other factor that separated ponds according to Trumpeter Swan use. Pond salinity was highest for three of the consistently used ponds (Jumping Pound, Sibbald, and Sibbald East) and may reflect their proximity to roads. The other consistently used pond, Beaver, is isolated on private land, with no roads nearby, which may explain its lower salinity. Variable use ponds had the lowest salinity on average, and these ponds are in general further from roadways. The unused ponds had an intermediate salinity value that was not significantly different from either of the other pond groups. Four of the five unused ponds do not have a source of water inflow, and evaporation will influence salinity. Additionally, *P. pectinatus* is limited to waters containing moderate to high levels of calcium (Hutchinson 1975), and although all ions were sampled together and not calcium specifically, there is a tendency for Ca > Mg > Na > K (Hutchinson 1957). Therefore, salinity differences might reflect pond location and *P. pectinatus* dominance in consistently used ponds may be at least partially due to higher salinity values. Conductivity also significantly differed among pond classes and paralleled differences in salinity. Conductivity is a general measure of ions present, and was correlated with salinity, as salinity measurements were a function of conductivity (Hydrolab Corporation 1997).

The two misclassified ponds, Bend and Goodwin, were not used by Trumpeter Swans in either 1999 or 2000, even though they appear to contain characteristics favoured by Trumpeter Swans. Bend had a salinity value close to that of the consistently

used ponds and had tubers present. In this pond, however, when rake samples were taken *Chara* spp., a non-rooted, non-vascular plant, was the only species recovered and the tubers recovered did not resemble those of *P. pectinatus*. Additionally, this pond is located approximately 20 m from the Trans-Canada Highway, between it and a gravel road, which is most likely the cause of its increased salinity. Roadway traffic. in addition to the lack of *P. pectinatus*, may contribute to the lack of use of this pond. Breeding Trumpeter Swans typically avoid areas that are prone to disturbance (Shea 1979, Holton 1982), and although some consistently used ponds were located near roads, the traffic passing in close proximity to this pond would be the greatest. The other misclassified pond, Goodwin, was not used by Trumpeter Swans even though it contains *P. pectinatus* as its dominant macrophyte. A possible explanation for this is that Goodwin is located on the shaded north-east side of a hill so that the ice on it does not melt until approximately two weeks after Trumpeter Swans arrive, by which time the bulk of swans have moved though the area. Persistent ice-cover is a factor that will influence pond suitability, as Goodwin pond is essentially unavailable when Trumpeter Swans are present.

Many of the limnological features measured were not significantly related to Trumpeter Swan use of ponds. These variables included: pond open water area, area <1 m deep, shoreline length, pond length and width, pH, TP, chlorophyll a, macrophyte cover, tuber density, tuber + rhizome density, and nonrhizome/nontuber dry mass. There was little variation in these properties among ponds in the different Trumpeter Swan use groups. Maj (1983) compared the properties of unused, historically used, and presently used ponds on breeding grounds in the Tri-state area, and Holton (1982) studied presently used, presently unused, and historically unused ponds in Grande Prairie. Neither found a

significant difference in pond area. At breeding sites, Trumpeter Swans defend territories up to 400 ha, (Holton 1982). The only indication of territoriality in stopover areas was for a localized feeding location, and there was no sign of defense of an entire pond. Occasionally when a cygnet or a Tundra Swan foraged in close proximity to a Trumpeter Swan adult, it bit at the tail feathers of the intruding swan causing them to move away, and then resumed foraging.

Trumpeter Swans arrive in migratory stopover areas shortly after the ponds have open water in early spring, before macrophyte growth has begun (Wetzel 1983). Therefore, the only food available is the underground structures of macrophytes, and the depth that swans can reach limits their feeding-areas. The reach of an upending Trumpeter Swan is ~100 cm (Scott 1972, Holton 1982), and the area <1 m deep is a factor influencing Trumpeter Swan use in breeding and wintering areas (Squires et al. 1992). However, pond area <1 m deep was not a factor that differentiated stopover ponds according to use, most likely because all study ponds were relatively shallow. Shoreline length of ponds was not a factor that Trumpeter Swans select for in breeding areas (Maj 1983) or migratory areas. The length and width of ponds did not significantly differ among pond groups in migratory stopover or breeding areas (Maj 1983). However, Trumpeter Swans may select against very small ponds, as they typically require a minimum distance of 100 m for take-off (Mitchell 1994).

Pond pH did not influence habitat preferences of Trumpeter Swans in migratory or breeding areas. In the Calgary area all ponds were alkaline, ranging from a pH of 8.0 to 9.6, near the upper end of the pH range documented for *P. pectinatus* of 6.3 to 9.0 (Hutchinson 1975). The pH of ponds in breeding areas of the Tri-state region ranged

between 4-8 (Maj 1983), but Trumpeter Swans avoid breeding habitats in acidic waters (Mitchell 1994).

There are conflicting classifications of pond trophic status based on TP versus chlorophyll. The ponds studied in the Calgary area were generally eutrophic based on TP (Wetzel 1983), and mesotrophic based on chlorophyll a measurements (Forsberg and Ryding 1980). However, in both cases there is a lot of overlap between trophic status classifications (Wetzel 1983). Conflicting results in trophic status can be common when abundant macrophytes are present, as macrophytes compete for nutrients that would otherwise be used by algal cells (Hoyer and Canfield 1994). There have been conflicting results with regards to pond use by Trumpeter Swans based on eutrophic conditions. Maj (1983) found that Trumpeter Swans used eutrophying lakes for breeding, while others state that breeding Trumpeter swans avoid eutrophic waters (Mitchell 1994). Neither of these studies reported their method for determining trophic status. Additionally, chlorophyll a has been used as a bird abundance indicator (Hoyer and Canfield 1990).

Macrophyte coverage was not a good indicator of Trumpeter Swan abundance even though they rely on underground structures of macrophytes for forage. Hoyer and Canfield (1994) found no correlation between macrophyte coverage and waterfowl numbers and attributed this to preferences for particular macrophyte species. Since Trumpeter Swans prefer *P. pectinatus*, and *P. pectinatus* produces tubers and rhizomes that are consumed during spring migration, Trumpeter Swans do not prefer ponds with simply more macrophyte coverage, but rather those with more *P. pectinatus*. Additionally, as Trumpeter Swans are limited to areas <1 m deep, total macrophyte coverage may not be an important factor.

Tuber abundance has been reported to be an important factor in swan habitat selection (Anderson and Low 1976, Squires et al. 1992), however, I did not find a significant difference in tuber abundance in ponds with differing use. Tuber dry mass in feeding sites of wintering Trumpeter Swans (2.0 $g \cdot m^{-2}$; Squires et al. 1992) was much higher than in the consistently used ponds in the Calgary area (approximately 0.3 $g \cdot m^{-2}$). Tubers are not uniformly distributed throughout sediments. Larger tubers of *P. pectinatus* are typically located from depths of 10 cm to 20 cm in the sediment (Anderson and Low 1976), and consequently I may have underestimated the presence of tubers. Tuber + rhizome density did not differ significantly among usage categories, but rhizome density was significantly greater in consistently used ponds. The average dry mass of tubers + rhizomes in consistently used ponds was 4.98 ± 1.11 $g \cdot m^{-2}$, over twice what Squires et al. (1992) found for tuber density in wintering areas to a depth of 35 cm. In springtime migratory stopover areas Trumpeter Swans select for the mass of forage available, and not merely tuber and rhizome density.

Additional factors that may play a role in habitat preferences of Trumpeter Swans are ice persistence, disturbance, instinct and learned behaviour. Instinct and learned behaviour is difficult to quantify, but in 1999 unaccompanied cygnets were observed on two ponds that were not occupied by adults in 1999. Neither of these ponds had *P. pectinatus* present, and Jumping Pound East had 0 % macrophyte cover, although there was a little of the non-rooted *U. vulgaris*, while Horseshoe had 15.16 % cover, so these cygnets selected habitat with little in the way of food resources. Trumpeter Swan cygnets that are in flocks with adults may gain knowledge of ponds that carries over into later years and perpetuates the consistent use of some ponds over the years.

CHAPTER IV

TRUMPETER SWAN ENERGETICS, FORAGING, AND SUSTAINABILITY OF POND USE IN SPRING MIGRATORY STOPOVER AREAS

INTRODUCTION

During the second half of the 20th century, the Rocky Mountain Population (RMP) of Trumpeter Swans steadily increased (Figure 4.1, Subcommittee on Rocky Mountain Trumpeter Swans 1998). This increase was largely attributed to the growth of the migratory Canadian subpopulation, which reached a size of 2500 swans in 1995. In contrast, the largely nonmigratory Tri-state subpopulation appears stable near 400 individuals, or may be experiencing a slight decline. With an overall increase in the RMP, there is concern regarding habitat availability and its influence on Trumpeter Swan survival. While the status of wintering and breeding areas has received much attention as factors limiting the continued growth of the RMP (Shea 1979, Holton 1982, Maj 1983, Squires 1991), migratory stopover habitat has been overlooked. Trumpeter Swans, like other waterfowl species, are assumed to gather energy reserves prior to reproduction, as little feeding occurs by females after egg laying, and female condition upon arrival at breeding grounds directly relates to successful rearing of offspring (Ankney and MacInnes 1978, Raveling 1979, Krapu 1981, Davies and Cooke 1983, Gammonley and Heitmeyer 1990). At spring migratory stopover areas, foraging is the dominant activity (Chapter II), and Trumpeter Swans prefer ponds with a higher biomass of tubers and rhizomes (Chapter III). With continued growth of the RMP, increased numbers of Trumpeter Swans on migratory ponds may increase impacts on food resources, and over time may limit the availability of migratory stopover habitat.

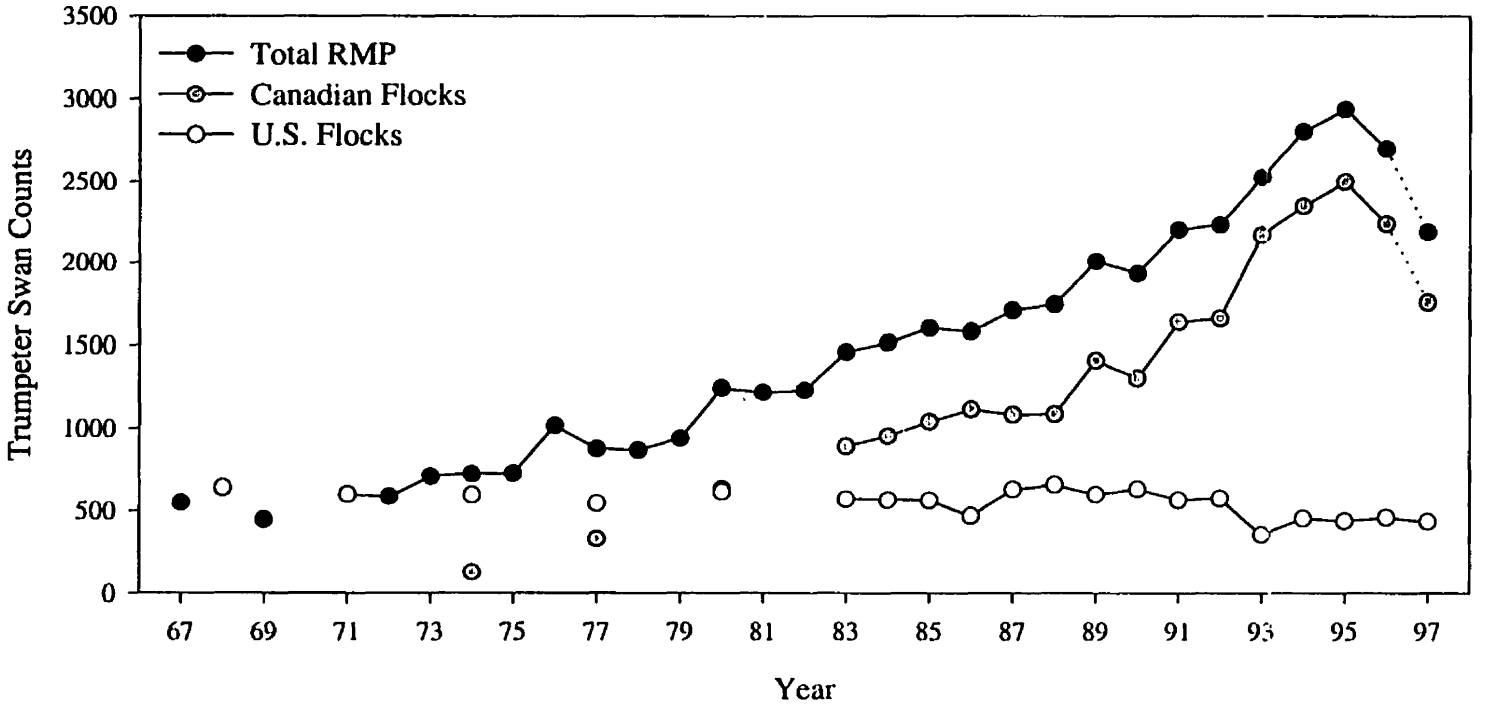

Fig. 4.1: Trends in Rocky Mountain Populations (RMP) of Trumpeter Swans, 1967-1997. Counts of U.S. Flocks were conducted in September surveys and Total RMP surveys were completed in February of the following year. Canadian Flocks were calculated by subtracting U.S. Flock counts from Total RMP counts. February counts are plotted on the year prior because they estimate production in the earlier year. Yellowstone National Park was not surveyed in February 1998 due to weather (from Subcommitte on Rocky Mountain Trumpeter Swans 1998).

My goals in this part of my study were to estimate the energetic demands of Trumpeter Swans and relate this to the removal of rhizomes and tubers though foraging, and to estimate foraging efficiencies in relation to forage removal. I also investigated impacts from Trumpeter Swan foraging on the macrophyte community in stopover areas, and discuss potential long-term consequences of spring tuber and rhizome consumption by Trumpeter Swans.

METHODS

Study area.- I investigated Trumpeter Swan energetics, and impacts of foraging by swans on tuber and rhizome density and macrophyte growth in 13 ponds located approximately 50 km west of Calgary, Alberta (51°05'N, 114°30'W to 51°09'N, 114°42'W). This site is located in the foothills of the Rocky Mountains and ranching is the main land-use practise. There are many ponds in the area, some of which are reportedly used every spring by Trumpeter Swans and other ponds that never appear to be used (G. Beyersbergen, pers. comm.; conversations with landowners).

Trumpeter Swan energetic requirements.- During the time that Trumpeter Swans were present in spring 1999, I conducted daily counts and observations using focal-animal techniques (Chapter II). Here I discuss in detail the four ponds that I identified as consistently used between years, and make only limited reference to ponds classified as variably used or unused between years (see Chapter III). I calculated the Basal Metabolic Rate (BMR) of Trumpeter Swans as: $BMR = 73.5W^{0.73}$, where W is mass in kilograms (calculation in kcal, 1kJ = 4.187kcal; Aschoff and Pohl 1970). I used 10 kg as the average mass of adults and cygnets (Bellrose 1976). I used the average time-budget of

swans on the four study ponds and created an energy-budget by assigning a value to each behaviour that was a function of BMR (Dolnik 1980; cited in Kritsov and Mineyev 1991). Trumpeter Swans are active at night (Squires 1991) so I assumed that their time-budget remains constant over 24 h. I calculated Trumpeter Swan energy requirements for a single day by multiplying the proportion of time allocated to each behaviour and the value of the behaviour relative to BMR. I summed over all behaviours, and multiplied the sum by the BMR. I did not differentiate between the activities of adults and cygnets as there was no significant difference in their time-budget (Chapter II). I then estimated the total amount of forage required by all Trumpeter Swans to satisfy their daily energetic requirements. I calculated the total energy requirements of all swans present on consistently used ponds, and divided by the average energy content of a dry gram of tubers and rhizomes.

Food consumption by Trumpeter Swans.- In two of the consistently used study ponds, Sibbald and Sibbald East, I used exclosures to assess forage availability and the consumption of tubers and rhizomes by Trumpeter Swans. I placed 10 60cm x 60cm rebar and plastic-mesh exclosures on the surface of the frozen sediment, in areas where Trumpeter Swans had been observed to forage in the past (L. Hills, pers. comm.), prior to the swans' arrival. After all Trumpeter Swans had left the study area, I randomly selected five exclosures to be removed and I sub-sampled the sediment within each excluded area 6 times with an Eckman grab (15 cm x 15 cm x 15 cm). I also selected additional sites where Trumpeter Swan foraging was observed, and took 6 Eckman samples from each of five 0.6-m^2 areas. In the other two consistently used ponds, Jumping Pound and Beaver, the placement of exclosures prior to the arrival of Trumpeter

Swans was not possible and I estimated tuber and rhizome availability in fall 1999. I estimated corrections for rhizome and tuber decomposition from the difference in mean tuber and rhizome biomass from Eckman samples taken in Sibbald and Sibbald East in fall 1999 (following the procedure for Beaver and Jumping Pound) and spring 1999 samples in excluded areas. I also took Eckman samples, as described above, in the spring of 1999 from the nine ponds that I classified as variably used or unused. Eckman samples were sorted in the lab using a 4 mm sieve and tubers and rhizomes were dried at 60°C for 48 hours. I calculated the total dry mass of tubers and rhizomes available to Trumpeter Swans as the total dry mass in the pond <1 m deep (Chapter III), because Trumpeter Swans can only reach ~100 cm to forage (Scott 1972, Holton 1982).

Tubers and rhizomes were analysed by Norwest Labs in Lethbridge, Alberta, for gross energy ($kJ \cdot g^{-1}$), metabolizable energy ($kJ \cdot g^{-1}$), crude protein, crude fat, and crude fibre. Metabolizable energy is equal to gross energy – (fecal + urinary energy) (Alisauskas and Ankney 1992) and is considered to be the most meaningful expression of dietary content (Burton et al. 1979). Nitrogen was measured by Kjeldahl digestion; crude protein was then determined by multiplying %N by 6.25 (Tecator Kjeltec 1035/38 Analyzer Manual 1990). Crude fat was determined by extracting fat from a known weight of sample using hexane, and then the hexane was distilled off and the remaining fat weighed (Association of Official Analytical Chemists 1990a). Crude fibre was measured using the Ankom method; it is the residue remaining after a sulfuric acid and sodium hydroxide digestion, followed by oven-drying and ignition (Association of Official Analytical Chemists 1990b). Ash content was determined through ignition at 600°C for 2 h to estimate mineral content (Association of Official Analytical Chemists

1996). Gross energy and metabolizable energy were calculated from crude protein, crude fat, and crude fibre measurements. Parameters for poultry ration were used, in the absence of captive Trumpeter Swans with which to estimate energy losses to feces and urine. However, the metabolizable energy of foods eaten by chicken and mallards is similar (Sugden 1971).

Foraging efficiencies of Trumpeter Swans.- I used the foraging behaviour of Trumpeter Swans (Chapter II) to estimate foraging efficiencies as the number of tubers and rhizomes that would have to have been removed by Trumpeter Swans during foraging tip-ups to remove the biomass that was estimated from direct samples of rhizome and tuber removal, and energy-budget requirements.

Impacts of Trumpeter Swans on the macrophyte community.- After all Trumpeter Swans had left, I measured turbidity in all study ponds during early June 1999, with an Orbeco-Hellige portable Turbidimeter (Orbeco Analytical Systems Inc., Farmingdale, N.Y.). I removed the remaining exclosures that were not used to assess foraging of Trumpeter Swans on tuber and rhizome biomass (see above) and replaced them with 60cm x 60cm quadrats (exclosure minus the mesh). I also placed five quadrats in areas where I had observed Trumpeter Swans foraging. In August 1999, a 30cm x 30cm quadrat was placed in the center of the larger quadrat and I harvested the aboveground structures of all macrophytes and brought them back to the lab. Each plant was identified to species and its height and dry mass was measured.

Statistical analysis.- I compared the gross energy, metabolizable energy, crude protein, crude fibre, and crude fat of tubers and rhizomes using t-tests. I ln-transformed turbidity to meet the assumptions of normality, and compared the turbidity of consistently

used, variably used, and unused ponds using an ANOVA and Tukey test for multiple comparisons. Regression analyses were carried out in SigmaPlot (Version 4.0) to determine the influence of height on macrophyte dry mass. This analysis was only conducted on *Potamogeton pectinatus*, because it was the dominant macrophyte species in all samples. The slopes of regression lines for macrophyte growth in excluded and used areas were compared using paired t-tests. I compared the average density of *P. pectinatus* shoots, average biomass of *P. pectinatus*, and the average biomass of all macrophytes present in used and excluded areas using Mann-Whitney U-tests. I used SYSTAT (Version 7.0) and a probability of 0.05 to determine significance for statistical tests, unless otherwise indicated.

RESULTS

In 1999 there were 1150 Trumpeter Swan-days (where one swan-day is equal to a single swan present for a single day) counted on the four consistently used ponds. Jumping Pound had a total of 411 swan-days, Beaver had 320 swan-days, Sibbald had 223 swan-days, and Sibbald East had 196 swan-days. The remaining nine ponds combined for only 150 swan-days. There was an overall total of 1300 Trumpeter Swans-days counted on all 13 ponds in 1999.

The dominant activity on the four consistently used ponds was foraging, followed by swimming, sleeping, and preening. Resting and flying were uncommon during observations (Table 4.1, also see Chapter II). The basal metabolic rate of a 10 kg non-passerine bird is 1 652.68 $kJ \cdot day^{-1}$, and factoring in the daily activities of Trumpeter Swans, the daily energy requirement of an individual swan was 2 437.81 $kJ \cdot day^{-1}$

Table 4.1: Time-budgets and energy requirements for Trumpeter Swans on four study ponds west of Calgary in spring 1999. Energy value of activities relative to BMR are from Dolnik (1980; cited in Kritsov and Mineyev 1991).

Behaviour	Proportion of time activity performed	Value of Activity x BMR	Energy requirement BMR
Forage	0.543	1.6	0.869
Preen	0.135	1.3	0.176
Rest	0.023	1.12	0.026
Sleep	0.143	1.0	0.143
Fly	0.001	14.0	0.014
Swim	0.155	1.6	0.248

Daily energetic requirement = 1.475 BMR

= 1.475 * 1 652.68 $kJ \cdot day^{-1}$

= 2 437.81 $kJ \cdot day^{-1}$

Total energy requirements of all swans:

= 2 437.81 $kJ \cdot day^{-1}$ *1150 swan-days

= 2 803 481.50 kJ

(Table 4.1). The total energy requirement of the 1150 Trumpeter Swans on the four consistently used ponds in the stopover area west of Calgary was 2 803 481.50 kJ.

The relative abundance of tubers and rhizomes in Eckman samples prior to Trumpeter Swan foraging was 6.1 % and 93.9 %, respectively (Table 4.2). Tubers had a significantly higher metabolizable energy content than rhizomes (t-test, t=-27.25, df=4, P<0.001), however, gross energy was not significantly different (t-test, t=-0.56, df=4, P>0.05). Rhizomes had three times the ash, twice the crude protein (t-test, t=8.20, df=4, P<0.005), 15 times the crude fibre (t-test, t=7.27, df=4, P<0.001), and three times the crude fat content (t-test, t=3.067, df=4, P<0.001), compared to tubers. The average metabolizable energy content per gram of forage based on the relative abundance of tubers and rhizomes was 11.86 $kJ \cdot g^{-1}$. Therefore, the total dry mass of forage required to meet the energy requirements of 1150 Trumpeter Swans in the four consistently used ponds in the Calgary stopover area in 1999 was 236.38 kg.

The total dry mass of forage available per pond was highest in Beaver followed by Jumping Pound, and then Sibbald and Sibbald East with similar amounts of total available forage (Table 4.3). However, the available area for Trumpeter Swan foraging was largest in Jumping Pound, followed by Beaver, and again Sibbald East and Sibbald were similar. The total dry mass of forage available to Trumpeter Swans in the Calgary area, to a depth of 15 cm in the sediment, was 359.90 kg, or 36.53 $kg \cdot ha^{-1}$. After the swans had continued their migration, the total dry mass of tubers and rhizomes remaining was 155.10 kg, or 16.61 $kg \cdot ha^{-1}$. Subtracting these values provides an estimate of 204.80 kg, or 56.9 % of the tubers and rhizomes available in spring were consumed by Trumpeter Swans in 1999, only 30 kg less than the estimated expected consumption

Table 4.2: Mean (SE) energy content and composition of tubers and rhizomes collected from Sibbald, Sibbald East, and Ibbotson ponds west of Calgary. Three 1-g samples of tubers and rhizomes were analysed, except for ash where only one sample of each was analysed.

	Tuber	Rhizome
Gross Energy ($kJ \cdot g^{-1}$)^{ns}	17.66 (0.01)	17.61 (0.07)
Metabolizable Energy ($kJ \cdot g^{-1}$)*	13.29 (0.04)	11.77 (0.04)
Ash (%)	4.6	13.7
Crude Protein (%)*	10.9 (0.2)	19.1 (0.9)
Crude Fibre (%)*	0.5 (0.2)	7.7 (0.4)
Crude Fat (%)*	1.4 (0.1)	4.5 (0.1)
Relative proportions in Eckman samples prior to swan foraging	0.061	0.939

* $P < 0.05$ from t-tests

^{ns} $P > 0.05$

Table 4.3: Total dry mass (rhizomes + tubers) available and remaining after Trumpeter Swans departed, in consistently used ponds west of Calgary.

Pond	Area of pond <1 m deep (ha)	Total dry mass (kg) available	Total dry mass (kg) remaining	% removed
Jumping Pound[a]	3.543	90.12	21.00	76.7
Beaver[a]	2.850	155.92	47.29	70.0
Sibbald	1.399	59.28	46.22	22.0
Sibbald East	1.548	54.58	40.59	25.6
Total	**9.340**	**359.90**	**155.10**	**56.9**

[a] - estimates of available dry mass have been adjusted for decomposition.

based on energetic requirements. The percentage of tubers and rhizomes removed was highest for Jumping Pound and Beaver, which also had the most swan-days, while Sibbald and Sibbald East had lower swan-use, and a lower percent removal of tubers and rhizomes (Table 4.3). For the nine ponds classified as variably used or unused, there was a total dry mass of 190.34 kg of forage available in 15.827 ha. or 12.03 $kg \cdot ha^{-1}$.

Trumpeter Swans foraged 54.3 percent of the time, or 781.92 min per day, and tipped-up at an average rate of 3.4 min^{-1} (Chapter II), for an estimated total of 3 057 307.2 tip-ups combined for 1150 swan-days. To remove the estimated 204.80 kg dry mass of forage taken by the swans in the four consistently used ponds, each Trumpeter Swan must consume tubers and rhizomes at a rate of 7.42 $g \cdot h^{-1}$ (88.0 $kJ \cdot h^{-1}$). With an average dry mass of tubers and rhizomes of 0.018 g, weighted in relation to relative abundance, they must remove an overall total of 11 377 778 tubers and rhizomes, at a rate of 3.72 tubers or rhizomes per tip-up. Since Trumpeter Swans spend an average of 12.43 s submerged during each tip-up (Chapter II), they must remove a tuber or rhizome every 3.34 s that they are submerged. To remove the 236.38 kg estimated to be required from energy-budgets, swans must remove a total of 13 132 222 tubers and rhizomes at a rate of 8.56 $g \cdot h^{-1}$ (101.5 $kJ \cdot h^{-1}$), 4.30 per tip-up, or one every 2.89 s.

Trumpeter Swans did not significantly alter the growth of *P. pectinatus* (Paired sample t-test, $t = 3.00$, df=1, $P > 0.05$). Although this was based on a small sample size, the slopes were similar (Figure 4.2). In Sibbald pond, the density of *P. pectinatus* was 284.44 ± 66.63 $shoots \cdot m^{-2}$ in excluded areas, compared to 122.22 ± 37.52 $shoots \cdot m^{-2}$ in used areas. This was a 57 % decrease, although it was not statistically significant (t-test, $t=2.12$, df=8, $P=0.067$). *P. pectinatus* shoot dry mass was 156.54 ± 22.16 $g \cdot m^{-2}$ in

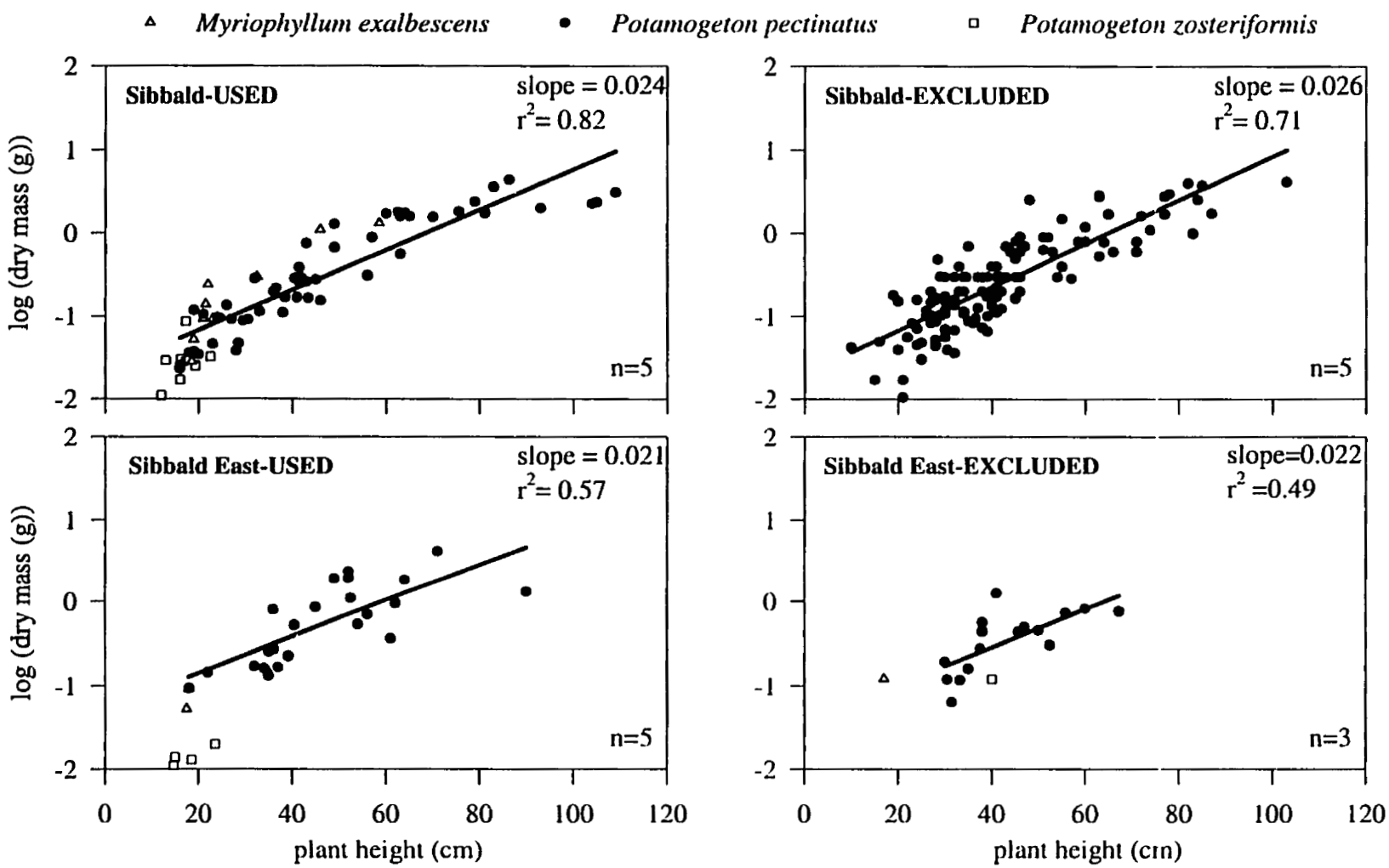

Figure 4.2: Macrophyte growth in areas used by Trumpeter Swans compared to areas where swans were excluded. Regression lines represent the variation in log(dry mass) explained by plant height for *P. pectinatus*. Each symbol represents an individual plant and n is the number of quadrats sampled.

excluded areas and 96.08 ± 33.34 $g \cdot m^{-2}$ in areas where Trumpeter Swans had fed, again not significantly different (t-test, t=-1.51, df=8, P=0.169). I plotted the size distribution of *P. pectinatus* in excluded and used areas of Sibbald pond. Trumpeter Swans appeared to only influence the number of smaller plants (<1.0 g) present and there were similar numbers of large plants (>3.0 g) in both areas (Figure 4.3). *Myriophyllum exalbescens* and *P. zosteriformis* were present in areas used by Trumpeter Swans, but not in excluded areas. There was no significant difference in the dry mass of all macrophytes present in the excluded (156.54 ± 22.16 $g \cdot m^{-2}$) and used (104.12 ± 34.23 $g \cdot m^{-2}$; t-test, t=-1.29, df=8, P>0.05) areas.

In Sibbald East only three of the five quadrats in excluded areas were recovered. There was no significant difference in *P. pectinatus* density in used (51.11 ± 19.12 $shoots \cdot m^{-2}$) versus excluded (48.15 ± 20.62 $shoots \cdot m^{-2}$; t-test, t=0.10, df=6, P>0.05) areas, or *P. pectinatus* dry mass (excluded: 22.16 ± 12.36 $g \cdot m^{-2}$, used: 46.64 ± 19.10 $g \cdot m^{-2}$; t-test, t=0.91, df=6, P>0.05) in Sibbald East. There was also no significant difference in the dry mass of all macrophyte species present in excluded (25.90 ± 12.38 $g \cdot m^{-2}$) and used (48.64 ± 18.29 $g \cdot m^{-2}$) areas. More *P. zosteriformis* was present in used areas compared to excluded areas of Sibbald East and in all cases there was actually a higher density and biomass of macrophytes in areas used by foraging Trumpeter Swans compared to excluded areas. Macrophytes in these ponds were also patchily distributed, with great variation between samples (quadrats). Overall, more variance in log (dry mass) was explained by plant height in Sibbald pond than Sibbald East (Figure 4.2).

Tubidity was significantly higher in consistently used ponds (15.38 ± 7.95 NTU) compared to unused ponds (2.98 ± 1.01 NTU), and variable use ponds (6.68 ± 2.00

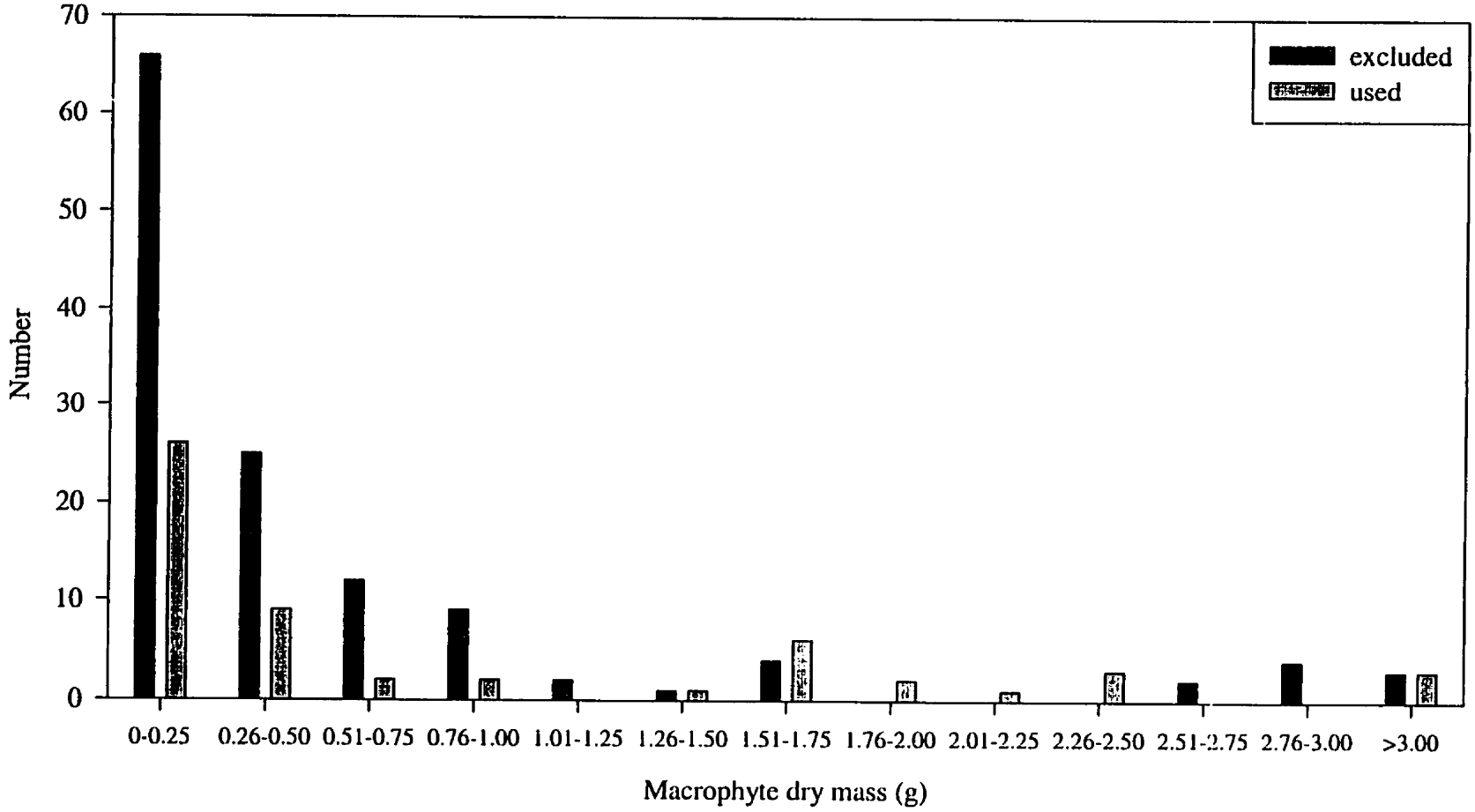

Figure 4.3: Distribution of *P. pectinatus* dry mass harvested in areas used by Trumpeter Swans compared to areas where Trumpeter Swans were excluded.

NTU) were not significantly different from the other groups (ANOVA, F=4.17, df=12, P<0.05).

DISCUSSION

The estimated amount of total forage required by 1150 Trumpeter Swans for daily activities (236.38 kg), and the estimated amount of forage consumed in the consistently used ponds (204.80 kg) was remarkably similar, even though the estimate of forage removed was likely conservative. Trumpeter Swans create craters up to 30 cm deep and 1 m across, by scratching at the sediment to remove tubers (Shea 1979) and I did not sample in cratered areas. Therefore, there were areas where Trumpeter Swans may have more completely depleted tubers and rhizomes that I did not factor into forage removal. In addition, I only sampled the top 15 cm of the sediment, although Trumpeter Swans may forage to depths below 15 cm, if the water depth is less than ~85 cm, and larger tubers occur between 10-20 cm depth (Anderson and Low 1976). Since my results demonstrate that foraging requirements for maintenance could be satisfied by the amount of forage used, any additional forage not accounted for in my conservative measurements would be available for allocation to energy reserves for migration and reproduction.

In stopover ponds, rhizomes were much more abundant than tubers, and although rhizomes were slightly lower than tubers in metabolizable energy, they were higher in ash, crude fibre, crude fat, and crude protein. Metabolizable energy of *P. pectinatus* tubers (13.29 ± 0.04 kJ·g^{-1}) was significantly higher than that found by Squires (1991) (11.72 ± 0.29 kJ·g^{-1}; t-test, t=3.69, df=7, P<0.05). However, my estimate for rhizomes (11.77 ± 0.04 kJ·g^{-1}) was not significantly different (t-test, t=0.12, df=7, P>0.05).

Additionally, McKelvey (1985) found the metabolizable energy of *Carex lyngbei* rhizomes eaten by Trumpeter Swans was 10.38 ± 0.92 kJ·g^{-1}, which is not significantly different from the rhizomes (t-test, t=0.73, df=13, P>0.05) or tubers (t-test, t=1.54, df=13, P>0.05) in my study.

Increased ash and fibre decreases the digestibility of the diet (Muztar et al. 1977, Thomas and Prevett 1980), and may help to explain why the metabolizable energy of rhizomes was lower than for tubers, even though their gross energy contents are similar. Rhizomes had significantly higher proportions of fat and protein compared to tubers. Fat fuels flight during migration, and the energy content of protein and carbohydrates is less than half as that liberated by fat (Alerstam 1993). Additionally, fat can be carried without storing extra water (Alerstam 1993). Fat and protein reserves are also important in their contribution to egg production, and food selection by waterfowl is influenced by the need to satisfy nutrient requirements for reproduction (Krapu and Reinecke 1992). Fat reserves possessed by females at the onset of the breeding season are an important determinant of clutch size in waterfowl (Ankey and MacInnes 1978, Krapu 1981). Therefore, the relatively high protein and fat content of rhizomes should better meet nutritional demands of Trumpeter Swans than tubers.

The daily energetic requirement of Trumpeter Swans, based on time-budgets, was estimated to be 2437.81 kJ. This value is similar to the existence energy of 2393.88 kJ·day^{-1}, calculated for a 10 kg Trumpeter Swan using Kendeigh's (1970) equation (log M = 0.6372 + 0.5300 log W, where W is weight in g and M is existence energy in kcal; 1kJ = 4.187kcal). In calculating existence energy, daily activities were factored in from behaviours of caged birds (Kendeigh 1970). Therefore, the assumption that the daily

time-budget could be used over 24 h in the calculation of the energy-budget seems plausible, as the energy-budget and existence energy requirements were similar.

To remove a total of 204.80 kg of tubers and rhizomes, each Trumpeter Swan would have to remove on average 7.42 $g \cdot h^{-1}$ during foraging. This value seems realistic as Lesser Snow Geese (*Chen caerulescens caerulescens*) have been recorded to consume 14.3 $g \cdot h^{-1}$ dry mass of stembases of tall cotton-grass (*Eriophorum angustifolium*) in Alaska (Hupp et al. 1996), and Greater Snow Geese (*Chen caerulescens atlantica*) consume *Scirpus* rhizomes at a rate of 17.8 $g \cdot h^{-1}$ (146.7 $kJ \cdot h^{-1}$; Bédard and Gauthier 1989). It is thus not unreasonable that Trumpeter Swans removed forage at a higher rate than estimated, and gained additional energy for migration and reserves for breeding. If the assumption that the time-budget is consistent over 24 h is not correct, and Trumpeter Swans only sleep during the night, their foraging efficiencies would have to increase to remove the estimated amount of forage, but not to unreasonable levels.

Interactions between herbivorous waterfowl and aquatic macrophytes have recently received attention in studies of macrophyte dynamics and in studies of habitat use and sustainability. Although it has been established that birds often reduce macrophyte abundance (Anderson and Low 1976, Squires 1991), long-term impacts of seasonal plant depletion remain largely unknown (Lodge et al. 1998). Because of the nature of my study regarding consumption of overwintering structures and impacts of foraging on macrophyte growth in the following growing season, I will discuss the potential long-term consequences of Trumpeter Swan foraging, but my data do not allow me to provide a direct answer regarding the long-term sustainability of macrophytes in my study ponds.

The timing of herbivory with respect to the growing season, tissue consumption, and cycling nutrients, affects macrophyte dynamics (Mitchell and Perrow, 1998). For example, the future productivity of a plant would not be directly affected by foraging on aboveground parts in autumn, when the plants are senescing (Kiørboe 1980). However, Trumpeter Swans arrive at migratory stopover areas in Southern Alberta while ice still covers a large proportion of the ponds and macrophyte growth has not begun. The plants from the previous year have senesced, hence the only available food source for Trumpeter Swans in April is tubers and rhizomes (Wetzel 1983), and consumption of these overwintering structures removes the future growth potential of that material (Mitchell and Perrow 1998).

Within stopover areas, Trumpeter Swans select ponds based on the abundance of available forage (Chapter III). Although Trumpeter Swans consistently use some ponds year after year, they also move among ponds (B. Anderson, pers. comm.). The consistently used ponds had a biomass of tubers and rhizomes three times that of variable and unused ponds. In fact, when Trumpeter Swans continued their migration they left the consistently used ponds with 16.61kg·ha^{-1} of tubers and rhizomes, which is greater than the 12.03 kg·ha^{-1} present in variable and unused ponds. Beekman et al. (1991) found that Bewick's Swans (*Cygnus columbianus bewickii)* moved to new areas when tubers fell below a threshold level, and Squires (1991) observed Trumpeter Swans in the Tri-state population shift to new areas, presumably in search of higher tuber densities. Therefore, the variable and unused ponds in the Calgary area may start out with tuber and rhizome densities below the threshold biomass that is profitable for the swans.

Potential impacts of herbivory on a macrophyte community range from a shift in community composition and a reduction in the favoured macrophyte species, to an increase in phytoplankton associated with lowered macrophyte biomass (Mitchell and Perrow 1998). Macrophytes can cover an entire lakebed if the water is shallow and transparent (Horne and Goldman 1994) and dense macrophytes can inhibit phytoplankton growth (Faafeng and Mjelde 1998). In areas where there is high nutrient loading, algal production may increase water turbidity and decrease macrophyte abundance by shading (Faafeng and Mjelde 1998). Sediment resuspension by swimming actions of waterfowl directly reduces the available light for macrophytes, and indirectly increases the rate of nutrient supply from the sediment to phytoplankton (Søndergaard et al. 1992). Mitchell and Wass (1996) found little influence of nutrient recycling and bioturbation due to Black Swan (*Cygnus atratus*) foraging on macrophytes, in relation to sediment resuspension generated by wind and wave action. Trumpeter Swans probably contribute little in terms of nutrient loads from faecal deposition, as they forage within ponds and would only recycle nutrients, not bring additional loads that originated in terrestrial environments. Turbidity was highest in the consistently used ponds, and Jumping Pound, the consistently used pond that was almost hypereutrophic, had algal blooms in both 1999 and 2000. Smaller blooms were observed on Sibbald and Sibbald East, but macrophytes were, and are, still abundant in all these ponds.

Foraging on overwintering structures may have important implications to macrophyte abundance and community composition in subsequent growing seasons (Lodge 1991, Perrow et al. 1997). In Sibbald and Sibbald East, there was no significant impact of foraging on the density or biomass of macrophytes in excluded and used areas,

and the growth patterns of *P. pectinatus* were not altered in used compared to excluded areas. *P. pectinatus* was the dominant species in excluded areas, while there were other species present in the used areas. Because foraging by Trumpeter Swans results in the removal or damage of overwintering structures, macrophytes from used areas may be at a disadvantage in terms of using the energy stored in overwintering structures, or the plants may sprout from seed. It would then be expected that these plants would have a smaller mass to height relation because macrophytes grow up to the surface of the water first and then allocate energy into spreading out (Van Wijk 1988). Although there was a higher density of *P. pectinatus* in excluded areas of Sibbald pond, most of the plants had a small biomass, while the number of large-biomass plants was no different than in used areas. A possible underlying mechanism is that the plants propagated from tubers or rhizomes reach the water surface earlier and then shade the remaining plants. In excluded areas, there was increased plant density and competition for light, resulting in a few large plants and a large number of smaller ones. In used areas, there were fewer plants and less competition, but plants from tubers or rhizomes that remained after the swans left, would grow to the surface and shade the remaining plants, and again, the majority of the plants would have a small biomass. In addition, the large plants may be the ones that allocate energy to overwintering structures in the fall, and thus provide forage to swans the next spring. I found that the biomass of tubers and rhizomes sampled in Sibbald and Sibbald East in the fall was greater than that found in spring exclosures (Chapter III), therefore there was no evidence of a carry-over effect of spring foraging on fall tuber and rhizome density. Hampton (1981) found no significant difference in the composition or abundance of macrophytes taken from within and outside exclosures for wintering

Trumpeter Swans. However, in a 30 year period a slight shift in the macrophyte community had occurred (Shea 1979, Hampton 1981).

Potamogeton pectinatus flourishes in areas that have been heavily grazed by waterfowl for over 20 years (Kantrud 1986). Near Calgary, yearly variation in the timing and pattern of pond melt relative to the swans' arrival provides foraging refuges to macrophytes. Beaver, for example, was used by Trumpeter Swans beginning 7 April 1999, but remained frozen until 22 April 2000, and there was ice coverage on a portion of Sibbald pond in 2000 that was a primary foraging area for Trumpeter Swans in 1999 (Chapter III). The pond area >1 m deep may function as a source of seeds or fragments that reproduce vegetatively. As there were still tubers and rhizomes present after Trumpeter Swans had left the area, recolonization of macrophytes could occur from those tubers and rhizomes that remained, in addition to seeds (Anderson and Low 1976, Van Wijk 1988), and thus the macrophyte community would be sustainable. However, if there are further increases in the Trumpeter Swan population, it is unlikely that the consistently used ponds in this study will be able to accommodate all Trumpeter Swans that pass through the Calgary area. With the 359.90 kg of forage available in the four consistently used ponds in 1999, and an average energy content of 11.86 kJ per gram of forage, the total number of swan-days that could have been supported, assuming that all forage in usable areas was consumed, is 1750 swan-days on the four ponds, based on 1999 energy-budgets. Recall that there were 1150 swan-days of use on these ponds in 1999, so a 50% increase in swans over 1999 levels could have been supported. In reality I expect the total number of swans that could be supported would be less because of threshold food levels, below which foraging would no longer be profitable. Therefore,

with further increases in Trumpeter Swans numbers, I expect that individuals may have to expand their range within the Calgary area to find suitable habitats. Another possibility is to actively manage other ponds in the area to produce properties desirable to Trumpeter Swans (Chapter III).

CHAPTER V

PROJECT SUMMARY

Trumpeter Swans were hunted almost to the point of extinction by the early 1900s (Coale 1915). However, in the latter part of the 20th century, Trumpeter Swan populations have rebounded, and the Rocky Mountain Population has increased at a steady rate (Chapter IV). Due to the threatened nature of this species, many research projects have been conducted to determine habitat selection and use, and factors limiting Trumpeter Swan population growth. Much of this research has been carried out in breeding and wintering habitat (Shea 1979, Holton 1982, Maj 1983, Squires 1991). Mine is the first study to consider Trumpeter Swan migratory stopover areas in Canada. I investigated time-budgets of Trumpeter Swans in migratory stopover areas of Southern Alberta (Chapter II), determined what characteristics were present in ponds that are used by Trumpeter Swans consistently between years (Chapter III), I also related energy requirements of Trumpeter Swans to the quantity of forage removed, and I discussed the sustainability of macrophyte communities (Chapter IV).

It has been assumed that Trumpeter Swans use energy reserves during the breeding period, because Trumpeter Swans arrive at breeding areas and begin nest construction while ponds are still ice-covered (Holton 1982, Shandruk 1991, Mitchell 1994), and egg-laying begins shortly after ponds open (Pinel et al. 1991, Squires 1991). Little information has been documented to determine when the collection of energy reserves for breeding takes place. Squires and Anderson (1997) found that Trumpeter Swans in the nonmigratory Tri-state subpopulation of the Rocky Mountain Population increased the proportion of time allocated to foraging from winter (0.296 ± 0.027) to

spring (0.445 ± 0.021). I found the mean proportion of time allocated to foraging was 0.486 ± 0.012, close to the spring value for Trumpeter Swans in the Tri-state area (Squires and Anderson 1997). The similarity in time-budgets of migratory and nonmigratory Trumpeter Swans in spring suggests that swans have to build up energy reserves before breeding. Trumpeter Swans in the Canadian subpopulation take up to two months to complete their relatively short 1400 km migration. This allows considerable time for foraging (Mackay 1978, Mitchell 1994), and suggests either that stopover sites are rich in food (Shea 1979) and worth exploiting, and (or) that swans must stay to recoup energy reserves lost during each stage of migration. If migratory stopover sites are richer in food than spring-use areas in the Tri-state region, swans in the migratory Canadian subpopulation may gather more energy reserves than their Tri-state counterparts and produce larger clutch sizes, and/or provision eggs with greater resources. This could result in greater cygnet production in the Canadian subpopulation and may be responsible for the steady increase in the Canadian subpopulation, compared to the Tri-state subpopulation that has remained near ~400 swans.

I found little difference in the activity budgets of adults and cygnets, contrary to my expectation that adults would forage for a larger proportion of the time to build up energy reserves for breeding. However, there were indications that foraging efficiencies may differ, as adults rocked a significantly higher proportion of the time prior to a tip-up, and this may reflect the adult's experience and result in gathering more food per tip-up compared to cygnets.

I found no difference in Trumpeter Swan time-budgets between stopover sites (Cardston-Mountain View-2000 versus Calgary-2000) that had an obvious biological

meaning. It may be of interest, however, to compare time-budgets of Trumpeter Swans at stopover sites closer to wintering grounds and just prior to breeding grounds to determine if foraging intensity changes over space and time relative to the timing of egg-laying. Although there was little effect of stopover site on time-budgets in this study, temperature was a significant factor on time allocated to foraging and sleeping. When temperatures dropped below -4° C, the proportion of time allocated to foraging dropped sharply, and sleeping increased (Chapter II). Time of day did not strongly influence behaviour of adults or cygnets in stopover areas.

Within spring migratory stopover areas, Trumpeter Swans preferred ponds with a higher biomass of tubers plus rhizomes compared to ponds that were used intermittently or not at all (Chapter III). This was not surprising, considering that the dominant activity of Trumpeter Swans was foraging. Salinity also contributed to separating ponds into use categories and may be a function of pond location, indicating that the remoteness of ponds is not a critical factor in selection. This was contrary to breeding areas where Trumpeter Swans select sites with low human disturbance (Shea 1979, Holton 1982, Mitchell 1994). Salinity may also promote the presence of *P. pectinatus* as it is restricted to waters with high ion concentrations (Hutchinson 1975). I found little variation in the values of most limnological variables between pond groups. Nevertheless, water chemistry may play an important role in driving macrophyte growth and ultimately in the forage available to migrating Trumpeter Swans. Learned behaviour may also play a role in the selection of ponds, although consistently used ponds were also those with higher food availability.

Trumpeter Swan energetic requirements, based on time-budgets, provided an

estimate of 2437.81kJ·day^{-1} for an individual swan (Chapter IV). The total biomass of tubers and rhizomes required to meet the energetic demands for 1150 swan-days on the four consistently used ponds was 236.84 kg. This was remarkably close to the conservative estimate of 204.80 kg consumed by Trumpeter Swans. This estimate was conservative because during sampling I avoided areas where feeding craters were created, and my sampling procedures involved extracting only the top 15 cm of sediment, while Trumpeter Swans can forage below this depth if the water was less than ~85 cm deep. This means that more forage could be consumed than was directly sampled, and excess forage could be allocated to energy reserves for continued migration and reproduction. Further research could be conducted to examine habitat preferences, energetic requirements, and forage removed by Trumpeter Swans during the fall migration, as they will not be building up breeding reserves.

Impacts by Trumpeter Swans on the macrophyte community were not significant. Although the density of shoots decreased 57% due to swan foraging, there was only a 33% drop in macrophyte biomass. The only difference in the distribution of plant biomass was seen in the dominance of smaller plants in exclosures compared to used areas. The same number plants in excluded and used areas became large (>3.00 g dry mass) and these plants may be the ones to allocate energy to produce overwintering structures the following fall, and the forage for swans the next spring. I also found an increase in tuber and rhizome densities from spring to fall in Sibbald and Sibbald East, so the impact of swans on their forage within the year was not significant. Therefore, it appears that the swans are harvesting the macrophytes in a sustainable fashion.

To date, migratory stopover areas have been largely overlooked in Trumpeter Swan studies. Here, I have demonstrated that migratory stopover habitat plays an important role in Trumpeter Swan biology. With only 4 of 13 study ponds in the Calgary area being consistently used by Trumpeter Swans (and I know of 10 additional ponds not used by swans and 2 ponds that have intermittent use in the region), the sustainability of forage resources in consistently used ponds will be key to ensuring successful reproduction, and continued increase of this population. But with further increases in this population, and increased consumption of tubers and rhizomes, migratory stopover habitat may become a limiting factor. Trumpeter Swans may find new, suitable ponds in the area. The knowledge gained through my study can also be used in active management of ponds to assure that ponds in the area meet the preferences and requirements of Trumpeter Swans.

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APPENDIX A: Trumpeter Swan use, morphometric measurements, water chemistry and biotic conditions of ponds in the Cardston area.

Pond	Total swan-days	Total calendar days used	Open Water Area (ha)	Area <1m deep (ha)	Shoreline Length (m)	Pond Length (m)	Pond Width (m)
Romeril	528	16	12.791	-	2371.6	760.0	490.0
Long	72	5	18.149	4.486	3002.3	950.0	475.0
Wolsey	44	6	17.617	17.617	1934.5	675.0	340.0
Walburger	16	4	9.828	-	2001.0	680.0	300.0
Mountain View	9	2	0.433	0.433	346.6	108.0	79.0
Romeril NE	0	0	11.113	3.159	1409.7	375.0	367.5

	Elevation (m)	pH	Salinity (ppt)	Conductivity ($\mu S \cdot cm^{-1}$)	Chla ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)
Romeril	1325	8.72 (0.02)	0.08 (0.00)	184.4 (0.6)	3.29 (1.05)	6.20 (1.24)
Long	1324	8.50 (0.25)	0.25 (0.07)	491.1 (135.3)	18.33	114.08
Wolsey	1265	9.66 (0.35)	0.19 (0.01)	377.0 (9.0)	9.09 (3.63)	83.66 (44.00)
Walburger	1325	8.48 (0.23)	0.10 (0.01)	217.0 (16.8)	3.33 (0.34)	9.12 (3.72)
Mountain View	1320	6.92 (0.10)	0.90 (0.03)	1684.0 (48.0)	-	-
Romeril NE	1315	8.31 (0.06)	0.43 (0.02)	626.3 (23.9)	11.07	9.41

	Macrophyte Coverage (%)	Rhizome Density (m^{-2})	Tuber Density (m^{-2})	Tuber + Rhizome Drymass ($g \cdot m^{-2}$)	Nontuber, Nonrhizome Drymass ($g \cdot m^{-2}$)
Romeril	16.76	-	-	-	-
Long	11.26	17.78 (5.54)	4.44 (2.96)	2.22 (1.21)	43.11 (21.14)
Wolsey	95.57	22.22 (12.17)	23.70 (16.13)	0.66 (0.37)	4.24 (3.63)
Walburger	18.91	-	-	-	-
Mountain View	100.00	17.78 (8.95)	20.74 (10.05)	1.44 (0.71)	141.19 (28.70)
Romeril NE	29.06	121.48 (29.13)	22.22 (9.66)	8.44 (2.01)	324.89 (14.01)

APPENDIX B: Morphometric measurements, water chemistry, and biotic parameters of study pond west of Calgary, grouped according to use by Trumpeter Swans in spring 1999 and 2000.

Pond	Open Water Area (ha)	Area <1m deep (ha)	Shoreline Length (m)	Pond Length (m)	Pond Width (m)	Elevation (m)
Consistent use						
Jumping Pound	3.543	3.543	716.40	270.0	190.0	1250
Beaver	9.273	2.850	1323.39	502.5	257.5	1302
Sibbald	1.950	1.399	716.20	272.0	104.0	1330
Sibbald East	1.548	1.548	683.23	214.5	135.5	1332
Variable use						
Parks	3.268	1.634	917.07	334.0	150.0	1300
Pile-O-Bones	2.115	1.678	722.04	228.0	170.0	1289
Ridge	1.548	1.239	832.00	343.0	80.0	1318
Monster	9.066	4.119	1748.11	740.0	210.0	1312
Unused						
Horseshoe	1.415	1.392	580.88	226.0	118.5	1302
Jumping Pound East	1.828	1.828	594.70	154.0	125.0	1236
CL	3.777	2.943	1351.76	301.0	232.0	1242
Bend	0.633	0.633	440.30	208.0	44.0	1330
Goodwin	0.772	0.361	610.87	280.0	40.0	1332

APPENDIX B continued...

Pond	pH	Salinity (ppt)	Conductivity ($\mu S \cdot cm^{-1}$)	Chla ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)
Consistent use					
Jumping Pound	9.21 (0.01)	1.11 (0.02)	2069.0 (31.0)	1.55 (0.25)	90.80 (8.77)
Beaver	9.41 (0.05)	0.49 (0.00)	942.0 (0.3)	5.31 (0.60)	54.07
Sibbald	8.44 (0.10)	0.86 (0.01)	1605.0 (15.0)	2.66 (0.79)	26.77 (3.42)
Sibbald East	8.54 (0.09)	0.90 (0.01)	1680.0 (10.0)	1.65 (0.38)	34.09 (2.64)
Variable use					
Parks	8.83 (0.11)	0.31(0.01)	599.8 (6.8)	4.23 (0.42)	39.90 (3.03)
Pile-O-Bones	8.42 (0.10)	0.46 (0.00)	879.9 (1.2)	1.13 (0.23)	28.63 (2.73)
Ridge	8.12 (0.10)	0.35 (0.01)	675.7 (19.9)	1.98 (0.04)	32.37 (0.85)
Monster	9.63 (0.06)	0.45 (0.00)	869.5 (0.6)	4.05 (0.55)	65.97 (4.89)
Unused					
Horseshoe	9.52 (0.01)	0.79 (0.01)	1477.5 (7.5)	0.65 (0.05)	61.75 (2.37)
Jumping Pound East	8.20 (0.07)	0.64 (0.00)	1214.0 (5.0)	2.06(0.34)	70.29 (12.18)
CL	8.74 (0.13)	0.66 (0.02)	1245.5 (25.5)	3.97(1.43)	66.17 (7.83)
Bend	8.97 (0.12)	0.84 (0.01)	1659.3 (81.7)	0.35 (0.05)	19.23 (0.20)
Goodwin	7.97 (0.18)	0.47 (0.01)	896.0 (19.1)	0.60 (0.10)	24.00 (6.16)

APPENDIX B continued ...

Pond	Macrophyte Coverage (%)	Rhizome Density (m^{-2})	Tuber Density (m^{-2})	Tuber + Rhizome Drymass ($g \cdot m^{-2}$)	Nontuber, Nonrhizome Drymass ($g \cdot m^{-2}$)
Consistent use					
Jumping Pound	64.55	84.44 (42.59)	0.00 (0.00)	2.54 (1.40)	92.89 (28.10)
Beaver	72.35	137.78 (40.48)	25.19 (12.08)	5.47 (1.91)	265.33 (35.81)
Sibbald	40.25	97.78 (23.59)	0.00 (0.00)	4.24 (1.08)	212.00 (39.57)
Sibbald East	63.64	69.63 (15.47)	0.00 (0.00)	3.53 (1.06)	162.96 (16.25)
Variable use					
Parks	43.44	42.96 (14.70)	1.48 (1.48)	1.66 (0.66)	427.56 (65.52)
Pile-O-Bones	58.84	29.63 (16.06)	16.30 (12.70)	1.01 (0.56)	164.89 (94.14)
Ridge	59.62	40.00 (30.14)	0.00 (0.00)	1.19 (0.73)	538.37 (63.01)
Monster	84.48	1.48 (1.48)	0.00 (0.00)	0.18 (0.18)	193.78 (38.48)
Unused					
Horseshoe	15.16	4.44 (4.44)	0.00 (0.00)	0.09 (0.09)	177.63 (36.51)
Jumping Pound East	0.00	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	236.00 (27.32)
CL	42.54	41.48 (18.53)	0.00 (0.00)	2.80 (1.29)	185.93 (39.79)
Bend	44.21	93.33 (45.76)	50.37 (22.39)	2.65 (1.20)	278.07 (43.07)
Goodwin	24.07	10.37 (6.46)	5.93 (4.32)	0.33 (0.21)	262.96 (72.12)