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# Compensatory growth responses of *Potamogeton pectinatus* to foraging by migrating trumpeter swans in spring stop over areas

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## Abstract

We examined spring pond use by migrating trumpeter swans (*Cygnus buccinator*) to assess their short-term impact on tuber and rhizome density and biomass, and to evaluate the impact of spring foraging on summer macrophyte biomass and species composition. Trumpeter swans in the Canadian subpopulation of the Rocky Mountain population select ponds that are dominated by *Potamogeton pectinatus*, a macrophyte favoured for its energy-rich tubers and rhizomes. Swans significantly reduced the biomass of tubers and rhizomes present in the study ponds in spring by 24%, but there was no significant impact on overall *P. pectinatus* shoot density and biomass the summer following herbivory. However, there were significantly fewer small *P. pectinatus* shoots (<1.0 g DW) in used areas, and other macrophyte species (*Myriophyllum exalbescens*, *P. zosteriformis*) were present in areas where foraging had occurred. *P. pectinatus* may compensate for the effects of herbivory, as the number of larger shoots (range 1.0–5.0 g DW) were similar in areas where trumpeter swans had foraged and been excluded. These larger plants likely produce the tubers that will be consumed by trumpeter swans the next spring. Pond areas out of the reach of foraging swans provide a refuge for the tubers and rhizomes, also enabling the persistence of *P. pectinatus*.

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## 1. Introduction

Macrophyte growth dynamics are affected by the timing of herbivory with respect to the growing season, the amount of tissue consumed, and nutrient cycling that results from

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herbivory (Mitchell and Perrow, 1998). For example, the future productivity of a plant would be little affected by foraging on senescing aboveground parts in autumn, while foraging on overwintering structures during early spring would remove the future growth potential of the plant (Kiørboe, 1980). However, few studies have investigated the impact of the removal of overwintering structures on macrophyte growth in the following year (Mitchell and Perrow, 1998). Herbivores that substantially reduce the macrophyte standing stock in shallow lakes could cause a shift from a clear to a turbid state (Scheffer et al., 1993). Macrophyte abundance and community composition affects the role of vegetation in an ecosystem and lake stability (Carpenter and Lodge, 1986; Van Donk, 1998). In a turbid state, low light penetration caused by abundant phytoplankton and suspended sediment hinders the establishment of submerged macrophytes (Weisner et al., 1997). In contrast, dense stands of macrophytes are considered a key component in maintaining a clear state by reducing sediment resuspension and internal nutrient loading (Scheffer et al., 1993). Given the important role of macrophytes, it is necessary to understand macrophyte–herbivore interactions (Lodge et al., 1998), and their influence on the macrophyte community.

Trumpeter swans (*Cygnus buccinator* Richardson) are native to North America and are the largest species of swan, with an average mass of 10 kg (Bellrose, 1976). They are strict herbivores (Squires, 1991) and forage to a depth of ~1 m in lakes (Scott, 1972; Holton, 1982). The species was hunted to near extinction the early 1900s (Coale, 1915). Over the 20th century, their numbers have increased and the Canadian subpopulation of the Rocky Mountain Population is estimated at 2500 birds (Subcommittee on Rocky Mountain Trumpeter Swans, 1998). During spring, these swans migrate north from the greater Yellowstone area, along the east side of the Rocky Mountains to breeding sites in northern Alberta, or even further to the Yukon and Northwest Territories (Mackay, 1978). At spring migration stop over areas, trumpeter swans prefer ponds with a high biomass of tubers and rhizomes (LaMontagne, 2000). Foraging is the dominant activity, and it has been hypothesised that swans gather energy reserves for continued migration and reproduction in these ponds (LaMontagne et al., 2001).

The two main objectives of our study were to: (i) estimate the quantity of macrophyte overwintering structures present in early spring that were consumed by migrating trumpeter swans at a spring migration stop over site in south-western Alberta, Canada, and (ii) determine if the consumption of tubers and rhizomes affects the density and community composition of macrophytes the following summer, with a focus on *Potamogeton pectinatus*, the dominant macrophyte species in the study ponds (LaMontagne, 2000). We hypothesized that if tuber and rhizome density and biomass were reduced substantially in early spring shoot density and biomass the summer following herbivory would be lower as well. We also expected that grazing on the overwintering structures of the dominant species would reduce its competitive impact on other species, resulting in an increase of other species in areas where herbivory had occurred.

## 2. Materials and methods

### 2.1. Study site description

Our study was conducted in spring and summer 1999 on two ponds (Sibbald and Sibbald East) located approximately 50 km west of Calgary, Alberta (51°07'N, 114°42'W). Both

Table 1

Characteristics of Sibbald and Sibbald East ponds in July 1999, values represent means ( $n = 3$  for water chemistry, standard error is shown in parenthesis)

	Sibbald	Sibbald East
Surface area (ha)	1.95	1.55
Average depth (m)	0.8	0.5
Area >1 m deep (ha)	0.55	0
pH	8.44 (0.10)	8.54 (0.09)
Conductivity ( $\mu\text{S cm}^{-1}$ )	1605 (15)	1680 (10)
Total phosphorus ( $\mu\text{g l}^{-1}$ )	26.8 (3.4)	34.1 (2.6)

ponds are used annually by trumpeter swans during their spring migration (LaMontagne, 2000). These two shallow eutrophic ponds are separated by approximately 700 m, are relatively small (1.95 and 1.55 ha, respectively), and have similar morphometry and water chemistry characteristics (Table 1).

The study area was located in the Rocky Mountain foothills and pasture surrounds both ponds. There are many ponds in the area, some appear to be used every spring by trumpeter swans while others never appear to be used (Beyersbergen, personal communication; LaMontagne et al., 2001). During our study, we counted 223 swan-days of use on Sibbald and 196 swan-days on Sibbald East (1 swan-day is a single swan present for a single day), of a total of 1300 trumpeter swans-days counted on 13 ponds within our study area.

## 2.2. Methods

We used 60 cm  $\times$  60 cm rebar-framed, plastic-mesh enclosures (mesh width = 0.2 cm) to assess spring tuber and rhizome densities in areas without spring trumpeter swan foraging, and the influence of spring swan foraging on macrophyte growth patterns. Prior to the swans' arrival, 10 enclosures were placed on the surface of the frozen sediment in Sibbald and Sibbald East where trumpeter swans had been observed to forage previously (Hills, personal communications), allowing 10–15 m between enclosures to obtain independent samples of the weedbed (Nolet and Mooij, 2002). These enclosures prevented swans from obtaining tubers and rhizomes from the area within them. After all trumpeter swans had left the area to continue their migration, five enclosures were randomly selected, removed, and the sediment within each enclosure sub-sampled 6 times with an Eckman grab (15 cm  $\times$  15 cm  $\times$  15 cm). Sites were also selected where foraging was observed, and 6 Eckman subsamples were taken from each of five 0.6 m<sup>2</sup> areas. Eckman samples were also taken from nine other ponds that had little (<60 swan-days) or no use; however, there were no enclosures in these ponds. This included ponds where swan counts were conducted (see study area; LaMontagne et al., 2001). All Eckman samples were sorted in the lab using a 4 mm sieve. Tubers and rhizomes were removed from the sediment and dried at 60 °C for 48 h.

The remaining enclosures from Sibbald and Sibbald East were replaced with 60 cm  $\times$  60 cm quadrats (without mesh). Five quadrats were also placed in each pond in areas where foraging was observed. In August 1999, a 30 cm  $\times$  30 cm quadrat was placed in the center of the larger quadrat and the aboveground shoots of all macrophytes harvested. Each shoot

Table 2

Mean  $\pm$  S.E. characteristics of ponds with differential use by trumpeter swans. Turbidity was significantly different based on ANOVA. Pond-use categories with like letters are not significantly different.

Pond characteristic	Pond use by trumpeter swans <sup>a</sup>		
	Consistent ( $n = 4$ )	Variable ( $n = 4$ )	Unused ( $n = 5$ )
Open water area (ha)	4.08 $\pm$ 1.78	4.00 $\pm$ 1.73	1.69 $\pm$ 0.57
Area < 1 m deep (ha)	2.34 $\pm$ 0.52	2.17 $\pm$ 0.66	1.43 $\pm$ 0.46
Turbidity (NTU)	15.38 $\pm$ 7.95 a	6.68 $\pm$ 2.00 ab	2.98 $\pm$ 1.01 b

<sup>a</sup> Consistent: >100 swan-days in spring 1999 or 2000, Unused: 0 swan-days in 1999 or 2000, or <10 swan-days total (1999 + 2000), Variable: remainder of ponds (from LaMontagne et al., 2001).

was identified to species and its height measured. Dry mass was measured after drying shoots to constant weight at 60 °C.

During early June 1999, after all trumpeter swans had continued their migration, turbidity was measured in all 13 study ponds (Table 2) with an Orbeco-Hellige portable turbidity meter (Orbeco Analytical Systems Inc., Farmingdale, NY).

A nested analysis of variance was used to test the effect of sample variation on natural log-transformed tuber and rhizome drymass in areas used by swans compared to areas where swans were excluded. Analysis of covariance was used to determine the influence of swan foraging (use or excluded) and pond (Sibbald and Sibbald East) on ln-macrophyte dry mass, with natural log-transformed macrophyte height as a covariate, using backwards elimination to remove non-significant effects. This analysis was conducted on *P. pectinatus* because it was the dominant (numerically and by biomass) macrophyte species in all samples (>85%). The average tuber and rhizome biomass, density of *P. pectinatus* shoots, average biomass of *P. pectinatus*, and the average biomass of all macrophytes present in used and excluded areas were compared using Mann–Whitney *U*-tests. The average size distribution of *P. pectinatus* shoots in used and excluded areas were compared using Kolomogorov–Smirnov test, and Mann–Whitney *U*-tests were used to compare differences in the average number of shoots in used and excluded areas within size classes. Turbidity was natural log-transformed to meet the assumptions of normality, and we compared the turbidity of consistently used (Sibbald, Sibbald East and two others; LaMontagne et al., 2001), variably used, and unused ponds using an ANOVA and subsequent Tukey test for multiple comparisons. A probability of 0.05 was used to determine significance for statistical tests, unless otherwise indicated. Mean values are reported with 1 standard error (S.E.).

### 3. Results

By mass, rhizomes (94%) exceeded tubers (6%) in our samples, and in the absence of swan foraging their combined dry mass present to a depth of 15 cm in the sediment was  $4.2 \pm 1.1 \text{ g m}^{-2}$  in Sibbald and  $3.5 \pm 1.1 \text{ g m}^{-2}$  in Sibbald East. After the swans left, the dry mass of tubers and rhizomes in areas where swans had foraged in each pond was  $3.3 \pm 1.4$  and  $2.6 \pm 1.1 \text{ g m}^{-2}$ , respectively. Swan use had a significant effect on ln-transformed tuber and rhizome biomass in both ponds (Table 3), with swans consuming an average of 24%

Table 3

Results of nested ANOVAs on Sibbald and Sibbald East ponds for the effect of sample variation on natural log-transformed (tuber and rhizome dry mass) in areas where trumpeter swans had foraged and been excluded (use status)

Source	d.f.	MS	<i>F</i>	<i>P</i>
Sibbald				
Use status	1	68.711	4.885	0.032
Sample (use status)	8	49.827	3.543	0.003
Error	50	14.065		
Sibbald East				
Use status	1	134.546	6.910	0.011
Sample (use status)	8	17.797	0.914	0.513
Error	50	19.471		

of the tubers and rhizomes present. The percentage of tubers and rhizomes removed was remarkably similar for the two ponds, as was the use by trumpeter swans. For nine other ponds in the area classified as variably used or unused, there was an average dry mass of tubers and rhizomes available of  $1.2 \text{ g m}^{-2}$  was observed in a 16 ha area available for foraging, far below that available in the two study ponds.

The aboveground summer biomass of *P. pectinatus* was not significantly altered due to trumpeter swan herbivory in either study pond, but there was a significant effect of the covariate, plant height, and of pond on shoot biomass (Table 4). Macrophyte biomass was significantly higher in Sibbald, the deeper pond with taller plants. In Sibbald pond, the density of *P. pectinatus* was  $284 \pm 67$  shoots  $\text{m}^{-2}$  in excluded areas, compared to  $122 \pm 38$  shoots  $\text{m}^{-2}$  in used areas. This represents 57% fewer shoots in areas where swans foraged, which was close to being statistically significant ( $P = 0.067$ ). *P. pectinatus* shoot dry mass was  $157 \pm 22 \text{ g DW m}^{-2}$  in excluded areas and  $96 \pm 33 \text{ g DW m}^{-2}$  in areas where trumpeter swans had fed, this shows a similar trend, however the difference was not statistically significant ( $P = 0.169$ ). The overall distribution of *P. pectinatus* shoot dry mass in excluded and used areas of Sibbald pond was not significantly different ( $P = 0.987$ ). However, there were significantly more small shoots ( $<1.0 \text{ g}$ ) present in areas where trumpeter swans had fed compared to areas where they were excluded ( $P = 0.036$ ), while the number of larger shoots ( $>1.0 \text{ g}$ ) in both areas was similar ( $P$  all  $>0.05$ ; Fig. 1). Therefore, although there were many more shoots in excluded areas, these were only small shoots and therefore

Table 4

Results of a backwards stepwise ANCOVA for the main effects of trumpeter swan herbivory (used vs. exclusion) and pond (Sibbald vs. Sibbald East), and the covariate of shoot height on *P. pectinatus* summer shoot biomass ( $n = 221$ )

Variable	SS	d.f.	MS	<i>F</i>	<i>P</i>	Partial $r^2$
Herbivory	0.009	1	0.009	0.106	0.745	$<0.001$
Pond	0.983	1	0.983	11.648	0.001	0.014
Shoot height	48.897	1	48.897	579.249	$<0.001$	0.717
Error	18.318	217	0.084			
Total	68.20	220	0.310			

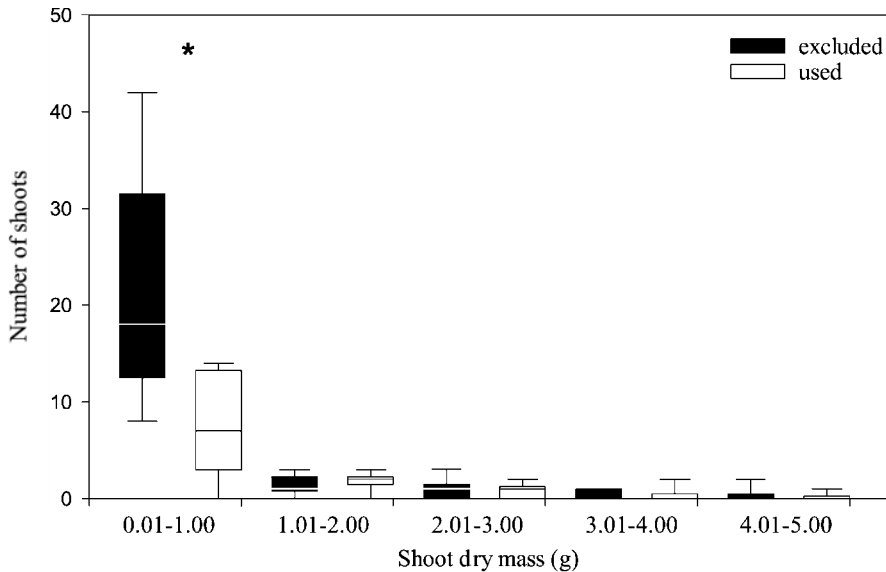


Fig. 1. Box plots of the distribution of *P. pectinatus* shoot dry mass in areas used by trumpeter swans compared to areas where trumpeter swans were excluded. Asterisk (\*) indicates a significant difference in the median number of shoots within a 1.0 g DW size class.

contributed less than larger plants would to the overall *P. pectinatus* shoot biomass resulting in non-significant differences in overall shoot dry mass between areas used for foraging and excluded from foraging. In addition, *Myriophyllum exalbescens* and *P. zosteriformis* were present in Sibbald areas used by trumpeter swans (combined biomass  $\sim 8$  g DW  $m^{-2}$ ), but not in excluded areas.

In Sibbald East pond, *P. pectinatus* density was similar in excluded ( $48 \pm 21$  shoots  $m^{-2}$ ) versus used ( $51 \pm 19$  shoots  $m^{-2}$ ;  $P > 0.05$ ) areas, and its dry mass did not differ significantly in excluded ( $22 \pm 12$  g DW  $m^{-2}$ ) versus used ( $47 \pm 19$  g DW  $m^{-2}$ ;  $P > 0.05$ ) areas. More *P. zosteriformis* was present in used areas compared to excluded areas of Sibbald East. In Sibbald East, only three of the five quadrats in excluded areas were recovered, and macrophytes in this pond were more patchily distributed, with greater variation between samples.

Turbidity was significantly higher in consistently used ponds compared to unused ponds, while variable use ponds were not significantly different from the other groups (Table 2,  $P < 0.05$ ).

#### 4. Discussion

Interactions between herbivorous waterfowl and aquatic macrophytes have become a recent focus in studies of macrophyte dynamics and alternative stable states, and in studies of habitat use by waterfowl (Van Vierssen et al., 1994; Perrow et al., 1997; Lodge et al.,

1998; Mitchell and Perrow, 1998; Van Donk, 1998; Jonzén et al., 2002; Santamaría and Rodríguez-Gironés, 2002). The potential impacts of herbivory on macrophyte communities range from a reduction in the macrophyte species favoured by waterfowl and a shift in community composition, 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 sufficiently transparent (Horne and Goldman, 1994), and dense macrophyte stands can inhibit phytoplankton growth (Faafeng and Mjelde, 1998). In areas of high nutrient loading, algal production may increase water turbidity and decrease macrophyte abundance by shading (Faafeng and Mjelde, 1998). Trumpeter swans likely contribute little new nutrient loading from their faecal deposition, as they forage within ponds and would recycle nutrients, rather than importing nutrient subsidies from terrestrial environments. We found turbidity to be higher in consistently used ponds than in lesser used ponds, which is likely due to sediment disturbance by swans during foraging (Søndergaard et al., 1992).

Trumpeter swans arrive at migration stop over areas in southern Alberta while ice still covers a large proportion of the ponds and macrophyte growth has not yet begun. The plants from the previous year have senesced, hence the only available food for swans in April is tubers and rhizomes, and consumption of these overwintering structures removes the future growth potential of that material (Mitchell and Perrow, 1998). Within stop over areas, trumpeter swans appear to select ponds based on the abundance of tubers and rhizomes (LaMontagne, 2000). Consistently used ponds had approximately three-times more tuber and rhizome biomass than variable and unused ponds. In fact, when trumpeter swans continued their migration, consistently used ponds still had twice the tuber and rhizome biomass remaining compared to variable and unused ponds. Therefore, it is possible that the variable and unused ponds in our study area had tuber and rhizome densities below a level that the swans deem profitable, which is not surprising as the tuber producing *P. pectinatus* was not abundant in the lesser used ponds (LaMontagne, 2000). Bewick's swans (*C. columbianus bewickii*) were reported to move to new areas when tuber density fell to a level similar to that of our unused areas (Beekman et al., 1991; Santamaría and Rodríguez-Gironés, 2002), and Squires (1991) observed trumpeter swans in Wyoming shift to new areas, presumably in search of higher tuber densities. Although trumpeter swans in our study area consistently use some ponds year after year, neck-banded individuals have been observed to move among ponds within a year (Anderson, personal communication).

Foraging on overwintering structures has important implications for macrophyte abundance and community composition in subsequent growing seasons (Lodge, 1991; Perrow et al., 1997). However, we detected no statistically significant impact of foraging on the density or biomass of macrophytes when we compared excluded and used areas, which were dominated by *P. pectinatus*. Because foraging by trumpeter swans results in the removal or damage of overwintering structures, macrophytes in used areas may experience a loss of energy stored in these structures. If so, these plants should have a smaller mass to height relationship because under eutrophic conditions *P. pectinatus* first grows to the surface of the water and then allocate energy to spreading horizontally (Van Wijk et al., 1988; LaMontagne personal observation). Although there was a higher density of *P. pectinatus* in excluded areas of Sibbald pond, this difference was only due to the number

of small shoots, while the number of large-biomass shoots was not different from used areas.

*P. pectinatus* can flourish in areas that have been heavily grazed by waterfowl for over 20 years (Kanutrud, 1990). Near Calgary, yearly variation in the timing and pattern of pond melt relative to the swans' arrival provides foraging refuges to macrophytes. For example, there was ice on a portion of Sibbald pond in 2000 that was a primary foraging area for trumpeter swans in 1999 (LaMontagne, 2000). The part of the pond deeper than 1 m, which is not accessible (Scott, 1972; Holton, 1982), may also function as a refuge. Because 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). Another mechanism that may have led to the lack of a difference in the number of large shoots in used and excluded areas is competition. In excluded areas, there was increased shoot density and hence increased competition that may then lead to a few large shoots and a large number of smaller ones.

In addition, large plants produce larger tubers in the fall (Santamaría and Rodríguez-Gironés, 2002), and thus provide forage to swans the next spring. Hampton (1981) found no significant difference in the composition or abundance of macrophytes taken from within and outside exclosures for wintering trumpeter swans. However, over a 30-year-period a slight shift in the macrophyte community had occurred (Shea, 1979; Hampton, 1981). In The Netherlands, the number of Bewick's swan wintering on lakes have been known to fluctuate with long-term changes in *P. pectinatus* biomass (Van Vierssen et al., 1994).

Swimming and foraging behaviours of waterfowl resuspend sediments and directly reduce the available light for macrophytes, and indirectly increase the rate of nutrient supply from sediments to phytoplankton (Søndergaard et al., 1992). In our consistently used ponds, turbidity was higher than in variably and unused ponds. However, Sibbald East is shallower than Sibbald (Table 2), therefore overall light penetration to the pond bottom is likely greater in Sibbald East. Increased light penetration may partially offset negative effects of herbivory as there was little difference in macrophyte growth in excluded versus used areas of this pond compared to the deeper Sibbald pond. However, as the trumpeter swan population continues to increase, swan foraging may negatively affect Sibbald East pond, which is completely within the foraging range of trumpeter swans (<1 m deep). Therefore, further studies should be conducted to determine threshold tuber and rhizome levels that lead to this species, the trumpeter swan, moving to another pond, or region, to forage.

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