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Reviewed work(s):

Source: *American Midland Naturalist*, Vol. 133, No. 2 (Apr., 1995), pp. 274-282

Published by: [The University of Notre Dame](#)

Stable URL: <http://www.jstor.org/stable/2426391>

Accessed: 04/02/2013 18:24

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Trumpeter Swan (*Cygnus buccinator*) Food Habits in the Greater Yellowstone Ecosystem

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ABSTRACT.—We documented the winter, spring and summer food habits of trumpeter swans (*Cygnus buccinator*) in the greater Yellowstone area (the intersection of Idaho, Montana and Wyoming) and studied the diet preference of nesting swans. Although 23 foods were detected in trumpeter swan diets during the winter, spring and summer, only 8 contributed at least 3% to the diet during any one season (Table 1). Dominant foods (over 10% of the diet in at least one season) included *Chara* spp. (21.7%, 4.1%, mean, SE), *Elodea canadensis* (11.4%, 3.1), *Potamogeton* spp. (32.3%, 4.2), and *Potamogeton pectinatus* tubers (15.7%, 3.6). *Potamogeton pectinatus* tubers were highly preferred by swans and tuber consumption significantly ($P = 0.03$) increased from winter (23.4%, 10.5) to spring (38.5%, 10.0). The primary food in summer was *Potamogeton* foliage which accounted for 48.2% of the summer diet. Nesting trumpeter swans significantly ($P = 0.039$) prefer *Potamogeton* spp. when it was available at feeding sites within their territories. *Chara* spp. was eaten in proportion to its availability, and swans avoided eating *Ceratophyllum demersum* and *Myriophyllum exalbescentis*.

INTRODUCTION

Trumpeter swans (*Cygnus buccinator*) were nearly extirpated across their historic North America range from over-harvest and habitat destruction (Banko, 1960). This decline ushered in conservation measures that were partially successful in restoring trumpeter swan populations. The Rocky Mountain population is composed of the Interior Canada subpopulation that nests in Canada and Tristate subpopulation that nests in the greater Yellowstone area (Gale *et al.*, 1987). Both subpopulations winter almost exclusively in the greater Yellowstone area and use common wintering sites. Before 1974, the number of wintering birds in the Tristate subpopulation approximately equaled the number of resident birds (Gale *et al.*, 1987); there was no large winter influx of migratory swans from Canada. However, from 1974 to 1990, the number of wintering birds in the Tristate subpopulation increased from 700 to 2000 due to the rapid expansion of the Interior Canada subpopulation (Mitchell, 1990).

The dramatic increase in the number of wintering swans in the greater Yellowstone area has heightened concerns regarding potential impacts of their herbivory on food stocks. Wildlife managers have initiated range expansion programs to help disperse the number of wintering swans (Shea *et al.*, 1991). In addition, Tristate swans typically nest on national forest lands where conflicting land-use practices, such as grazing or timber harvest, heighten the need for land managers to identify and protect wetlands potentially valuable to nesting swans. Despite the importance of understanding trumpeter swan food habits when assessing impacts of herbivory and when identifying potentially important wetlands for nesting, their

food habits have never been quantitatively studied in the greater Yellowstone area. Existing data on swan diets in the greater Yellowstone area are from observational studies (Banko, 1960; Leach, 1975; Page, 1976) or postmortem examinations (Hampton, 1981). Determining swan diets from visual observations is difficult because trumpeter swans typically feed on submerged plants. Postmortem examination is limited to natural mortalities, and is hindered by small sample size or biased samples (*i.e.*, starved birds).

Our primary objective was to determine the seasonal (winter, spring and summer) food habits of trumpeter swans in the greater Yellowstone area by microhistological fecal analysis. This is a reliable technique for determining diets of rare birds like trumpeter swans, which cannot be collected (Owen, 1975; Rosenberg and Cooper, 1990). Fecal analysis has been used to study the diets of geese (Owen and Kerbes, 1971) and trumpeter swans in Canada (McKelvey, 1981). Foods eaten by trumpeter swans pass rapidly through the gut leaving plant epidermal residues intact which facilitates microhistological identification (Squires, 1991). Our second objective was to study the diet preference of nesting trumpeter swans among dominant foods present at feeding sites.

STUDY AREA

The study area in the western United States is bordered by the Teton Range to the south and west, the Yellowstone Plateau to the north, and the Gros Ventre Mountains to the east. Average air temperature in May through August is 12 C; average summer precipitation is 3.6 cm per month (30-yr average, NOAA Climatological Data Annual Summary, Moran, Wyoming).

Trumpeter swan wintering sites are located in Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, the National Elk Refuge, and on private lands near Jackson, Wyoming. Elevation of wintering areas is approximately 2000 m. Average air temperature in December through February is -9.3 C; average winter precipitation (mostly snow) is 7.4 cm per month (30-yr average, NOAA Climatological Data Annual Summary, Moran, Wyoming). During winter, most trumpeter swans feed in low velocity streams (Squires *et al.*, 1992). Nest sites are located in western Wyoming and eastern Idaho.

METHODS

Fecal samples ($n = 467$ feces) were collected throughout the winter, spring, and summer of 1989. Samples were collected from 8 winter sites (December–February), 7 spring sites (March–May), and 21 summer sites (June–August). Winter fecal samples were collected mainly from the National Elk Refuge, near Jackson, Wyoming and on Fish Creek, approximately 10 km south of Wilson, Wyoming. Spring samples were collected in Teton National Park and on adjacent U.S. National Forest Service lands. Summer fecal samples were collected from 14 nest sites in northwestern Wyoming and 7 sites in eastern Idaho. Summer fecal collections were primarily from breeding birds; most samples were collected at nest and resting sites within territories.

Feces were dried and ground to pass through a 1-mm Wiley Mill screen. On a given collection day, one fecal sample was collected from each site. A sample was an aggregation of an equal quantity of feces taken from each fecal dropping (mean = 5.5 feces/composite sample). Composite samples ($n = 14, 20, 48$ for winter, spring and summer, respectively) were the sampling units.

The Composition Analysis Laboratory (CAL, Colorado State University, Fort Collins, Colorado) conducted the microhistological analyses (Sparks and Malechek, 1968). The percent relative density of food items was determined at 20 systematic and equally-spaced fields on each of five slides (100 total fields per composite sample, Sparks and Malechek, 1968). Plant

fragments were identified by comparison with an aquatic plant reference that contained plants collected on our study area. CAL could not distinguish among the different species of *Potamogeton* present in samples so they were identified only as *Potamogeton* spp. Species of *Potamogeton* present at feeding sites include *P. pectinatus*, *P. pusillus*, *P. berchtoldi*, *P. natans*, and *P. richardsonii*.

DATA ANALYSIS

Determining correction factors.—Microhistological analysis assumes that the relationship of dry mass to surface area of all forages is the same (Johnson, 1982). This assumption may be invalid when comparing *Potamogeton pectinatus* tubers with aquatic plant foliage. Regression analysis was used to relate actual percent composition of hand-ground plant mixtures to laboratory estimates of the mixtures – corrected % composition = $\beta_0 + \beta_1$ (laboratory estimate). Correction procedures, when applied to microhistological estimates, provide less biased estimates of diet composition (Dearden *et al.*, 1975; Rumble and Anderson, 1993). The percent compositions used to establish regression equations ranged between 4% to 100% for each forage. Correction equations were determined only for the foliage of *Ceratophyllum demersum*, *Chara* spp., *Elodea canadensis*, *Myriophyllum exalbescentis*, *Potamogeton pectinatus* foliage and tubers of *Potamogeton pectinatus*. If the initial regression indicated that the intercept did not differ significantly ($P < 0.05$) from zero, the analysis was repeated, forcing the regression through the origin (Neter *et al.*, 1985). If a non-zero intercept was significant, as was the case with *Chara* spp. and *Potamogeton pectinatus* foliage, the intercept was retained in the final equation. Regression equations relating measured plant species composition to microhistological estimates initially contained squared polynomial terms for each forage (Neter *et al.*, 1985); polynomial terms were dropped if not significant ($P > 0.05$). We assumed the correction equation that was derived for *Potamogeton pectinatus* foliage was applicable to other *Potamogeton* spp.

Seasonal dietary differences.—Statistical analyses of seasonal diet shifts among dominant forages were performed on the corrected percentages (see above). Both raw and arcsine-transformed food habits data (percentage) were non-normally distributed with heteroscedastic variances. Therefore, multiresponse permutation procedures (MRPP) were used on non-transformed data. We tested for differences in seasonal use of dominant forages both between winter and spring and between spring and summer ($\alpha = 0.05$). MRPP is a distribution-free statistical procedure based on Euclidean distance-functions, which have greater power for detecting differences in skewed distributions than variance-based statistics (Zimmerman *et al.*, 1985; Mielke, 1986). The “BLOSSOM” statistical software was used for these analyses (Slauson *et al.*, 1991).

Diet preference of nesting swans.—Foraging sites used by each pair of nesting swans were plotted on low-level aerial photographs throughout the nesting season. A sample of 15 feeding points was randomly selected for each pair. Aquatic macrophytes present at these feeding points were sampled from a floating blind using snorkeling gear and a 0.1-m² sampler equipped with a draw knife. Samples were later washed, sorted to species, dried (40 C for 24 h), and weighed.

Diet preference among foods present at feeding sites was determined by comparing the forage composition at feeding sites to the swan's diet as determined by microhistological analysis of feces present at each site. Food items were considered preferred if they were eaten in greater proportion to their availability. The percent composition of potential foods present at swan feeding sites was compared to percent occurrence in the diet using a paired MRPP analysis (Slauson *et al.*, 1991). If more than one fecal collection was gathered at a given site, the results from the fecal analysis were averaged for that site. Food items had to

TABLE 1.—Food habits of trumpeter swans in the greater Yellowstone area during winter, spring, and summer (tr = <3% of sample)

Food Item	Winter (n = 14 composite fecal collections)		Spring (n = 20)		Summer (n = 48)	
	Mean percent diet com- position	SE	Mean percent diet com- position	SE	Mean percent diet com- position	SE
<i>Carex</i> spp.	tr	—	3.2	3.0	4.4	2.7
<i>Chara</i> spp.	36.8	13.1	27.4	8.8	14.9	4.4
<i>Cruciferae</i> (unknown forb)	7.5	5.1	3.5	3.3	0	—
<i>Eleodea canadensis</i>	29.6	12.1	5.6	3.6	8.5	3.4
<i>Equisetum</i> spp.	0	—	tr	—	3.7	2.6
<i>Potamogeton pect.</i> tubers	23.4	10.5	38.5	10.0	3.9	2.1
<i>Potamogeton</i> spp.	3.0	1.1	16.3	6.7	48.2	5.5
Seeds (unknown)	0	—	4.9	4.8	tr	—

comprise at least 10% of the diet in at least one season, or contribute at least 5% dry mass to the sample of potential forages, before being considered a dominant forage and included in these comparisons. Nesting swans are territorial and exclude other pairs from their territory. Thus, feces collected in nesting territories were from resident birds that fed entirely within that territory.

Determining the abundance of potential winter forages.—Ten staked transects were systematically established on each of three wintering areas (National Elk Refuge, Fish Creek, and Pole Creek, near Yellowstone National Park) and were sampled in 1988 and 1989. Each transect consisted of four sample points located at 20%, 40%, 60%, and 80% across the stream channel width. Sample points were averaged per transect and transects averaged per wintering area. Statistical comparisons of winter-forage use versus availability were impossible due to limited sample size (n = 2, wintering areas); only descriptive statistics are discussed for these data.

RESULTS

REGRESSION EQUATIONS FOR CORRECTING DIET ESTIMATES

Regression equations used to correct for laboratory biases in determining percent composition (Table 1) were as follows:

Chara spp.;

$$\text{Corrected (\%)} = -0.038 + 1.134(\text{Chara spp. (lab result)})$$

$$(F_{1,16} = 506, \quad r^2 = 0.97, \quad P < 0.001)$$

Elodea canadensis;

$$\text{Corrected (\%)} = 1.039(\text{Elodea canadensis})$$

$$(F_{1,17} = 479, \quad r^2 = 0.97, \quad P < 0.001)$$

Potamogeton pectinatus foliage;

$$\text{Corrected (\%)} = -125 + 1.052(\text{Potamogeton pectinatus})$$

$$(F_{1,16} = 513, \quad r^2 = 0.98, \quad P < 0.001)$$

TABLE 2.—Seasonal composition changes [mean percentage, (SE)] of trumpeter swan diets

	Winter (A) (n = 14)	Spring (B) (n = 20)	Difference A, B	Summer (C) (n = 48)	Difference B, C
<i>Chara</i> spp.	36.8 (13.1)	27.4 (8.8)		14.9 (4.4)	
<i>Elodea canadensis</i>	29.6 (12.1)	5.6 (3.6)	P = 0.04	8.5 (3.4)	P = 0.01
<i>Potamogeton pectinatus</i> tubers	23.4 (10.5)	38.5 (10.0)	P = 0.03	3.9 (2.1)	P < 0.01
<i>Potamogeton</i> spp.	3.0 (1.1)	16.3 (6.7)	P = 0.03	48.2 (5.5)	P < 0.01

Potamogeton pectinatus tubers;

Corrected (%) = 2.335(tuber) - 1.331(tuber²)
(F_{2,15} = 531, df = 17, r² = 0.98, P < 0.001).

Equations for *Ceratophyllum demersum* and *Myriophyllum exalbenscens* were unnecessary because these forages were not important foods in any season. Correction equations for *Potamogeton* spp. foliage were based on the foliage (narrow leaf growth form) of *Potamogeton pectinatus* (i.e., we assumed other species of *Potamogeton* had visibility biases similar to *Potamogeton pectinatus*).

FOOD HABITS

Although 23 foods were detected in trumpeter swan diets during the winter, spring, and summer, only 8 contributed at least 3% to the diet during any one season (Table 1). Dominant foods (over 10% of the seasonal swan diet) included *Chara* spp., *Elodea canadensis*, *Potamogeton* spp. and *Potamogeton pectinatus* tubers (Table 1). The overall consumption of these foods was *Chara* spp. (21.7%, 4.1%, mean, SE), *Elodea canadensis* (11.4%, 3.1), *Potamogeton* spp. (32.3%, 4.2), and *Potamogeton pectinatus* tubers (15.7%, 3.6).

SEASONAL DIETARY SHIFTS

Winter to spring.—Trumpeter swans ate similar (P = 0.511) percentages of *Chara* spp. in winter (mean = 36.8%, SE = 13.1) and spring (27.4%, 8.8 SE, Table 2). Swans consumed significantly (P = 0.04) more *Elodea canadensis* in the winter (29.6%, 12.1 SE) than in the spring (5.6%, 3.6 SE). *Potamogeton* foliage became increasingly (P = 0.03) important in the spring (16.3%, 6.7 SE) compared to the winter (3.0%, 1.1 SE) as this forage became available after its winter senescence. Trumpeter swans also increased (P = 0.03) their consumption of *Potamogeton pectinatus* tubers in the spring (38.5%, 10.0 SE) compared to the winter (23.4%, 10.5 SE).

Spring to summer.—*Potamogeton* foliage was the primary food eaten by nesting swans during the summer (48.2, 5.5 SE, Table 1). Swans increased (P = 0.001) their consumption of *Potamogeton* spp. from 16.3% (6.7 SE) in the spring to 48.2% (5.5 SE) in the summer. Tubers of *Potamogeton pectinatus*, as they sprout, become less available to swans during the summer (Kantrud, 1990). The decline in tuber consumption from spring to summer was significant (P < 0.001). Although *Elodea canadensis* contributed little (8.5%, 3.4 SE) to the summer swan diet, the increased use from spring to summer was significant (P = 0.01).

DIET PREFERENCE

Summer diets.—The overall diet composition of nesting trumpeter swans significantly (P = 0.008) differed from forage availability. At nest sites where *Chara* spp. was present at foraging sites, it was eaten approximately in proportion to its availability (Table 3). Trumpeter swans significantly (P = 0.011) avoided *Ceratophyllum demersum* since it was commonly

TABLE 3.—Diet preference of trumpeter swans nesting in the greater Yellowstone area among dominant macrophytes present at feeding sites (n = number of sites where both forage availability and fecal samples were collected)

	Mean composition available forages at swan feeding sites (SE)	Mean composition of swan diet at sites with forage species present (SE)	
<i>Chara</i> spp. (n = 22)	37.1 (12.0)	37.6 (8.8)	
<i>Ceratophyllum demersum</i> (n = 11)	23.1 (6.0)	3.5 (2.4)	P = 0.011
<i>Myriophyllum exallescens</i> (n = 17)	5.0 (2.9)	0.4 (0.1)	P = 0.002
<i>Potamogeton</i> spp. (n = 22)	35.5 (6.3)	52.3 (7.4)	P = 0.039

present at feeding sites (23.1%, 6.0 SE) but contributed little to the swan diet (3.5%, 2.4 SE). *Myriophyllum exallescens* was relatively uncommon at foraging sites (5.0%, 2.9 SE) and was not preferred by swans ($P = 0.002$). Of the four dominant forages present at swan feeding sites, only *Potamogeton* spp. was preferred ($P = 0.039$) in greater proportion to its availability. There were insufficient data to statistically test swan diet preference of *Elodea canadensis*.

Winter diets.—The percent composition (mean dry mass, SE) of dominant forages present on swan wintering ranges were *Chara* spp. (28%, 17 SE), *Elodea canadensis* (32.7%, 16 SE), *Myriophyllum exallescens* (14%, 13 SE), and *Potamogeton* spp. (12%, 11 SE). *Ceratophyllum demersum* was rare in wintering areas, only contributing 2% to the total forage biomass. *Potamogeton pectinatus* tubers comprised less than 1% of the forage biomass, but contributed 23.4% (10.5 SE) to the winter diet.

DISCUSSION

FOOD HABITS

Unlike many other swan populations that augment their diet by feeding on agricultural crops (Bortner, 1985; Dirksen *et al.*, 1991), trumpeter swans in the greater Yellowstone area fed almost exclusively on aquatic macrophytes throughout the year. They fed primarily on *Chara* spp., *Elodea canadensis*, *Potamogeton* spp. foliage, and *Potamogeton pectinatus* tubers. There are few published data on trumpeter swan food habits for comparison. At Red Rock Lakes National Wildlife Refuge in Montana, Banko (1960) cited qualitative field observations of swans foraging on a variety of aquatic plants and Page (1976) believed nesting swans primarily ate aquatic forages, possibly preferring *Elodea canadensis*. In Idaho, Hampton (1981) examined the digestive tracts of three wintering swans that died from unknown causes and found that *Myriophyllum exallescens*, *Potamogeton richardsonii*, *Potamogeton pectinatus*, and *Elodea canadensis* were dominant foods. In British Columbia, Canada, McKelvey (1981) quantified trumpeter swan diets using fecal analysis and found they ate *Zostera* (33.8%), *Scirpus* (30.8%), grass (18.5%), and *Carex* (13.8%). Trumpeter swans nesting in Alaska fed predominantly on submerged aquatic plants before and during egg laying, but shifted to emergent horsetail (*Equisetum fluviatile* and *E. arvense*) and sedge (*Carex lyngbyaei*) during incubation (Grant *et al.*, 1994).

SEASONAL DIETARY SHIFTS AND DIET
PREFERENCE

Nesting swans.—In an earlier paper, we reported that nesting trumpeter swans preferred shallow water feeding sites (0.74 m mean depth) with a greater biomass of *Chara* spp., *Potamogeton* spp., and total macrophytes, and less *Nuphar luteum* (water lilies) compared to random points within nest ponds (Squires *et al.*, 1992). We suggested that both *Chara* spp. and *Potamogeton* spp. were important forages based on their prevalence at swan feeding sites. More detailed food-habit analysis from this study allows us to state more conclusively that nesting swans do prefer *Potamogeton* spp. when it is available at feeding sites ($P = 0.039$). *Chara* spp. is eaten in proportion to availability. *Ceratophyllum demersum* had lower true metabolizable energy compared to four other forages we tested during previous feeding trials (Squires, 1991). This might explain why swans avoided this forage. We can not explain why swans ate little *Myriophyllum exalbescens*, except that it was relatively uncommon (approximately 5% dry mass) at feeding sites used by nesting swans.

Wintering swans.—Approximately 90% of the diet of wintering swans was composed of *Chara* spp. (36.8%), *Elodea canadensis* (29.6%) and *Potamogeton pectinatus* tubers (23.4%). Trumpeter swans consumed *Chara* spp. (28% of biomass present on wintering areas) and *Elodea canadensis* (32%) approximately in proportion to their abundance on winter ranges, whereas they avoided eating *Myriophyllum exalbescens*. By midwinter, *Potamogeton pectinatus* is senescent (Verhoeven, 1980) and the foliage is unavailable to wintering swans which explains its absence in the winter diet. *Potamogeton pectinatus* tubers comprised less than 1% of the biomass of aquatic macrophytes present on wintering areas, yet represented 23.4% of the winter diet. This indicates that tubers are a highly preferred forage of wintering swans.

Potamogeton pectinatus tubers are high in energy, consisting primarily of carbohydrates, high in protein, and have a high digestive efficiency compared to aquatic macrophytes (Squires, 1991). Other investigators have also found that tubers are an important swan food (Paullin, 1973; Anderson and Low, 1976; Jupp and Spence, 1977). Beekman *et al.* (1991) found that Bewick's swans (*Cygnus columbianus bewickii*) only grazed in areas where tubers were most abundant. When tuber stocks were grazed below 7.2 g drymass m⁻², the swans shifted to feeding in agricultural fields. The National Elk Refuge, which is the primary wintering area for trumpeter swans in Wyoming, produces tuber stocks that average 11.7 g drymass m⁻² (avg. 1988, 1989) before swan herbivory.

One reason why trumpeter swans in Wyoming did not shift to other foods as winter tuber stocks were reduced is that agricultural lands that provide high-protein foods are not adjacent to their wintering areas. A second reason is that icing patterns on the National Elk Refuge are in constant flux because of changes in weather and water conditions. Tuber beds may be exposed and then protected by ice from swan herbivory, several times during the winter. This apparently prevents swans from reducing tuber stocks below a threshold where searching for tubers becomes energetically unprofitable. In the spring, swans readily move to spring-use areas as they thaw to exploit tuber stocks that were protected by winter ice.

The significant ($P = 0.03$) increase in tuber consumption that we observed from 23.4% in the winter to 38.5% in the spring may be important to trumpeter swans for securing the endogenous reserves necessary for reproduction. Bewick's swans also prefer energy-rich foods in the autumn and protein-rich foods in the form of winter wheat and grasses in the spring (Dirksen *et al.*, 1991). The feeding behavior of trumpeter swans may be consistent with the "condition hypothesis" which states that nutrient reserves accumulated on spring

staging areas are important in determining reproductive output (Ebbinge *et al.*, 1982). Other waterfowl depend on spring-use areas to establish the lipid and protein reserves needed for reproduction (Raveling, 1979; Krapu, 1981; McLandress and Raveling, 1981).

Acknowledgments.—We acknowledge the following agencies for their financial contributions to the project: Wyoming Game and Fish Department, Grand Teton National Park, Bridger-Teton National Forest, and the Friends of Elk Island National Park Society. This study was conducted as part of a Ph.D. dissertation by John Squires at the Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming. Many people helped with the project, but we especially thank B. Heath, D. Lockman, B. Long, B. Wood and B. Smith.

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SUBMITTED 21 FEBRUARY 1994

ACCEPTED 9 DECEMBER 1994