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EVALUATION OF TRANSLOCATION CRITERIA FOR TRUMPETER SWANS  
REINTRODUCED TO NORTHERN UTAH: HABITAT QUALITY  
AND INTERACTIONS WITH TUNDRA SWANS

by

Katharina A. M. Engelhardt

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Fisheries and Wildlife Ecology

Approved:

UTAH STATE UNIVERSITY  
Logan, Utah

1997

## ABSTRACT

Evaluation of Translocation Criteria for Trumpeter Swans Reintroduced to  
Northern Utah: Habitat Quality and Interactions with Tundra Swans

by

Katharina A. M. Engelhardt, Master of Science

Utah State University, 1997

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Department: Fisheries and Wildlife

Fifty-seven Trumpeter swans (*Cygnus buccinator*) were translocated to the Bear River Migratory Bird Refuge and the Bear River Club Company in northern Utah. The purpose of this effort was to encourage dispersal of the Rocky Mountain population of Trumpeter swans during the winter, and to reestablish a migratory route to southern wintering grounds. I assessed the success of the translocation by evaluating 13 translocation criteria proposed in the literature. In this study I addressed two of these criteria in detail by evaluating habitat quality at the translocation sites and by analyzing potential competitive interactions with Tundra swans (*Cygnus columbianus*).

Habitat quality was determined by analyzing the spatial distribution of sago pondweed (*Potamogeton pectinatus*) tubers in wetland sediments before the fall and after the spring migration of Tundra swans. Sixty-four transects were established within the study sites with 10 sediment cores per transect. Geostatistical procedures were employed

to account for autocorrelation between samples. Tuber biomass was not randomly distributed within the studied wetlands. In fact, discrete areas of high values appeared to exist before and after swan foraging. It is not likely that sago pondweed tubers are limiting swan abundance in this system. Thus, the habitat quality of the study sites is sufficient for Trumpeter swan translocation.

Potential competitive interactions with Tundra swans were evaluated by examining differences in resource utilization patterns of the two species. I measured body size differences, dietary overlap, resource availability, and the efficiency of extracting available resources. Trumpeter swans appear to benefit from a larger body size and a longer neck because they are more efficient in extracting tubers from the sediment, and are able to exploit tubers to a greater sediment depth than Tundra swans. However, Trumpeter swans incur higher traveling costs due to the larger body size. The trade-off between higher foraging efficiency of Trumpeter swans and higher traveling efficiency of Tundra swans may be a potential mechanism for coexistence.

Lack of support by governmental and non-governmental agencies did not allow for more than one year of translocation. Even though the Trumpeter swan translocation in 1996 was successful, I concluded that the Utah translocation program failed because the translocation did not meet translocation goals.

## ACKNOWLEDGMENTS

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Katharina A. M. Engelhardt

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## CHAPTER 1

### INTRODUCTION

Observed and projected increases in extinction rates within recent years (e.g., Myers 1988, Wilson 1989) focus attention on the value of biological diversity and techniques of conserving this diversity. Translocations, the "intentional release of individuals to the wild in order to establish, reestablish, or augment a population" (World Conservation Union 1987 *in* Kleiman et al. 1994), appear to be an increasingly important conservation technique because human activity is fragmenting habitats and therefore animal and plant populations (Griffith et al. 1989). However, the need to establish or augment a population is not sufficient justification for a translocation to proceed (Kleiman et al. 1994) because a translocated species, through its interactions with the new ecosystem, may severely affect the established community (e.g., Simberloff 1981, Van Driesche 1994, Case 1996, Ramos 1996). Alternatively, local environmental conditions, such as food supply and potential competitors, may severely influence the success of the translocation (e.g., Griffith et al. 1989, Kleiman et al. 1994).

In this study we translocated 57 Rocky Mountain Trumpeter Swans to northern Utah to encourage establishment of a migratory pathway to southern wintering grounds. Translocation was necessary because the persistence of the Rocky Mountain Trumpeter Swan Population (RMP) is questionable, even though the population has increased from an estimated 66 individuals in 1933 (Banko 1960) to approximately 3,000 individuals in 1996 (United States Fish and Wildlife Service unpub. data). Apparently, 90% of the RMP winter on thermal springs and rivers in the tristate area (Subcommittee on Rocky

Mountain Trumpeter Swans 1992), located where the borders of Idaho, Wyoming, and Montana meet. The tristate area provides only limited resources during winter (Subcommittee on Rocky Mountain Trumpeter Swans 1992) due to overgrazing by waterfowl and drought since 1987 (Kadlec 1991). Even though Trumpeter swans wintering in the tristate area may face starvation in harsh winters, most RMP Trumpeter swans do not appear to disperse into more favorable southern habitats. Obviously, there is a need to translocate Trumpeter swans to decrease the population pressure on the tristate area and to establish a tradition of migrating south of the tristate area. However, translocations may not only affect Trumpeter swan survival; Trumpeter swans may also affect the ecosystem and community structure at the translocation sites. Thus, attempting translocations of Trumpeter swans to northern Utah without evaluating introduction criteria is unwise (Kleiman et al. 1989, Sarrazin and Barbault 1996). Kleiman et al. (1989) suggested 13 criteria for planning and executing species translocations (Table 1). In order to understand the ecological implications of the translocation, I focused on evaluating habitat quality (criteria 5) in chapter 2, and quantifying potential competitive interactions with Tundra swans (criteria 6) in chapter 3. In chapter 4 ("Conclusions") of this thesis, I analyzed all criteria to evaluate whether the goals of the translocation were met.

## HABITAT EVALUATION

Trumpeter swans preferentially feed on sago pondweed (*Potamogeton pectinatus*) tubers when available (Limpert and Earnst 1994, Mitchell 1994). Craner (1964) demonstrated that sago pondweed was the most abundant submersed aquatic macrophyte

Table 1. Reintroduction criteria as proposed by Kleiman et al. (1994).

| Condition of the species       |   |
|--------------------------------|---|
| 1                              | Augmentation of the wild population is necessary                                      |
| 2                              | Stock is available  |
| 3                              | The wild population is not jeopardized  |
| Environmental conditions       |   |
| 4                              | Causes of decline are removed   |
| 5                              | The habitat is ecologically suitable  |
| 6                              | The habitat is unsaturated with members of the same species and other similar species |
| Biopolitical considerations    |   |
| 7                              | The local human population is not negatively impacted                                 |
| 8                              | Community support exists  |
| 9                              | Governmental and nongovernmental organizations are supportive                         |
| 10                             | The reintroduction program complies with all laws and regulations                     |
| Biological and other resources |   |
| 11                             | Reintroduction technology is known or in development                                  |
| 12                             | Sufficient information exists about species' biology                                  |
| 13                             | Sufficient resources exist for the program  |

at the Bear River Migratory Bird Refuge (BRMBR) and the Bear River Club Company (BRC), the translocation sites in northern Utah. Current productivity of sago pondweed, however, is not known. Flood water from the Great Salt Lake eliminated a majority of the wetlands and food resources on BRMBR and BRC from 1983 to 1989. Inevitably, the flood in 1983 changed soil substrate, water depths, water currents, and salinity. Some or all of these factors may have a pronounced effect on the establishment, reproduction, and survival of sago pondweed. In order to evaluate the quality of the habitat and the appropriateness of BRMBR and BRC as translocation sites, abundance and distribution of sago pondweed tubers in the sediment column were quantified using geostatistical procedures. The information gained from the geostatistical analysis has management implications (e.g., describing the number of swans BRMBR and BRC can support), as well as theoretical implications (e.g., linking spatial structure to swan foraging behavior and resource utilization).

#### COMPETITIVE INTERACTIONS

Northern Utah is a major staging area for Tundra swans (*Cygnus columbianus*). About 30,000 Tundra swans staged in northern Utah in November 1996; numbers dropped to 15,000 a month later (Utah Division of Wildlife Resources unpub. data). Interactions between Trumpeter and Tundra swans are likely because both species appear to feed exclusively on sago pondweed tubers at BRMBR, and because both species feed in areas dominated by sago pondweed. Additionally, body measurements (e.g., weight, bill length, neck length, leg length) are reasonably similar for both species. Trumpeter swans



are about 1.2 times the size of Tundra swans (calculated from Limpert and Earnst 1994, Mitchell 1994). However, the Hutchinsonian ratio of 1.3 (Hutchinson and MacArthur 1959) suggests that these two species should not coexist in the same environment when resources are limited. So, is the Utah translocation program doomed to failure because the two species are very similar, or might other community level processes (e.g., different foraging efficiencies, different microhabitat selection, temporal separation, etc.) enable these species to coexist on staging and wintering grounds?

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CHAPTER 2  
PREDICTING THE SPATIAL DISTRIBUTION OF SAGO PONDWEED  
TUBERS USING GEOSTATISTICAL PROCEDURES

*Abstract:* Analysis of spatial pattern is a crucial component in understanding population, community, and ecosystem dynamics and stability, yet, it is rarely considered in wetland ecological studies. I analyzed the spatial distribution of sago pondweed (*Potamogeton pectinatus*) tubers within the sediment of four Great Salt Lake (Utah) marshes before the fall and after the spring migration of Tundra swans (*Cygnus columbianus*) in September 1996 and March 1997. Sixty-four transects were established within the study area with 10 sediment cores extracted per transect. Tuber biomass was recorded for each 5 cm section within each core. Geostatistical procedures were used to account for the lack of independence (autocorrelation) between samples. Geostatistics takes advantage of this autocorrelation to find spatial patterns within the data and to interpolate between sample points. Variograms were calculated to analyze the degree of similarity ( $\gamma$ ) between pairs of samples as a function of distance between the pairs. Variograms were then fitted with a least squares function and kriged to create a surface plot of the study areas. Variograms and kriged surface maps analyzing total tuber biomass per sediment core in September suggested that sago pondweed tubers were distributed in gradients and large patches, whereas March variograms showed weaker autocorrelation between samples in some units and no autocorrelation in others. A spatial trend before swan foraging versus a weak spatial trend after swan foraging suggests that high tuber biomass areas were

exploited to a greater extent than low tuber biomass areas. Kriged surface plots allowed calculation of total tuber biomass per wetland before and after swan foraging. This suggested the number of swan-days (one swan-day is defined as an area where a swan spends most of its day foraging; this can be converted to the amount of biomass consumed per swan per day) the wetlands could potentially support and how much biomass was actually depleted by swans. Even though speculative, the results suggested that tuber resources were not limiting swan abundance in winter 1996/1997. With this study I demonstrate how spatial information has implications both in ecological theory as well as in management.

## INTRODUCTION

Ecologists in recent years increasingly have become aware that the spatial distribution of plants and animals is critically important in explaining ecosystem patterns and processes because spatial structure often determines how strongly components of an ecosystem are linked in space (Allen and Starr 1982, Legendre and Fortin 1989). Thus, the analysis of spatial structure has implications in population, community, and ecosystem ecology, as well as sampling design considerations, and should be an important component of many ecological studies. Spatial structure analysis on wetland ecosystems, however, has been neglected. The spatial structure of aquatic macrophytes, for example, is only rarely mentioned (e.g., de Szalay and Resh 1996) or described (e.g., Lehmann et al. 1994, Harlin et al. 1996, Pall et al. 1996), but very seldom quantified. Macrophytes are an important component in wetland ecosystems because they can substantially modify energy and

material flow between land and water (Carpenter and Lodge 1986). Additionally, aquatic macrophytes have major effects on fresh water productivity and biogeochemical cycles because they provide food and structure for other living organisms, e.g., algae and invertebrates, and generally have an annual production-decomposition cycle (Carpenter and Lodge 1986). However, the spatial structure of aquatic macrophytes needs to be quantified so that wetland ecologists can begin to understand how the heterogeneity of wetland ecosystems might affect the dynamics and stability of wetland processes.

Conventional statistical methods assess spatial pattern either by fitting a discrete probability distribution to sample count frequency data or by computing various indices of dispersion that measure the degree of nonrandomness in spatial patterns (Rossi et al. 1995). However, these methods do not take into account the actual location of sampling points with respect to each other and thus neglect to consider autocorrelation between sampling points. A variable is said to be autocorrelated if measures derived for one sample are not independent of neighboring samples. Conventional statistical methods are not valid if samples are autocorrelated because the assumption of independence is violated. Thus, ecologists need to use other statistical tools to address spatial dependence (Legendre and Fortin 1989, Rossi et al. 1992). Geostatistics takes advantage of autocorrelation by describing the degree of similarity between sample points at varying distances between the sample points, thereby assessing the spatial pattern within the data set (Legendre and Fortin 1989, Rossi et al. 1992, 1995). This information may then be used by ecologists to understand how the observed spatial pattern might influence ecosystem processes.

The objective of this study was to describe the distribution and abundance of sago

pondweed (*Potamogeton pectinatus*) tubers in four Great Salt Lake (Utah) wetlands before and after Tundra swan (*Cygnus columbianus*) fall and spring migrations, respectively. Tundra swans preferentially feed on sago pondweed tubers when staging on northern Utah wetlands because sago pondweed is the dominant submersed aquatic macrophyte in these wetlands (Craner 1964) and sago pondweed tubers are high in starch and therefore high in energy (Kantrud 1990). I decided to study the spatial distribution of tubers within wetland sediments to understand how distribution and abundance of tubers affects tuber utilization patterns by swans. In particular, I was interested in differential utilization of high versus low tuber biomass areas, and the level of tuber depletion by swans during staging to detect potential resource limitation in northern Utah. I also studied tuber distribution to devise hypotheses regarding the dominant abiotic and biotic mechanisms contributing to the observed spatial pattern. With this study, I demonstrate how analysis of spatial pattern is important in ecological theory and in management.

#### STUDY AREA

The study was conducted on units 1, 2, and 4 of the Bear River Migratory Bird Refuge (BRMBR) and on the Bear River Club Company (BRC). All four of these freshwater wetlands are located on the delta of the Bear River entering the Great Salt Lake, Utah (Figure 1). Each wetland includes a permanently submersed area between 8 (Unit 4) and 23 km<sup>2</sup> (BRC). Sago pondweed and widgeon grass (*Ruppia maritima*) were the most abundant submerged aquatic macrophytes on BRMBR and BRC in 1963 (Craner 1964), but their abundance and distribution has not been quantified recently. It is likely

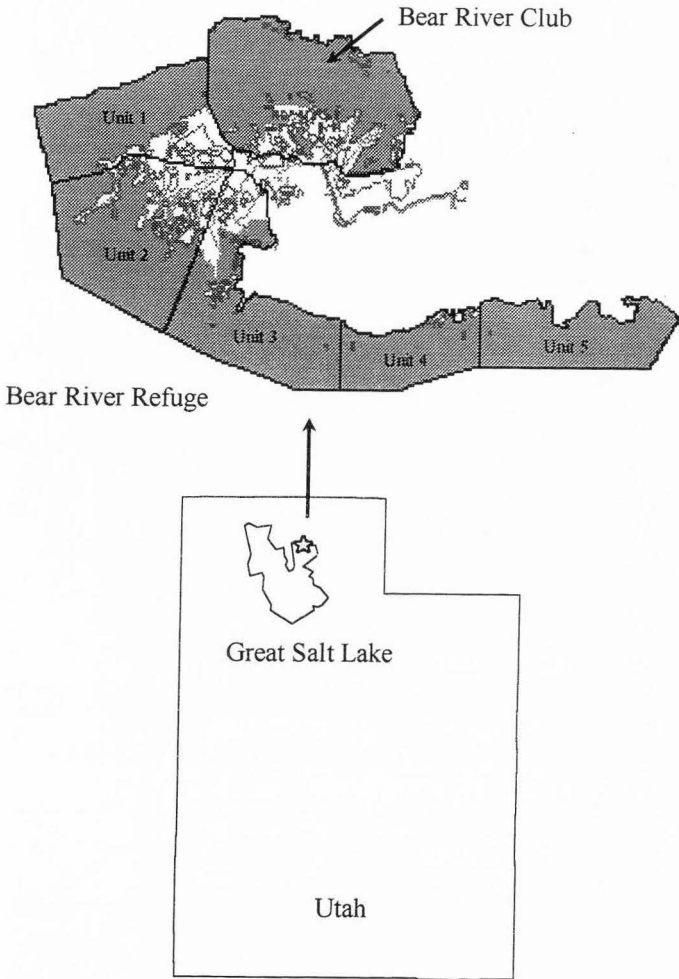


Figure 1. Map of the Bear River Migratory Bird Refuge and Bear River Club Company.

that aquatic macrophyte distribution and productivity have changed since 1964 because a flood of the Great Salt Lake in 1983 to 1989 inundated the marshes with salt water and subsequently destroyed the submersed aquatic plant community and altered abiotic conditions (Foote 1991).

## METHODS

Sediment cores were collected from each wetland in September 1996 after sago pondweed senescence, and in late March 1997 before sprouting of tubers to assure that all wintering tubers were at the same stage of development (i.e., dormant). In September, I sampled before Tundra swan foraging because Tundra swans staging in Utah appear to feed preferentially on sago pondweed tubers (Limpert and Earnst 1994) and therefore may deplete the tuber resources. To confirm that swans prefer to forage on sago pondweed tubers at BRMBR and BRC, I extracted the esophagus and gizzard from swans killed by hunters. In March, I sampled after most Tundra swans migrated to breeding grounds. Sixty-four 200 m transects were selected by *a priori* dividing all wetlands into a grid of 1 km squares and placing transects randomly within each square if greater than 75% of the square was submersed. With this sampling design I was assured that the submersed wetlands were sampled adequately in space (systematic component) and that all points in the wetlands had an opportunity to be chosen (random component). The direction of every transect was chosen randomly. One sediment core (5.2 cm diameter) was taken every 20 m so that 10 cores were extracted per transect. Cores were extracted to the depth of the wetland hardpan. Thus, cores varied in length between 15 and 60 cm



depending on the depth of the hardpan. Every core was divided into 5 cm sections that were washed through a 1 mm sieve in the lab. Tuber lengths, as well as wet and dry weights were recorded for each section. Dry weights were determined by drying the tubers at 60° C for at least 24 hours to obtain a constant weight.

### Geostatistical Analysis

Geostatistical analysis is generally a two-step procedure. First, variograms examine the variance between sample pairs at different distances between pairs to quantify the range (distance at which autocorrelation disappears), nugget (presence of residual variation), and sill (sample variance). The variogram identifies whether a spatial structure (e.g., patches, gradients) is present and whether directionality (anisotropy) in the spatial structure is present. Once a spatial structure is identified, the observed variogram is described with a suitable model (e.g., linear, exponential, spherical, power, gaussian, or some combination thereof). Least squares methods are then used to fit the models to the variograms. The kriging procedure uses the residuals derived from the variogram to interpolate between sampling points and to create a surface plot (Legendre and Fortin 1989, Rossi et al. 1992, 1995, Pohlmann 1993).

*Creating Variograms.* I analyzed every wetland separately because I assumed autocorrelation was insignificant between wetlands. To determine whether directionality (anisotropy) existed within a data set, I ran directional variograms at 90 degree angles. I then created omnidirectional variograms (considers all directions simultaneously) for the total biomass per sediment core before and after swan foraging, and plotted the

variograms to the maximum distance. Usually, variograms are plotted to half the maximum distance because estimates of autocorrelation become unreliable as distance between samples increases and therefore number of possible pairs incorporated in the estimate decreases. However, larger distances may potentially elucidate patterns not apparent when plotting only half the maximum distance. To assure reliable variance estimates, I only accepted estimates that incorporated a minimum of 100 sample pairs. I set two lag distances (distance between successive distance classes of which autocorrelation is calculated): 600 m and 20 m to emphasize between and within transect autocorrelation, respectively. I ran two different variograms with different lags to compare within transect variograms (small scale) to the variograms created for entire units (large scale). I also created variograms for all 5 cm depth intervals separately to determine whether certain depths showed greater spatial autocorrelation than others.

*Modeling Variograms and Kriging.* Variograms were only modeled when a spatial trend was apparent because it is inappropriate to model a variogram with random trend (Burrough 1986). I chose a Gaussian model for Unit 2 and a Spherical model for Unit 1, Unit 4, and BRC. The models were fitted with nonlinear least squares. I modeled the variograms to the range of the variograms because at larger distances variances decreased again. Residuals of the models were used to interpolate between samples and to create a kriged surface. Within-transect variograms were not modeled and kriged due to low sample size (10 stations per transect).

### Calculating Biomass Ingested by Swans

I calculated mean tuber biomass for each grid cell within the kriged surfaces and multiplied by the submersed portion of the respective wetlands to obtain an estimate of total tuber biomass for each wetland before and after swan foraging. I compared this estimate with an estimate obtained by calculating the mean tuber biomass per core directly without using geostatistics. I calculated tuber biomass loss during the swan season by subtracting March foraging biomass estimates from September biomass estimates. About 25% of total biomass is lost through decomposition (Beekman et al. 1991); thus, an estimate of biomass ingested by waterfowl was obtained by subtracting biomass lost through decomposition from total biomass lost.

To obtain an estimate of swan use of every wetland, aerial surveys were conducted by the Utah Division of Wildlife Resources from 8 am to 10 am once every 2 weeks in October 1996, for every week in November and December 1996, and once in January and in March 1997 (Aldrich and Manes unpub. data.). To convert observed numbers to swan-days (wetland where a swan foraged more than 50% of its total foraging time within one day), it was necessary to correct for intermarsh migrations and daily behavioral patterns. Swans appeared to migrate extensively starting at 6 am from BRC to Unit 1 and from Unit 2 to Unit 1. The swans appeared to use Unit 1 exclusively for resting (except in March 1997). A reverse migration occurred starting 1 hour before sunset. These local but often extensive migrations are most likely due to hunting pressure in BRC and Unit 2 in November and December. Therefore, I supplemented the aerial surveys with migration counts that counted every swan flying over the dike between BRC and Unit 1 and over the

dike between Unit 2 and Unit 1. I also counted birds immigrating and emigrating from Unit 4. Migration counts were performed beginning at sunrise and 1 hour before sunset. Once local migrations were accounted for, I estimated the number of swan-days per wetland. I did not count days when tubers were not accessible to swans due to greater than 90% ice cover of the wetlands. I calculated tuber biomass ingested per wetland by multiplying the number of swan-days per wetland by the biomass of tubers ingested by a swan per day to meet its daily energy requirements. Bortner (1985) suggests that a Tundra swan requires between 2,157 to 2,856 kJ per day to meet its daily energy expenditures. This estimate suggests that Tundra swans should ingest between 184 g and 244 g (average = 214 g) of dry tubers per day assuming one gram of tubers contains 2.80 kcal or 11.7 kJ (Squires 1991). Beekman et al. (1991) suggest that Bewick's swans (*Cygnus columbianus bewickii*) require 254 g to 318 g (average = 283 g) of dry tubers per day while staging. This estimate seems more reasonable because staging swans do not forage to merely meet daily energy expenditures, but to exceed them and store energy for winter survival and increased fecundity.

## RESULTS

### Geostatistical Analysis

Directional variograms suggested no apparent directional trend because gamma, a measure of variance between sample pairs, did not increase as distance between sample pairs increased. Thus, omnidirectional variograms were run for all subsequent analyses. Variograms analyzing the variance of tuber biomass per core with increasing distance

between cores indicated that sago pondweed tubers were not randomly distributed before swan foraging (Figure 2). Rather, all four variograms showed that variance generally increased with distance until the distance between cores reached 1,500 m in Unit 1, 2,000 m in Unit 2, 3,500 m in Unit 4, and 2,000 m in BRC. After these distances, variances decreased for all wetlands except Unit 4. The same analysis after swan foraging (Figure 3) indicated that a spatial structure can only be defined for BRC where variance increased up to 1,500 m. Variance then leveled out up to 3,500 m, after which variance decreased. Within-transect variograms before swan foraging (Figure 4) indicated that cores within a transect were not autocorrelated in Units 1 and 2. Variograms for Unit 4 and BRC, on the other hand, indicated that spatial structure appears to be random up to approximately 100 m after which variance between cores increased. Within-transect variograms after swan foraging (Figure 5) suggested no apparent within-transect spatial structure for any of the wetlands. Variograms analyzing tuber distribution by depth suggested a spatial autocorrelation at most depths before swan foraging, except Unit 4 (Figures A.1, A.2, A.3, and A.4). However, the variograms did not suggest that some depths consistently showed higher autocorrelation than others. After swan foraging variograms (Figures A.5, A.6, A.7, and A.8) showed a random spatial pattern for most sections and most wetlands, except for BRC sections between 20 and 40 cm sediment depth.

Kriged surfaces of before foraging tuber biomass distribution (Figures 6 to 9) indicated that tuber biomass peaks were located in the middle of Unit 1, Unit 2, and BRC. Unit 4 tuber biomass decreased steadily from the SE corner to the NW corner of the wetland before swan foraging. The variograms for Units 1, 2, and 4 after swan foraging

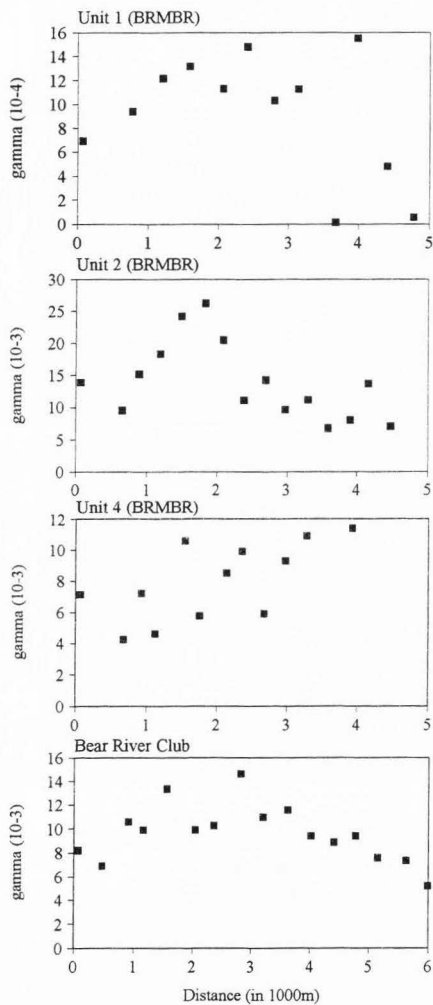


Figure 2. Variograms of the four study sites before swans started feeding on sago pondweed tubers. Variograms are plotted to the maximum distance.

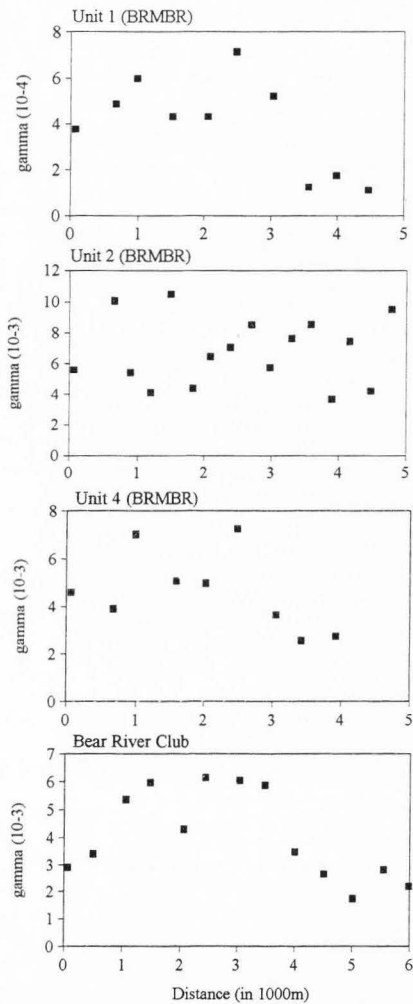


Figure 3. Variograms of the four study sites after swan foraging on sago pondweed tubers. Variograms are plotted to the maximum distance.

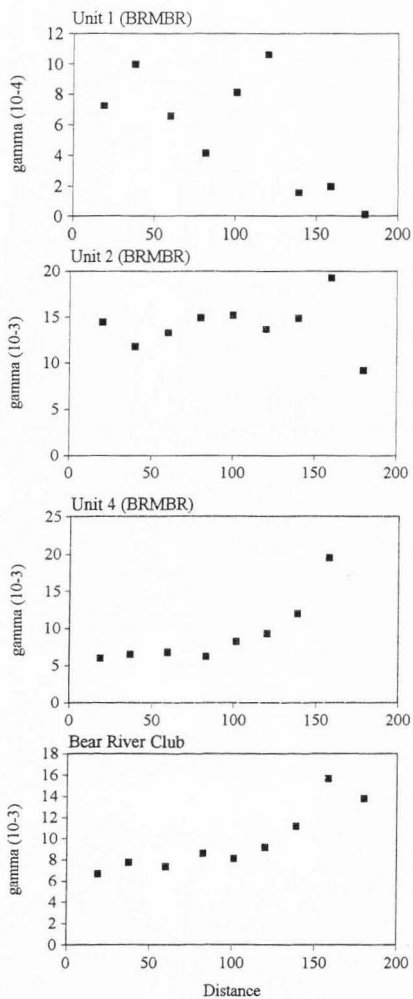


Figure 4. Within-transect variograms of the four study sites before swans started foraging on sago pondweed tubers.



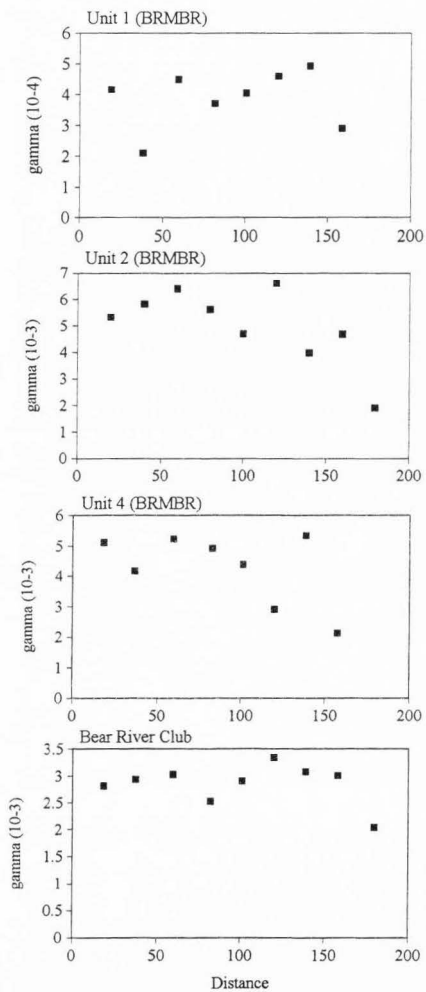


Figure 5. Within-transect variograms of the four study sites after swan foraging on sago pondweed tubers.

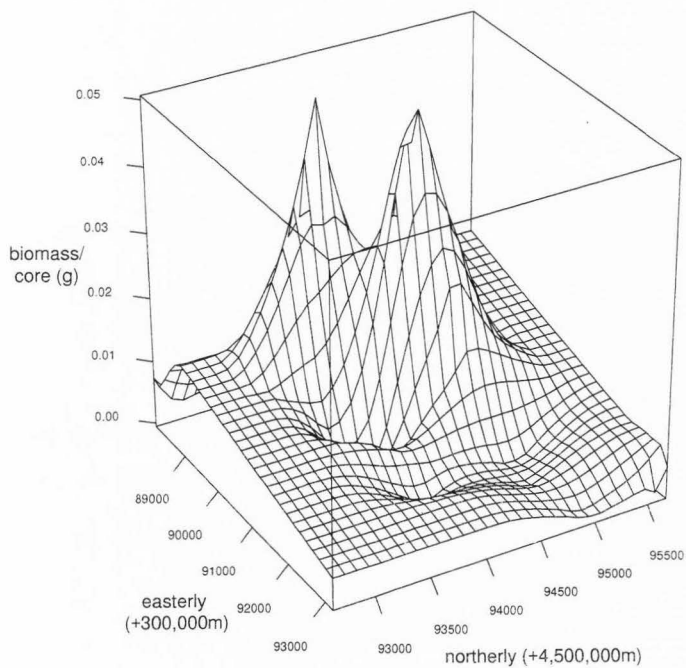


Figure 6. Kriged surface map of tuber biomass in Unit 1 before swan foraging. Biomass is 100 % dry matter. Easterly and northerly are UTM coordinates.

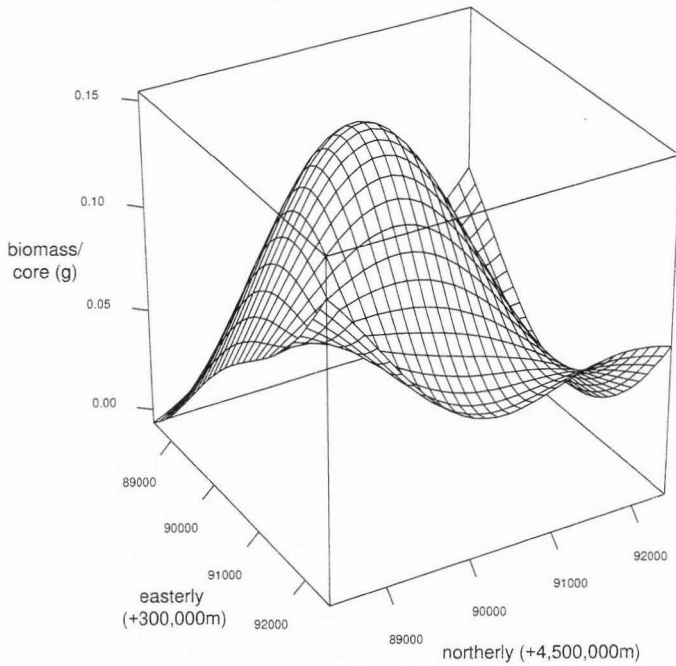


Figure 7. Kriged surface map of tuber biomass in Unit 2 before swan foraging. Biomass is 100 % dry matter. Easterly and northerly are UTM coordinates.

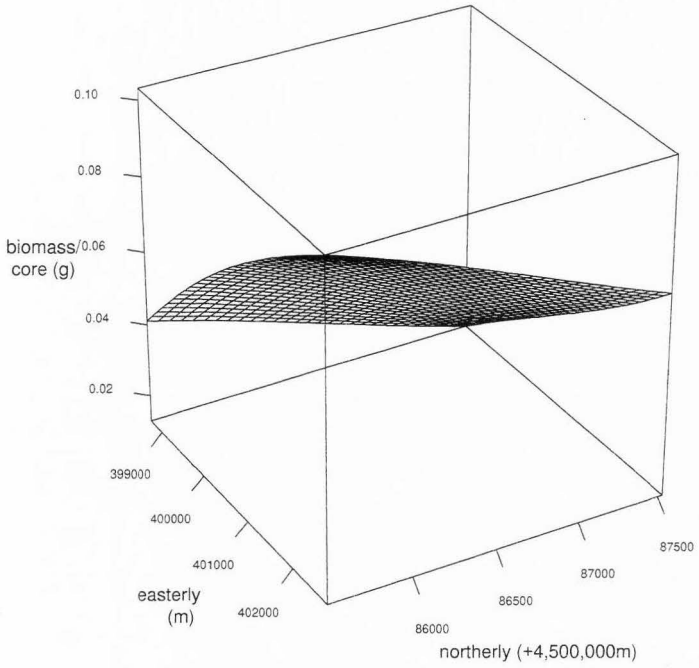


Figure 8. Kriged surface map of tuber biomass in Unit 4 before swan foraging. Biomass is 100 % dry matter. Easterly and northerly are UTM coordinates.

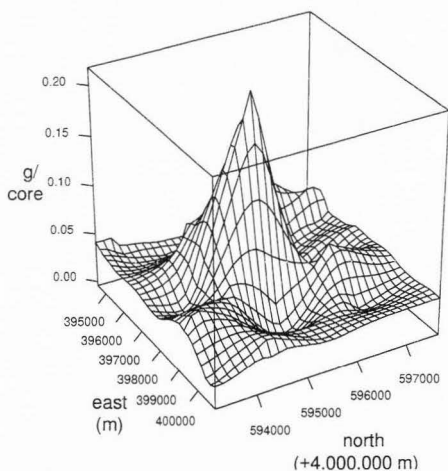
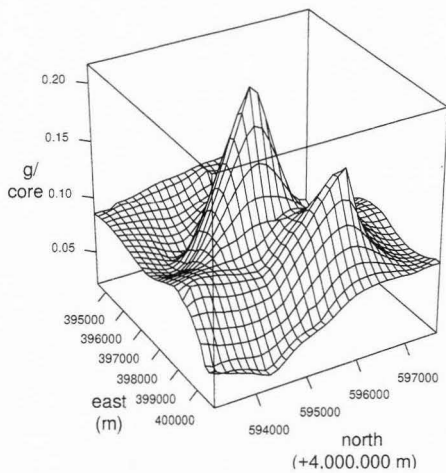


Figure 9. Kriged surface maps of tuber biomass in BRC before (top) and after (bottom) swan foraging. Biomass is 100 % dry matter. Easterly and northerly are UTM coordinates.

were not modeled and kriged because the variograms suggested a random tuber distribution (Figure 3). The kriged surface map for BRC after swan foraging showed one peak in the middle of the unit.

#### Tuber Biomass Calculations

Tundra swans appeared to exclusively feed on sago pondweed tubers while staging at BRMBR and BRC. Out of 50 gizzards and esophagi collected, seven gizzards and two esophagi contained 100% sago pondweed tubers, and all other gizzards and esophagi were empty. Additionally, all swans were observed feeding within the sediment of submersed wetlands. Between October and March, these wetlands provide sago pondweed tubers as the predominant food resource. Besides swans, other waterfowl, e.g., Canvasbacks (*Aythya valisineria*) among other diving ducks, may feed on sago pondweed tubers. However, compared to swans, tuber utilization by diving ducks should be minimal because diving ducks can only feed in shallow sediment depths (e.g., maximum 10 cm depth), whereas swans are able to feed deeper in the sediments (e.g., 60 cm depth). Also, diving ducks are generally not present in large numbers during the winter compared to swans (U.S. Fish and Wildlife Service unpub. data).

All biomass measurements were recorded as 100% dry matter (mean dry weight = 34.3434% of wet weight). In September, Unit 1 exhibited the lowest average tuber biomass per square meter area (5 g) followed by Unit 4 (27 g), Unit 2 (37 g), and BRC (42 g). In March, 50% of the tuber resources were depleted in Unit 1 (2.5 g/m<sup>2</sup> after swan foraging), 43% in Unit 2 (20 g/m<sup>2</sup>), 29% in Unit 4 (19 g/m<sup>2</sup>), and 59% in BRC (17 g/m<sup>2</sup>).

Comparison of tuber biomass per area calculations between geostatistical analysis and direct calculations showed no apparent differences. After calculating tuber biomass loss between September and March and after determining tuber biomass loss due to decomposition, I determined that 15,777 kg were ingested in Unit 1, 116,893 kg in Unit 2, 10,236 kg in Unit 4, and 327,661 kg in BRC. These estimates were compared to estimates derived from converting observed swan-days to tuber biomass ingested within each wetland. These estimates suggest that 25,536 kg were ingested in Unit 1, 118,346 kg in Unit 2, 35,848 kg in Unit 4, and 232,231 kg in BRC (Table 2).

#### DISCUSSION

Variograms that first increase and then decrease suggest that samples separated by a large distance are more similar than samples separated by a shorter distance. Isaaks and Srivastana (1989) call this a "hole effect" and suggest that it is a common natural phenomenon when discrete areas of high values exist, as is the case in many ore deposits (Isaaks and Srivastana 1989). Moisen (pers. comm.) found when studying Aspen (*Populus tremuloides*) production that a hole effect occurs when crossing from one mountain range to another. As abiotic conditions such as slope and aspect approximately repeat when a new mountain range starts, the variogram values repeat as well. The range value of a variogram suggests the distance at which samples are autocorrelated; thus, the range describes the distance between a "valley" and a "peak" on a kriged surface map. Two times the range would suggest the distance between two valleys or two peaks, i.e., the "frequency" in mathematical terms, assuming the data are cyclical or repetitious (Isaaks

Table 2. Summary of tuber biomass calculations. All biomass is recorded as 100% dry matter.

| Site   | Area (m <sup>2</sup> ) | g/m <sup>2</sup><br>before | g/m <sup>2</sup><br>after | kg<br>before | potential<br>swan days | kg<br>after | kg<br>loss | kg de-<br>comp. <sup>b</sup> | kg<br>ingested <sup>c</sup> | swan<br>days | kg<br>ingested <sup>d</sup> |
|--------|------------------------|----------------------------|---------------------------|--------------|------------------------|-------------|------------|------------------------------|-----------------------------|--------------|-----------------------------|
| Unit 1 | 12,985,309             | 5<br>(5) <sup>a</sup>      | 2.5<br>(2) <sup>a</sup>   | 64,611       | 228,307                | 32,682      | 31,929     | 16,153                       | 15,777                      | 90,234       | 25,536                      |
| Unit 2 | 15,491,246             | 37<br>(35.5) <sup>a</sup>  | NA<br>(20) <sup>a</sup>   | 571,151      | 2,018,201              | 311,471     | 259,680    | 142,788                      | 116,893                     | 418,183      | 118,346                     |
| Unit 4 | 8,909,258              | 27<br>(27) <sup>a</sup>    | 19<br>(20) <sup>a</sup>   | 243,048      | 858,827                | 172,050     | 70,998     | 60,762                       | 10,236                      | 126,672      | 35,848                      |
| BRC    | 23,318,746             | 42<br>(41) <sup>a</sup>    | 17<br>(17) <sup>a</sup>   | 971,888      | 3,434,233              | 401,255     | 570,633    | 242,972                      | 327,661                     | 820,605      | 232,231                     |
| Total  | 60,704,559             | NA                         | NA                        | 1,850,698    | 6,539,569              | 917,458     | 933,240    | 462,675                      | 470,567                     | 1,455,694    | 411,961                     |

<sup>a</sup> estimate of mean biomass per area calculated without geostatistical procedures.

<sup>b</sup> assumed decomposition rate of 25% (Beekman et al. 1991).

<sup>c</sup> calculated from biomass loss minus biomass decomposed.

<sup>d</sup> calculated from observed swan days assuming swans require 238 grams of tubers per day (Beekman et al. 1991).



and Srivastana 1989). Table 3 provides the range values of all variograms after they were modeled. The range value for Unit 1 in September suggests that the distance between two tuber biomass peaks is approximately 1,760 m (2 X 880 m). The kriged surface map (Figure 6) shows two definite peaks that may be approximately 2,000 m apart. The Unit 2 September variogram suggests a range of approximately 1,022 m; thus, the distance between peaks at approximately 2,050 m. The kriged surface map of Unit 2 (Figure 7) shows a biomass peak in the middle of the wetland and two smaller peaks in the NW and SE corners. The same phenomenon appears to occur for Bear River Club September data where the range equals 1,674 m, and thus biomass peaks are separated by approximately 3,350 m (Figure 9). The September variogram for Unit 4 does not exhibit a hole effect. The kriged surface map is smooth with no apparent peaks.

What are the implications of the observed tuber distribution on swan foraging behavior? In the studied system sago pondweed tuber biomass appears to be distributed in gradients. In Unit 4, this gradient decreases continuously and regularly from the south-east corner to the north-west corner of the wetland. In Unit 1, Unit 2, and BRC, the gradient increases and decreases within the wetland, creating peaks and valleys in the tuber biomass map. At the wetland-wide scale, these peaks and valleys may be interpreted as large patches between 1,600 to 3,000 m in diameter. These patches may be selected by swans when individuals select habitats to forage in, i.e., swans are likely to select high tuber biomass areas within a wetland because these areas offer the highest energy gain per unit time. However, once an area within a wetland is selected, foraging swans probably perceive the spatial distribution of tubers as gradients rather than as large patches. Optimal

Table 3. Summary of variogram and model parameters.

|                             | Unit 1                          | Unit 2                      | Unit 4                          | Bear River Club                 |
|-----------------------------|---------------------------------|-----------------------------|---------------------------------|---------------------------------|
| <b>Variogram parameters</b> |                                 |                             |                                 |                                 |
| lag                         | 500                             | 300                         | 500                             | 500                             |
| maximum distance            | 3,500                           | 2,000                       | 3,900                           | 4,500                           |
| minimum pairs               | 100                             | 100                         | 100                             | 100                             |
| <b>Model parameters</b>     |                                 |                             |                                 |                                 |
| model type                  | spherical                       | gaussian                    | spherical                       | spherical                       |
| range (m)                   | 880<br>(1,060) <sup>a</sup>     | 1,022<br>(NA) <sup>a</sup>  | 4,193<br>(1,115) <sup>a</sup>   | 1,675<br>(1,508) <sup>a</sup>   |
| sill <sup>b</sup>           | 0.0006<br>(0.0002) <sup>a</sup> | 0.0088<br>(NA) <sup>a</sup> | 0.0026<br>(0.0019) <sup>a</sup> | 0.0035<br>(0.0030) <sup>a</sup> |
| nugget <sup>b</sup>         | 0.0006<br>(0.0003) <sup>a</sup> | 0.0126<br>(NA) <sup>a</sup> | 0.0065<br>(0.0043) <sup>a</sup> | 0.0076<br>(0.0027) <sup>a</sup> |

<sup>a</sup> values in parantheses are for March model parameters.

<sup>b</sup> sill and nugget values are average squared tuber biomass differences between sample pairs ( $\gamma$ ).

foraging theory predicts that as distance between similar patches increases, the time spent within a patch increases (Charnov 1976, Stephens and Krebs 1986). Sago pondweed tubers are distributed in gradients, and small scale patches are nonexistent, or at least not detected by the tuber sampling. Thus, according to optimal foraging theory, swans should move constantly while foraging because "time between patches" is nonexistent. This kind of foraging behavior was not observed. In fact, I observed swans feeding continuously within a 1 to 2 m diameter area for 0.5 to 4 hours. By foraging in one spot, swans create foraging holes by paddling with their webbed feet and subsequently digging deeper with their bills. The created foraging holes may be perceived as patches. Optimal foraging theory predicts that a forager should leave a patch when the rate of capturing a prey in the patch falls below the average rate of capture in all patches within the environment (Charnov 1976). Swan foraging holes are rarely depleted because swans may simply scrape at the sides of the hole for more tubers. This is also energetically more favorable to swans than to create a new foraging hole. Thus, according to optimal foraging theory, swans are predicted to forage within a hole until satiated. This kind of foraging behavior was observed in the field.

Optimal foraging theory predicts that a forager should leave a patch when the rate of capturing a prey in the patch falls below the average rate of capture in all patches of the environment (Charnov 1976). Thus, high tuber biomass areas are predicted to be depleted to a greater extent than low tuber biomass areas. This may indeed be the case because variograms generated from March tuber biomass data generally suggest that spatial patterns are absent, and thus "peaks" and "valleys" are absent (Units 1, 2, and 4) or are

less evident (BRC). By separating the sediment depth strata in BRC, spatial trend in March was only evident between 21 to 40 cm (Appendix A.4). This wetland is the deepest of the four, so swans may not have been able to deplete the tuber biomass at these depths. Thus, a different spatial pattern in March may suggest that the tuber resource has not yet been depleted to the lowest level possible, and, therefore, resources are not limiting swan abundance.

Sago pondweed tubers may not be limiting in this system for other reasons as well. Table 2 suggests that observed Tundra swan-days (1,500,000 for BRMBR and BRC combined) appear to be well below the potential maximum swan-days calculated for the entire area (6,500,000). Also, Tundra swans abandoned BRMBR and BRC in March when resource densities were 20 g/m<sup>2</sup> in Unit 2, 19 g/m<sup>2</sup> in Unit 4, and 17 g/m<sup>2</sup> in BRC (Table 2). However, Beekman et al. (1991) determined that Bewick's swans (*Cygnus columbianus bewickii*), the European subspecies of the Tundra swan, exploited sago pondweed tubers until tuber biomass reached 7 g/m<sup>2</sup>.

The spatial distribution exhibited by sago pondweed tubers may be caused by abiotic and biotic variables that vary in space. For example, water depth (e.g., Craner 1964, Anderson and Low 1976, van Wijck and De Groot 1993), wave action (e.g., Jupp and Spence 1977, Anderson 1978), turbidity (e.g., van Dijk et al. 1992), sediment and water characteristics (e.g., Craner 1964, Van Wijk 1988, Van Wijk et al. 1988, van Wijk et al. 1992), fish (e.g., Crivelli 1983), and waterfowl (e.g., Jupp and Spence 1977) determine reproduction and survival of sago pondweed populations (see Kantrud 1990 for in-depth literature review). Another explanation of the observed spatial distribution may

be that sago pondweed primarily propagates vegetatively (Spencer and Anderson 1987, Van Wijk 1989, van Wijk et al. 1992); thus, high biomass patches may be the center of a sago pondweed clone. This is possible in Unit 1 where sago populations are only starting to establish because the unit has been permanently wet only since fall 1995. Thus, observed patches may be chance colonizations by sago seed and subsequent outward radiation through vegetative propagation. Finally, the repetitious behavior of tuber biomass distribution may be attributed to intraspecific competition. As a plant population matures, root systems may overlap increasingly, which may cause competition for nutrients ("self-thinning"; Kays and Harper 1974). This may cause the spatial distribution to change from clumped, to random, to regular (Philips and MacMahon 1981 *in* Giller 1984). Maturing sago pondweed populations may undergo self-thinning due to sago pondweed's extensive vegetative propagation. In fact, one tuber may produce more than 12 tubers after an 8-week period (Spencer and Anderson 1987). In a culture experiment, Yeo (1965 *in* Kantrud 1990) grew 36,000 tubers from one tuber within one season. Peaks and valleys on the kriged tuber biomass maps may correspond to different levels of self-thinning, which may be caused by the environmental conditions discussed above. Swan herbivory may or may not counter self-thinning at BRMBR and BRC, depending on the level of tuber depletion by swans in relation to the carrying capacity of the studied areas. Unfortunately, a carrying capacity cannot be calculated for BRMBR and BRC because the time at which swans should leave an area due to perceived resource limitation is unknown.

I calculated the tuber biomass ingested by waterfowl by calculating how much tuber biomass was lost between September 1996 and March 1997, assuming

approximately 25% of biomass is lost to decomposition. I also calculated ingested biomass by estimating the number of swan-days the different wetlands were used until March. Ingested biomass estimates for Unit 2 are close; however, Unit 1 and Unit 4 biomass estimates, calculated from converting observed swan days into biomass ingested, were severely overestimated and BRC was underestimated. BRC and Unit 2 were hunted and Tundra swans abandoned these wetlands and sought refuge in non-hunted areas. Unit 1 and Unit 4 biomass may therefore have been overestimated because some swans were using these areas as refuges but were counted as feeding birds. BRC biomass may have been underestimated because it is a large wetland. Corridors of local migrations may have been overlooked such that local movements in and out of BRC were underestimated. Nevertheless, discrepancies in the calculations suggest that swans move extensively during the day.

Ecologists have recently become concerned about choosing appropriate spatial scales to analyze ecological problems (e.g., Allen and Starr 1982). For example, conclusions and management decisions derived at one scale may be completely inappropriate at another scale due to some abiotic and/or biotic interaction(s) not readily apparent at one scale. Analysis of spatial population distribution patterns at various spatial scales would help in choosing the correct scale of study and in designing effective experiments (Biondi et al. 1994). I decided to analyze tuber biomass spatial distribution on a transect scale (200 m) to explore possible spatial structures at this smaller scale. Only Unit 4 and BRC show autocorrelation in the variogram; however, the transects are too short to determine when a sill and range would be reached. Overall, the within-transect

variograms are inconclusive because they either show no trend (Unit 1 and Unit 2) or only partially describe a trend (Unit 4 and BRC). On the other hand, the variograms calculated for entire wetlands showed a spatial pattern. This suggests that spatial scales need to be chosen wisely because a variable may not exhibit a spatial structure at one scale but it may at a different spatial scale. The spatial scale chosen for a study depends on the question one wants answered. Because I was interested in how swans exploit tuber resources within entire wetlands, the wetland-wide scale was more appropriate than the within-transect scale. However, I was also interested in swan foraging behavior at a smaller "patch" scale. My sampling did not show any conclusive spatial trends within transects. This suggests either that the sampling was inadequate for the smaller scale, or that tubers are distributed randomly at the smaller scale. I could have extracted cores closer together to understand small-scale spatial trends; however, extracting additional cores was not feasible due to time constraints.

Spatial pattern analysis is critically important in ecological studies because it often elucidates how components of an ecosystem are connected spatially. Spatial structure provides a "habitat template" for other species (Southwood 1977). Submersed aquatic macrophytes, for example, often occur in patches (Sand-Jensen and Mebus 1996). This spatial structure affects the spatial distribution patterns of invertebrates and therefore the distribution of waterfowl feeding on the vegetation and the invertebrates. Additionally, macrophyte patches change water as well as sediment chemistry and alter other physical characteristics, which may affect wetland ecosystem processes. The description of spatial patterns also allows ecologists to better track the decline or recovery of a population

because recovery efforts will not only be focused on absolute numbers but also on other "spatial" factors contributing to population persistence. Accurate knowledge of spatial patterns and changes of these patterns in time can help in making management decisions for the long-term sustainability of a species (Biondi et al. 1994).

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CHAPTER 3  
MECHANISMS OF COEXISTENCE BETWEEN  
TUNDRA AND TRUMPETER SWANS

*Abstract:* Coexistence often is assumed to be caused by the degree of similarity between species. Body size often is used as an indicator of similarity because body size is closely related to the energy requirements of an animal and the amount of resources available to the animal. As similarity between species increases, interspecific competition often is assumed to increase, and to affect the likelihood of coexistence between the species. The link between body sizes of species and potential competition appears to be well established in ecological theory and empirical studies; however, the intermediate link to resource utilization patterns is considered less often. In this study I argue that patterns of resource use should be studied to fully understand mechanisms of coexistence between ecologically similar species. I examined patterns of resource use by Tundra (*Cygnus columbianus*) and Trumpeter (*Cygnus buccinator*) swans, two ecologically similar species staging and/or wintering in northern Utah. I measured body size differences, dietary overlap, resource availability, and the efficiency of extracting available resources. Body and appendage length ratios ranged between 1.1 and 1.2, and both species fed exclusively on sago pondweed (*Potamogeton pectinatus*) tubers that were distributed in large patches and gradients, and buried in wetland sediments between 0 and 50 cm deep. Four percent of total tuber biomass was available exclusively to Trumpeter swans, because they were able to feed in deeper water and exploit tuber resources growing deeper in the sediment,

whereas the shorter neck length of Tundra swans did not allow them to exploit those resources. Gain curves (tuber intake rate versus time within a patch) suggested that both species were equally efficient in extracting tubers from shallow sediment depths but Trumpeter swans became more efficient in deeper sediment. Studies of allometry and its effects on coexistence often suggest that larger species consume larger particle sizes. This appears to be a common way species partition resources and thus coexist. This chapter provides an interesting new perspective on how body size similarities may affect species coexistence. It suggests that larger body size may provide a support structure for long appendages such as wings and necks. My results suggest that the Trumpeter swans benefit from a larger body size and a longer neck because they generally can extract more from a patch within a given time, and have access to exclusive resources (deeper tubers). However, the species is likely to incur higher total costs (e.g., higher metabolic costs, higher flying costs) than Tundra swans because of the larger body size. The trade-off between higher foraging efficiency of Trumpeter swans and higher traveling efficiency of Tundra swans is likely to be a mechanism of coexistence between the two species.

## INTRODUCTION

Ecological theory predicts that the number of coexisting species within a community should be finite and that species differ in their morphological traits more than would be expected by chance (Lack 1947, Hutchinson 1959, Brown 1995). This pattern has indeed been observed among various guilds and communities (e.g., Bowers and Brown 1982, Brown and Bowers 1985, Hopf et al. 1993, Winston 1995) and across

ecosystems (e.g., Holling 1992, Brown 1995). In fact, the predicted and observed pattern appears to be general enough that ecologists have attempted to calculate minimum body size ratios between species to predict species coexistence (e.g., Hutchinson 1959, MacArthur and Levins 1967, Schoener 1974). Even though heavily debated (e.g., Wiens and Rotenberry 1981, Connell 1983, Schoener 1983, Gurevich et al. 1992), finite and nonrandom community structure is mostly attributed to interspecific competition. For example, Gause (1934) suggested that similar species ultimately cannot coexist in the same environment because one of the species will eventually prove to be superior in exploiting the resources and therefore will be superior in producing offspring. Diamond (1975) expressed as an assembly rule that some species will never coexist because similar species compete for resources. Hopf et al. (1993) and Brown (1995) argued that competition for resources is the most likely explanation for morphological segregation within a community. Winston (1995) argued that interspecific competition best explained why very similar species of stream fishes coexist less frequently than more dissimilar species. Interestingly, even though the link between interspecific competition and body size similarity within a community has apparently been established theoretically and empirically, the link between competition and resource utilization via differences in morphology is weak and rather speculative (Price and Heinz 1984, Nakano and Furukawa-Tanaka 1994). Giller (1984) explained that in ecological studies morphological differences are usually directly linked to competition for resources because resource utilization is hard to study. However, empirically linking interspecific competition to differences in resource utilization is crucial in understanding whether interspecific

competition is really driving observed community structure. In fact, Wiens and Rotenberry (1981) argued that the use of morphology when studying competitive interactions between similar species is only appropriate when actual resource utilization by the studied individuals is measured.

Body size is related to an animal's energy and nutrient requirements and its opportunities for acquiring resources (Calder 1983, Werner and Gilliam 1984, Letcher et al. 1994). Large-bodied species have higher nutrient requirements and therefore need to be more efficient in extracting energy and nutrients from the environment compared to their smaller counterparts (Peters 1983, Price and Heinz 1984, Brown 1995). This in turn may affect patterns of resource use and species coexistence. Brown (1989) proposed that a trade-off between foraging efficiency and the cost of travel may be a mechanism for coexistence. A larger species may be more efficient in extracting resources, but the smaller species may be able to travel between foraging sites more efficiently. Brown (1989) also suggested that species may coexist when foraging efficiencies for the species differ between habitats or seasons. Thus, similar species may coexist in the environment if they separate proximately by certain niche variables (e.g., Grinnell 1917, Hutchinson 1959).

Body size differences may not only determine energy requirements and feeding efficiencies but may also determine the nature of resources available to the species. Several studies on body size similarities suggested that larger species consume larger particle sizes because they have larger mouth parts (e.g., Schluter and Grant 1984, Grant and Grant 1989, Schluter 1993, Forsman and Lindell 1993, Forsman 1994, 1996). These studies suggest that gape size sets an upper limit to ingestible prey size and therefore an upper

limit to energy intake rates. Small species may only use a subset of the resources that can be consumed by larger species (Werner and Gilliam 1984, Gaston and Lawton 1988, Martin et al. 1994, Basset 1995, Brown 1995). In fact, it is possible that a small species shares all its resources with a larger species, but the larger species may still enjoy resources not available to the smaller species ("included niche": Miller 1967, Schoener 1974). For these species to coexist, the species with the included niche must be a superior competitor for the shared resources on a per-capita basis, and the species with the exclusive resources must not achieve sufficient density on exclusive resources to numerically outcompete the included-niche species for the shared resources (Chase and Belovsky 1994, Chase 1996a,b). Thus, coexistence and relative abundances of species in this scenario depend on the availability of exclusive resources and the per capita effects of both species on the shared resources (Chase and Belovsky 1994, Chase 1996a,b). Apparently, community structure cannot simply be explained by observed body size similarities. Rather, species coexistence may need to be determined by patterns of resource use, which may then (but not necessarily) lead to niche shifts and observed body size ratios.

The objective of this study was to link body size similarities with patterns of resource use to infer possible mechanisms of coexistence within a community. As an example, I examined patterns of resource use by Trumpeter (*Cygnus buccinator*) and Tundra (*Cygnus columbianus*) swans, similar species staging and/or wintering on marshes of the Great Salt Lake in northern Utah. This simple system is ideal for linking interspecific competition with resource utilization patterns via differences in morphologies:



Both species prefer to feed on sago pondweed (*Potamogeton pectinatus*) tubers (Limpert and Earnst 1994, Mitchell 1994) that are abundant in Utah marshes (see Chapter 2) and the only high-quality food source available between October and March when swans are most likely to be present. Additionally, both species are often sympatric on staging and wintering habitats (e.g., Shea 1979). In fact, the only apparent difference between the species is that Trumpeter swans are larger (Figure 10). This difference, however, may have tremendous consequences for swan foraging efficiencies and resource availability, and may affect outcome of interspecific competition when resources are limited.

## METHODS

Fifty-seven Trumpeter swans were translocated to the Bear River Migratory Bird Refuge (BRMBR) and the Bear River Club Company (BRC) in northern Utah (Figure 1). The translocation area is a traditional staging area for Tundra swans during fall and spring. In fact, 30,000 Tundra swans were counted during the 1996 fall peak migration (Utah Division of Wildlife Resources unpub. data). Trumpeter swans have only rarely been sighted in Utah. Trumpeter swans historically migrated through the area but may not presently because the population was drastically reduced in the early 1900's, possibly due to excessive hunting for their valued skins and habitat loss (Banko 1960). Survivors were artificially fed in the tristate area, located where the borders of Idaho, Montana, and Wyoming meet. Artificial feeding helped recover the population; however, it also established a tradition of wintering in the tristate area. Artificial feeding was stopped in 1992; however, Trumpeter swans have been reluctant to winter in more favorable

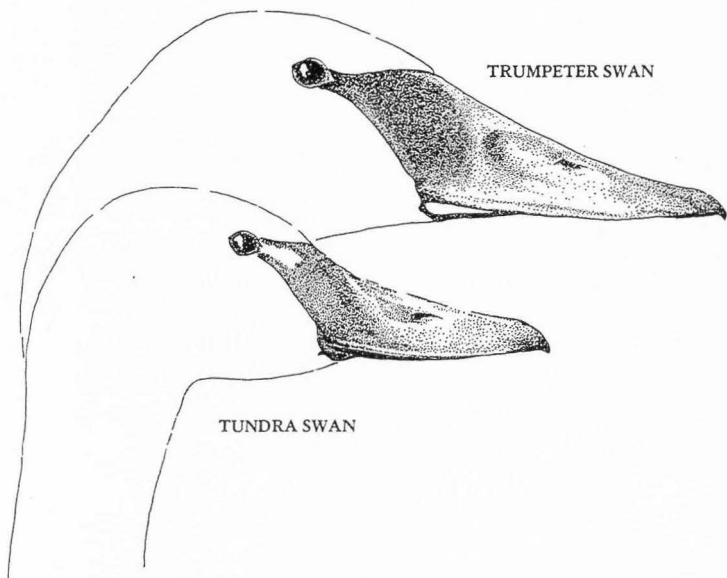


Figure 10. Head profiles of a Tundra and a Trumpeter swan showing relative differences in bill sizes (Trumpeter Swan Society identification flyer).

southern habitats, and are thus threatened with a catastrophic crash during a harsh winter. In November and December 1996, Trumpeter swans were reintroduced to northern Utah by the U. S. Fish and Wildlife Service in an effort to expand their present range, providing an opportunity to study mechanisms of coexistence between Trumpeter and Tundra swans.

### Morphology

In addition to morphological measurements cited in the literature, I measured the neck length and leg length of both species. Measurements were taken on translocated Trumpeter swans and on Tundra swans killed by Utah swan hunters. Neck length was measured to estimate the maximum depth each species can forage to by stretching its neck down through the water and sediment. Swans also "tip up" to reach deeper resources; the legs and tail are the only body parts remaining above the water surface. Neck length appeared to be as long as the length between the neck and legs. Thus, the maximum reach of a swan was estimated as two times the neck length. Leg length was measured to estimate the effectiveness of paddling in stirring the soil layers. Foraging swans as well as other waterfowl species commonly stir the sediment by paddling vigorously in place for several seconds. This behavior is likely to increase the efficiency of extracting food resources (Banko 1960).

### Food Resources, Diets, and Metabolic Rates

Biomass of sago pondweed tubers was quantified in Unit 1, Unit 2, and Unit 4 (BRMBR) and BRC in September 1996, before swans migrated through or wintered on

the study areas. Sixty-four transects were placed in these wetlands using a two-stage systematic-random sampling design. Transects were 200 m long with one core taken every 20 m. Cores were divided into 5 cm sections that were washed through a 1 mm sieve to extract all tubers. Dry weight (100%) was determined for all tubers. Tuber abundance and distribution for every wetland was determined with geostatistical procedures (see chapter 2 for more detail).

I determined the diets of both swan species by extracting the gizzard and esophagus of 50 swans killed by hunters. I supplemented this information by observing feeding swans during the day and locating them by radiotelemetry at night. I assumed that swans feeding on submersed vegetation were feeding on sago pondweed tubers because all aboveground vegetation senesces in September and sago pondweed is the only submersed macrophyte in these wetlands that produces tubers.

Metabolic rates of Tundra and Trumpeter swans were estimated using allometric equations. Peters (1983) explained that basal metabolic rate is the power required to maintain basic body functions. Each additional activity, such as locomotion, growth, and food processing increases the basal metabolic value. I calculated the basal metabolic rate for adult swans using the standard metabolic rate (SMR) equation for homeotherms by Hemmingsen (in Peters 1983, p. 29):  $R_{s(h)} = 4.1 W^{0.751}$ , where  $R_{s(h)}$  is SMR measured in watts, and  $W$  is weight of an individual measured in kg. Kendeigh, Dol'nik, and Govrilov (in Peters 1983, p. 39) suggested that the average realized metabolic rate (ARM) for birds is 1.6 to 2 times SMR in the thermal neutral zone. I calculated ARM for both species using the calculated SMR values to obtain an estimate of Tundra and Trumpeter swan

average energetic requirements. These estimates were compared to values in the literature.

### Evaluating Foraging Efficiencies

Foraging efficiency was determined for Trumpeter and Tundra swans by estimating time spent paddling and digging to a certain sediment depth. I was not able to observe this in the field because the water was too turbid to conduct any underwater observations. I therefore simulated swan paddling by attaching two Tundra and two Trumpeter swan feet to sticks (artificial swan legs). The artificial Tundra or Trumpeter legs were then pushed through two holes in a floating piece of wood. To assure that swan leg length was correctly simulated, crosspieces were pushed through the artificial legs above the float so that the artificial legs from the feet to the crosspieces were as long as measured Tundra and Trumpeter swan legs. I assumed that swan paddling occurs in a strict up-and-down motion because swans always paddled in strictly one spot, often swaying from side to side. Thus, when alternately pushing the artificial legs down through the water and sediment, Tundra and Trumpeter swan paddling was assumed to be simulated sufficiently. Swan paddling was simulated at every transect. I recorded initial water depth (distance between water surface and water-sediment interface) and then alternately pushed each leg down five times. Water depth was recorded within the created hole. This was repeated 15 times or until water depth did not significantly change. Paddling appeared to be ineffective once a certain water depth was reached. At that point I assumed that swans dig further into the sediment with their bills. The exact digging strategy is not known. However, swans appeared to stab into the sediment with their bills. Additional strategies are likely but were

not observed. In order to simulate bill digging, I measured the area of Tundra and Trumpeter swan feet to determine the area of a hole dug by paddling in one spot. I then determined the area of Tundra and Trumpeter swan bills at the base to estimate the number of bill stabs necessary to displace an area equivalent to an area dug by paddling. Finally, I created rules that assigned a time to every bill stab. The time depended on whether a swan was able to reach the sediment without tipping up or by tipping up, assuming tipping up costs additional time. The water depth at which each species was expected to tip up was determined by the measured neck length. Finally, I assumed that digging costs increase as water depth increases because swans must reach further down and dig through increasingly compact mud (see Appendix B for entire set of rules). Thus, time per bill stab changed the further swans dug into the soil column. Both species experienced the same time changes (e.g., from 1 sec to 2 sec per bill stab) as sediment depth increased so that error by arbitrarily assigning a time per bill stab was canceled out. However, times changed more quickly for Tundra swans (e.g., time per bill stab for Tundra swans increased by one second after digging through 5 cm of sediment, whereas for Trumpeter swans time increased by one second after digging through 10 cm of sediment) because bill stabs are in general 5 cm shorter, they are assumed to be not as strong as Trumpeter swans due to body size, and they need to tip up earlier than Trumpeter swans because of their shorter neck length. In fact, when observing Trumpeter and Tundra swans feeding side by side, Trumpeter swans tipped up approximately 10% of their total foraging efforts, whereas Tundra swans tipped up 90% of their foraging efforts. A foraging effort is defined as a foraging activity where a swan submerses part of its neck

for at least two seconds.

Gain curves were calculated for both species at each transect to estimate the time spent digging to reach a certain tuber biomass. I assumed this represented an estimate of Tundra swan foraging efficiency relative to Trumpeter swans, assuming time spent ingesting a tuber is negligible. It was inappropriate to calculate giving-up-times and therefore giving-up-depths of Tundra and Trumpeter swans using an optimal foraging approach. As chapter 2 indicates, tuber biomass appeared to be distributed in gradients rather than in distinct patches. Thus, swan traveling time between patches should be nonexistent. This scenario predicts that both species should move constantly while foraging. However, I often observed swans foraging continuously within a 1 to 2 m diameter circle for 0.5 to 4 hours, indicating that the gain curves are approximately linear and a point of diminishing returns does not exist or is so vague that a highly variable residence time within a patch (e.g., swan foraging hole) is observed. Giving-up-times should therefore be solely determined by swan morphology, i.e., swans should give up digging when they are physically unable to dig deeper. At that point it is probably energetically more favorable to scrape at the sides of the hole for more tubers rather than to create a new hole. Thus, swans are likely to forage within one hole until completely satiated.

#### Estimating Exclusive Resources

Exclusive resources were determined by calculating the maximum sediment depth at each transect to which an adult Tundra and Trumpeter swan might forage. Tuber

biomass at depths greater than the maximum Tundra swan depth but less than the maximum Trumpeter swan depth was summed for every transect. Every 200 m transect was assumed to be representative of a 1 km<sup>2</sup> area. Thus, exclusive tuber biomass was calculated for every 1 km<sup>2</sup> area and then summed for every wetland to obtain an estimate of total exclusive resources per wetland. I calculated shared resources by subtracting exclusive tuber biomass per wetland from total tuber biomass per wetland (see chapter 2).

### Surveys

All Trumpeter swans were collared and 37 were dyed pink on the left wing and neck for easier identification from the air and ground. Thirty Trumpeter swans also received radio transmitters for easier location during the day and night. Five Tundra swans received transmitters. Ground surveys were conducted every day between November 15 and December 30, 1996 and once every 2 weeks thereafter. Aerial surveys were flown once every week during November and December and once per month thereafter.

## RESULTS

### Morphology

Body morphology measurements extracted from the literature (Limpert and Earnst 1994, Mitchell 1994) and field measurements indicate that size ratios range from 1.1 to 1.2 for linear estimates (e.g., bill length and neck length) and 1.6 for mass measurements (Table 4).



Table 4. Summary of Trumpeter and Tundra swan morphology measurements found in the literature and this study.

|  | Trumpeter | Tundra | Ratio |
|--|-----------|--------|-------|
| <b>Body mass (kg)<sup>a</sup></b>                    |           |        |       |
| adult  | 10.9      | 6.8    | 1.6   |
| juvenile   | 9.3       | 5.9    | 1.6   |
| <b>Mid toe length (mm)<sup>a</sup></b>               |           |        |       |
| adult  | 148       | 122    | 1.2   |
| juvenile   | 143       | 122    | 1.2   |
| <b>Anterior nostril to bill tip (mm)<sup>a</sup></b> |           |        |       |
| adult  | 53        | 44     | 1.2   |
| juvenile   | 53        | 43     | 1.2   |
| <b>Bill length (mm)<sup>a</sup></b>                  |           |        |       |
| adult  | 114       | 102    | 1.1   |
| juvenile   | no data   | 89     | NA    |
| <b>Total body length (cm)<sup>b</sup></b>            | 1260      | 1092   | 1.2   |
| <b>Wing span (cm)<sup>b</sup></b>                    | 189       | 160    | 1.2   |
| <b>Neck length (cm)<sup>c</sup></b>                  | 510       | 470    | 1.1   |

<sup>a</sup> Values adapted from Limpert and Earnst (1994) and Mitchell (1994).

<sup>b</sup> Values adapted from Trumpeter Swan Society pamphlet "Swan identification: Trumpeter or Tundra (Whistling)? Reported values do not distinguish between adults and juveniles.

<sup>c</sup> this study. Reported values are from adult swans only.

## Diets and Metabolic Rates

I collected 50 gizzards and esophagi from Tundra swans killed by hunters. Seven gizzards and two esophagi contained 100% sago pondweed tubers, and the rest were empty. This is a common observation when studying bird diets because birds have a high food passage rate compared to other species and exhibit high post-mortem digestion. I collected the esophagus and gizzard of one Trumpeter swan which was completely empty. Ground and aerial observations indicated that both species exclusively fed in the sediments of submerged wetlands, which, in November and December, only provide sago pondweed tubers as a food resource for swans. Thus, both species most likely fed exclusively on sago pondweed tubers.

The standard metabolic rates are 17.2024 watts (356.71 kcal/day) for a 6.75 kg adult Tundra swan and 24.5861 watts (509.82 kcal/day) for a 10.86 kg Trumpeter swan. McKelvey (1985) in Mitchell (1994) suggested that a 10 kg Trumpeter swan at 0°C has a metabolic rate of 572 kcal/day. Basal metabolic rate estimates for Tundra swans could not be found in the literature. Average realized metabolic rate ranged from 571 to 713 kcal/day for a Tundra swan and 816 to 1020 kcal/day for a Trumpeter swan. Assuming sago pondweed tubers contain 2.8 kcal/g (Squires 1991), a Tundra swan requires 203 to 255 g tubers per day, whereas a Trumpeter swan requires approximately 291 to 364 g tubers per day. Beekman et al. (1991) suggested that Bewick's swans (*Cygnus columbianus bewickii*) require approximately 283 g tubers per day during staging in the Netherlands. This estimate is close to my 255 g per day estimate for Tundra swans when multiplying the calculated standard metabolic rate by two. I could not find

any similar measurements in the literature for Trumpeter swans.

#### Foraging Efficiencies and Gain Curves

Figure 11 suggests that at shallow water and sediment depths, Tundra swans may be more efficient in stirring the sediments through paddling than Trumpeter swans. However, Trumpeter swans, due to their longer legs, are able to create deeper holes within the sediment through paddling. Thus, when paddling, Tundra swans are efficient at shallower depths and Trumpeter swans are efficient at deeper depths. The rules created for bill digging assumed Trumpeter swans were stronger due to a larger body size, longer necks, and longer bills. Thus, Trumpeter swans in this simulation were always more efficient in digging with their bills than Tundra swans.

Figure 12 provides examples of typical gain curves. Efficiencies of foraging are approximately equal for Tundra and Trumpeter swans at shallower depths (i.e., shorter foraging times). However, as depth increases, the gain curves for the two species tend to drift apart with the Trumpeter swan becoming increasingly more efficient in extracting tubers than the Tundra swan. Gain curves are approximately linear. In fact, a point of diminishing returns may only be identified at depths where tubers are absent.

#### Exclusive Resources

BRC appeared to be the only wetland potentially providing exclusive tuber resources to Trumpeter swans (Table 5), accounting for 8% of total tuber biomass in BRC or 4% of total biomass in all four wetlands. Water depth at BRC was the highest of all four wetlands (610 mm maximum depth). Maximum tuber depth was also the greatest in

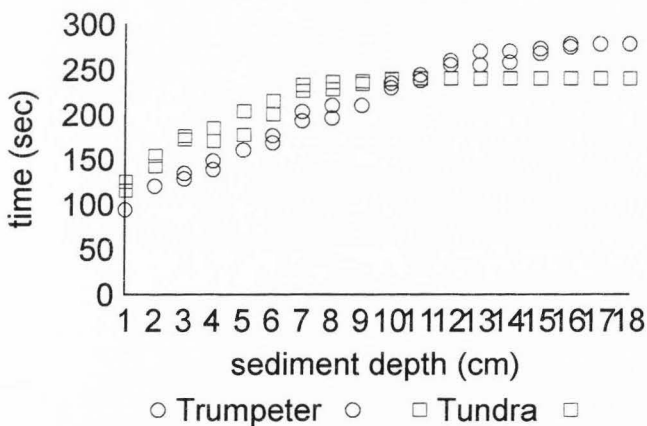
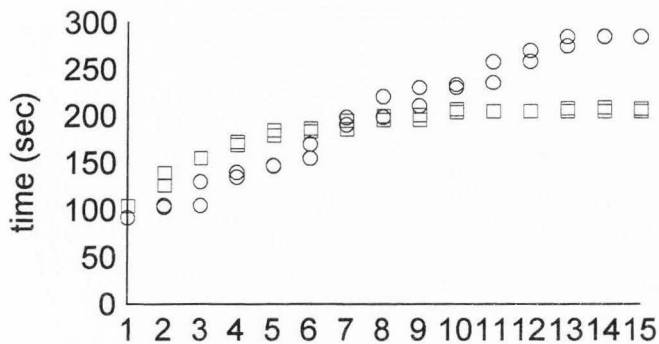


Figure 11. Examples of differing paddling efficiencies between Tundra and Trumpeter swans.

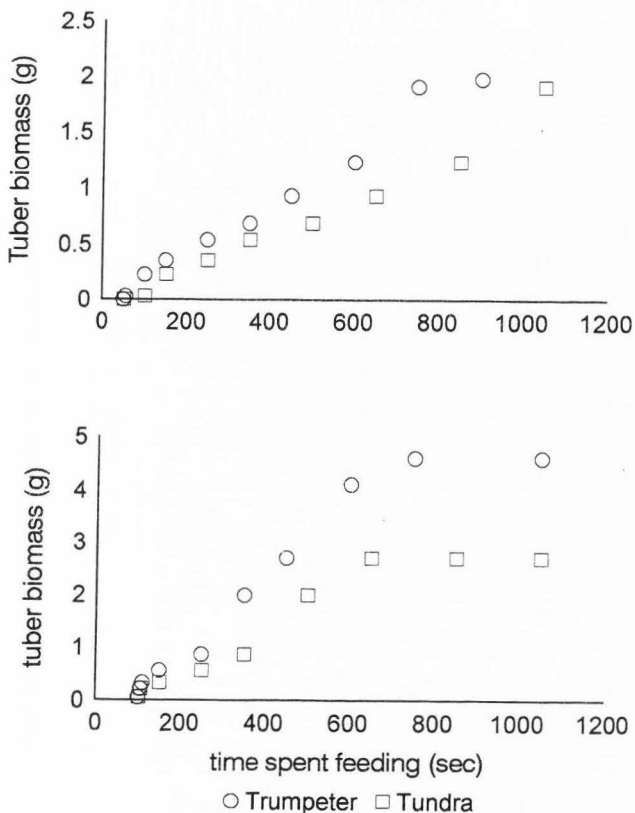


Figure 12. Examples of gain curves showing the different overall foraging efficiencies between Tundra and Trumpeter swans, assuming swans do not scrape at the sides of foraging holes created by paddling. If swans increase the size of a foraging hole by digging at the sides, the gain curves shown here should increase further and may never level out.

Table 5. Summary of exclusive and shared sago pondweed tuber biomass and the number of Tundra and Trumpeter swan days the resources can potentially support and actually support. All biomass is recorded as 100% dry matter.

| Site   | Area (m <sup>2</sup> ) | Total kg | Exclusive kg | Shared kg | Potential Trumpeter swan-days on exclusive resources <sup>a</sup> | Potential Tundra swan-days on shared resources <sup>b</sup> | Actual # Tundra swan-days | Actual # Trumpeter swan-days |
|--------|------------------------|----------|--------------|-----------|---|---|---------------------------|------------------------------|
| Unit 1 | 12,985,309             | 64,611   | 0            | 64,611    | 0   | 190,032   | 90,234                    | 0                            |
| Unit 2 | 15,491,246             | 571,151  | 0            | 571,151   | 0   | 1,679,856   | 418,183                   | 0                            |
| Unit 4 | 8,909,258              | 243,048  | 0            | 243,048   | 0   | 714,847   | 126,672                   | 0                            |
| BRC    | 23,318,746             | 971,888  | 80,119       | 891,769   | 165,080   | 2,622,850   | 820,605                   | 600                          |

<sup>a</sup> assuming each Trumpeter swan requires 364 g tubers/day (twice basal metabolic rate) and assuming 25% of tuber biomass is lost to decomposition.

<sup>b</sup> assuming each Tundra swan require 255 g tubers/day (twice basal metabolic rate) and assuming 25% of tuber biomass is lost to decomposition.

this wetland with tubers found up to 45 cm deep in some transects. Deep water and tuber depths were found in four transects on BRC, which were all located adjacent to each other in the middle of the wetland.

### Surveys

Trumpeter swans fed almost exclusively in the middle of BRC. Three swans were observed feeding in Unit 2 for a short time while the majority of wetland area was covered with ice. Trumpeter swans were observed resting in Unit 1. They were never located in Unit 4. Tundra swans fed in all four wetlands. In November, they appeared to feed preferentially in some areas of the wetland (e.g., middle of Unit 2), whereas in December and March they seemed to be distributed evenly over all wetlands.

## DISCUSSION

Gause's (1934) principle of competitive exclusion suggested that species need to partition limited resources to coexist. Resource partitioning and niche complementarity have indeed been found in a variety of systems. These studies usually claim that they have found evidence for competition and therefore a mechanism for species coexistence. I argue that species often partition resources in subtler ways than suspected, such that it may be more fruitful to study systems where similar species are able to coexist despite the principle of competitive exclusion (see also Brown 1995). Here, I present an example of two similar species, Tundra and Trumpeter swans, that often stage and winter sympatrically. Assuming resources are sometimes limiting during staging and wintering, I

decided to study potential mechanisms of swan coexistence. The Utah Trumpeter swan translocation program provided the opportunity to observe the two species while feeding exclusively on sago pondweed tubers. Sago pondweed tubers may not have been limiting in northern Utah in winter 1996/1997 (see chapter 2) except when the majority of the wetlands iced-up. I suggest that Trumpeter and Tundra swans can coexist because their slightly different body sizes allow them to utilize the same resources (e.g., sago pondweed tubers) in slightly different ways. This swan example is unique in two different ways. First, it suggests that a large body size may provide a support structure for longer appendages such as a longer neck and longer legs. Longer appendages in turn may enable the larger species to gain access to exclusive resources and may allow the larger species to extract resources more efficiently. Second, the example shows that body size similarities do not sufficiently predict whether two species can coexist. Rather, resource use by two similar species needs to be studied to fully understand mechanisms of coexistence.

Species that vary in body size often appear to differ in swallowing capacity, i.e., the gape size of different species determines the upper limit on food item size that can be consumed. Optimal foraging theory predicts that gape-size limited species should partition resources along a food size gradient because it is most efficient for species to exploit the largest item sizes and ignore smaller item sizes. This argument assumes that all species in the community have prior knowledge of the food resource. If this assumption is met, gape-size limitation may structure communities because interspecific competition forces species to narrow their fundamental niches into realized niches that only include food item sizes that are efficiently exploited. Tundra and Trumpeter swans are not gape size limited



because the length of sago pondweed tubers retrieved from Tundra swans gizzards were as long as the longest tubers extracted from the soil cores (13 mm). Because Tundra swans do not appear to be gape size limited, I inferred that Trumpeter swans are also not limited by gape size. Even though gape size does not seem to influence resource partitioning in swans, differences in swan body size may still play a role in resource utilization and therefore coexistence between the two species. The larger body size of Trumpeter swans appears to support a longer neck length which enables the species to extract tubers to a greater sediment depth than Tundra swans. Thus, Trumpeter swans benefit from a larger body size by gaining access to exclusive resources. This idea has also been documented by Darwin (1871, in Simmons and Scheepers 1996), who suggested that giraffes evolved long necks to outreach competitors when leaves are scarce. The swan/giraffe scenario is different from the gape-size limitation scenario because it does not lead to resource partitioning. Rather, Trumpeter swans (giraffes) forage most efficiently by ingesting tubers at all sediment depths (tree heights) while gaining access to exclusive resources. Thus, Tundra swans share all tuber resources with Trumpeter swans, i.e., Tundra swans are included within the niche of Trumpeter swans. Limiting similarity models assume that species partition resources along a continuous resource gradient. Because the included niche scenario violates this assumption, swans may actually be more or less similar in body size than predicted by limiting similarity body size ratios such as the Hutchinsonian ratio.

My results indicate that Tundra and Trumpeter swans are equally efficient in extracting resources from shallow sediment depths. Even though Tundra swans are more

efficient in paddling, Trumpeter swans may compensate with their greater bill digging efficiency. Additionally, shallow sediments are usually soft enough that larger body size does not produce a detectable advantage in extracting tubers, regardless of differences in paddling efficiency. Trumpeter swans, however, are more efficient in depleting tubers at greater sediment depths. This greater efficiency is a direct consequence of the Trumpeter swan's larger body size: This species has a longer bill (bill size ratio = 1.2) and therefore may be able to stab through more soil layers and search more efficiently for tubers than Tundra swans. Also, Trumpeter swans are probably able to displace more sediment per unit time than Tundra swans due to their longer and most likely stronger neck and bill. Judging from the gain curves, Trumpeter swans should be the overall superior competitors for sago pondweed tubers. Tundra swans, in fact, never are more efficient in extracting the resources. Additionally, even though Trumpeter swans enjoy exclusive resources and select areas that provide exclusive resources, they also appear to have a greater per-capita effect on the shared resources. This is evidenced by the gain curves and the higher metabolic rates of Trumpeter swans.

The above discussion suggests that Trumpeter swans are superior competitors for sago pondweed tubers; they enjoy exclusive resources, and they appear to exploit tubers more efficiently. So how can Tundra and Trumpeter swans coexist on staging and wintering grounds? Several scenarios are possible. First, Tundra swans, due to their lower body mass, enjoy lower traveling costs and are therefore able to find high tuber biomass patches more efficiently. Thus, a trade-off between higher foraging efficiency and higher traveling efficiency may be a likely mechanism of coexistence (Brown 1989). Second,

Tundra and Trumpeter swans may be able to coexist because sago pondweed tubers are not limiting during staging and wintering. In fact, chapter 2 suggested that tubers were not limiting in 1996 except during short periods of ice-up. Tubers are limiting when the majority of the wetlands ice up and only few pockets of open water remain. When this occurred in 1996, I observed both species feeding side by side within the open water pockets, with Trumpeter swans easily displacing Tundra swans from their foraging holes. Even if tuber resources become scarce during staging, individual swans may immediately move on to better habitats such that resource limitation is never experienced. In fact, in most winters, the majority of Tundra swans migrate further south when Utah wetlands ice up. The winter was mild in 1996, and 10,000 Tundra swans wintered in northern Utah. Third, Tundra and Trumpeter swans breed allopatrically in Alaska (Conant et al. 1991, but see Wilk 1993). Thus, the two species may coexist during staging and wintering because they separate on a different resource dimension, i.e., breeding habitat.

The goal of this study was not to prove or disprove that competition between Tundra and Trumpeter swans drives community structure. I also did not intend to criticize past and present approaches taken to explain community structure. However, I do suggest, using the Tundra-Trumpeter swan system as an example, that community ecology is due for a paradigm shift. Instead of calculating and proving limiting similarities which assume that similar species inherently compete for resources and therefore cannot coexist, community ecologists should focus more on patterns of resource use among similar species. Additionally, ecologists should study why species can coexist instead of why they cannot. Taking this approach might help community ecologists in finding mechanisms for

coexistence that are not apparent by merely studying body size differences between species.

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## CHAPTER 4

### CONCLUSIONS

Kleiman et al. (1994) proposed that translocation programs need to evaluate thirteen criteria (Table 6) so that researchers and managers can understand whether a species introduction furthers population or species persistence, whether the translocation is a waste of time and money, or whether the translocation actually hinders species persistence. Unfortunately, translocation criteria are rarely evaluated (Kleiman et al. 1994) because it is often impossible to determine the success or failure of a translocation. All translocation criteria were evaluated after releasing fifty-seven Trumpeter swans in northern Utah in 1996 to understand whether this translocation effort has the potential of being successful in future years (Table 6). Unfortunately, not all criteria were sufficiently evaluated because support from governmental and non-governmental organizations did not permit more than one field season for the project.

#### EVALUATION OF CRITERIA

##### Criterion 1: Augmentation Is Necessary

The Rocky Mountain Trumpeter Swan Population (RMTSP) is not threatened with extinction, so augmentation of the population is of secondary importance. However, the persistence of the Rocky Mountain Trumpeter Swan Population (RMP) is threatened because the population does not migrate to southern wintering grounds. Rather, the majority of Rocky Mountain Trumpeter swans winter on a small area at the borders of



Table 6. Evaluation of the reintroduction criteria as proposed by Kleiman et al. (1994)

| Number | Criteria  | Evaluation                           |
|--------|---|--------------------------------------|
| 1      | Augmentation of the wild Trumpeter swan population is necessary                                     | No, but range expansion is necessary |
| 2      | Appropriate Trumpeter swan stock is available   | Yes                                  |
| 3      | The wild Trumpeter swan population is not jeopardized   | Yes                                  |
| 4      | Causes of Trumpeter swan decline are removed  | No                                   |
| 5      | The habitat is ecologically suitable for Trumpeter swans  | Yes                                  |
| 6      | The habitat is unsaturated with Trumpeter swans and/or other similar species like Tundra swans      | Yes                                  |
| 7      | The local human population is not negatively impacted by the re-introduction                        | Yes                                  |
| 8      | Community support exists for the reintroduction   | Yes                                  |
| 9      | Governmental and non-governmental organizations are supportive of releasing Trumpeter swans in Utah | No                                   |
| 10     | The reintroduction program complies with all laws and regulations                                   | Yes                                  |
| 11     | Reintroduction technology is known or in development  | Yes                                  |
| 12     | Sufficient information exists about Trumpeter swan biology  | Yes                                  |
| 13     | Sufficient resources exist for the reintroduction program   | Yes                                  |

Idaho, Montana, and Wyoming (“tristate area”) and are therefore vulnerable to mass starvation and a catastrophic crash of the whole population in a severe winter. This wintering behavior is not natural. It most likely developed when the population was artificially fed in the tristate area to augment a severely reduced population in 1933 (Banko 1960). Artificial feeding was stopped in 1992, but the tradition of wintering in the tristate area still has not been broken. The RMTSP can only persist if the population learns to disperse into alternative areas during the winter and if it starts establishing migratory routes to southern wintering grounds in California and Arizona. Utah seemed to be an ideal translocation area because it is likely to be a first leg on a migratory route towards the south. Thus, the Utah translocation program is attempting to enhance the long-term persistence of the species by encouraging dispersal during winter, which indirectly supports Criteria 1.

#### Criterion 2: Appropriate Stock Is Available

Wild Trumpeter swans from the RMTSP were captured at Harriman State Park, Idaho, and immediately transported to northern Utah. These swans are appropriate transplanting stock because they were transplanted within their own flyway (Rocky Mountain Flyway). Whether Trumpeter swans from the Pacific Flyway would be appropriate stock for transplanting into Utah is unclear because the extent of natural exchange between the two flyways is unknown. Also, Trumpeter swans show low levels of genetic variability compared to other wild species (Marsolais and White 1997), which means Trumpeter swans from different flyways should not vary much genetically. On the

other hand, some differences in genetic variability were found between Trumpeter swan populations and subpopulations (Marsolais and White 1997). The results of Marsolais and White (1997), however, were inconclusive because they either suggest that populations are different genetically and should be managed accordingly, or that observed genetic differences reflect the natural genetic variability within the entire species. The Pacific and the Rocky Mountain Populations of Trumpeter swans may actually be one population, separated into two arbitrary populations by political boundaries. In fact, in an Environmental Assessment (Bartonek et al. 1995, p. 9), the United States Fish and Wildlife Service suggested that "Trumpeter swans are segregated for management purposes, not biological differences, into three different populations": the Rocky Mountain Population, the Pacific Population and the Interior Population. If this is indeed the case, Trumpeter swans may be taken out of the Pacific population to be transplanted into Utah.

### Criterion 3: The Wild Population Is Not Jeopardized

Whether the wild population of Rocky Mountain Trumpeter swans would be jeopardized by removing individuals from the tristate area for transplantation is debatable. The population wintering in the tristate area has steadily increased from 1,700 individuals in 1989 to 2,212 individuals in 1997 (Subcommittee on Rocky Mountain Trumpeter Swans 1997; Table 7). These swans winter on approximately 16 traditional sites and several expansion sites (Table 7). Management efforts, in the form of Trumpeter swan hazing and capturing for subsequent translocation, have focused mainly on Harriman State Park (HSP), one of the traditional wintering sites. In 1997, approximately 200 wintering

Table 7. Distribution of Rocky Mountain Trumpeter swans in February at tri-state region sites from 1989 to 1997. Data were obtained from United States Fish and Wildlife Service's Midwinter Rocky Mountain Population Trumpeter Swan Survey (Subcommittee on Rocky Mountain Trumpeter Swans 1997).

| Location           | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 |
|--------------------|------|------|------|------|------|------|------|------|------|
| <u>Montana</u>     |      |      |      |      |      |      |      |      |      |
| Red Rock Lakes NWR | 301  | 307  | 322  | 398  | 0    | 51   | 43   | 102  | 22   |
| Hebgen Lake        | 87   | 20   | 91   | 83   | 79   | 93   | 81   | 150  | 137  |
| Madison River      | 44   | 30   | 41   | 67   | 155  | 102  | 67   | 116  | 75   |
| <u>Wyoming</u>     |      |      |      |      |      |      |      |      |      |
| Yellowstone NP     | 117  | 110  | 75   | 112  | 217  | 161  | 182  | 154  | 77   |
| Jackson Hole       | 214  | 196  | 221  | 203  | 277  | 258  | 317  | 327  | 373  |
| Salt River         | 20   | 18   | 37   | 29   | 60   | 41   | 79   | 79   | 60   |
| Green River        | 0    | 0    | 14   | 2    | 20   | 21   | 13   | 20   | 15   |

Table 7. (continued)

| Idaho                                   |      |      |      |      |      |      |      |      |      |
|---|------|------|------|------|------|------|------|------|------|
| Harriman SP                             | 389  | 723  | 330  | 215  | 199  | 435  | 505  | 464  | 202  |
| Sheridan Reservoir                      | 49   | 31   | 47   | 16   | 8    | 67   | 18   | 36   | 21   |
| Island Park Reservoir                   | 22   | 47   | 44   | 0    | 0    | 28   | 0    | 24   | 65   |
| Henry's Fork River<br>(above reservoir) | 76   | 66   | 30   | 66   | 167  | 72   | 61   | 113  | 167  |
| Buffalo River                           | 96   | 30   | 13   | 11   | 65   | 22   | 18   | 12   | 18   |
| Henry's Fork                            | 118  | 142  | 168  | 309  | 362  | 206  | 344  | 354  | 329  |
| Teton Basin                             | 79   | 210  | 141  | 168  | 108  | 368  | 209  | 365  | 334  |
| Teton River                             | 77   | 60   | 72   | 60   | 148  | 212  | 271  | 135  | 152  |
| South Fork Snake River                  | 38   | 10   | 70   | 84   | 83   | 93   | 194  | 127  | 176  |
| Fort Hall                               | 8    | 4    | 78   | 128  | 85   | 37   | 117  | 63   | 223  |
| Soda Springs                            | 0    | 0    | 0    | 0    | 3    | 1    | 1    | 14   | 26   |
| Total core tristate area <sup>a</sup>   | 1713 | 1984 | 1665 | 1812 | 1868 | 2168 | 2390 | 2479 | 2212 |
| Total RMP <sup>b</sup>                  | 1797 | 2049 | 1995 | 2203 | 2235 | 2526 | 2803 | 2936 | 2699 |

Table 7. (continued)

<sup>a</sup> includes Trumpeter swans counted in areas not presented in table because data for these areas was incomplete or numbers counted were very low.

<sup>b</sup> includes expansion sites (e.g., Nevada, Oregon, and Utah) not previously mentioned.

Trumpeter swans were counted on HSP, versus 400-500 swans in the previous 3 years (Table 7). Due to the low number of Trumpeter swans on HSP in 1997, Idaho and Wyoming state agencies discontinued supporting the Utah translocation program, even though the total number of individuals wintering in the tristate area remained stable compared to previous years (see criterion 9 for further discussion). Some managers suggested that long-term hazing of Trumpeter swans encouraged Rocky Mountain Trumpeter swans traditionally wintering on HSP to disperse into alternative areas in 1997 (Subcommittee on Rocky Mountain Trumpeter Swans 1997). If this is the case, one should observe a steady decline in numbers on HSP from the time hazing was started in 1990 until the present. However, the trend appears to be random such that hazing can be ruled out. Unusual environmental conditions, i.e., unusually high water levels, may have created unsuitable wintering habitat for Trumpeter swans at HSP. If unsuitable habitat is the cause for a low number of wintering swans on HSP, Trumpeter swans should be able to disperse on their own when conditions are unsuitable such that hazing may not be necessary. Analysis of Table 7 suggests that the individuals missing from HSP in 1997 dispersed to other parts of the tristate area. Thus, the RMTSP still needs to learn to disperse into areas outside the tristate area and preferably establish a migratory route. This is best done by scientifically monitored translocations. Even though the number of Trumpeter swans wintering on HSP was low in 1997, the total number of Trumpeter swans wintering in the tristate area appeared to remain stable. Thus, the wild population would not be jeopardized by removing swans for translocation to Utah.

#### Criterion 4: Causes of Decline Are Removed

Trumpeter swans almost went extinct in the early 1900's due to excessive hunting for their valued skins (Banko 1960). Only individuals in inaccessible areas, e.g., parts of the tristate region, survived. Others recently speculated that the RMTSP does not migrate further south than the tristate area because all Trumpeter swans migrating through Utah are mistakingly killed by Tundra swan hunters. This inherently assumes that Trumpeter swans are more vulnerable to hunting than Tundra swans and suggests that the Utah Tundra swan hunt should be closed. However, swan bill measurement data collected by federal and state agencies in Utah over the last 5 years (United States Fish and Wildlife Service, Utah Division of Wildlife Resources unpub. data) indicate that Trumpeter swans are rarely killed: In 1994, zero Trumpeters were killed out of 464 examined swans; in 1995, three Trumpeters were killed out of 244 examined swans, and in 1996, one Trumpeter swan was killed out of 701 swans examined. Swan survey data from the ground and air also suggest that Trumpeter swans currently do not migrate through Utah in large numbers. Thus, hunting is not likely to be the cause for the lack of a migratory route towards the south.

I addressed the vulnerability issue by releasing 20 Trumpeter swans during the Tundra swan hunting season in November. Nine out of these 20 swans were killed directly (harvested) or indirectly (crippled or wounded) by hunters, whereas about 897 out of at least 30,000 Tundra swans were killed during the same period. Translocated animals generally are more mobile and may frequent unusual habitats after the release because translocated species are disoriented and do not have prior knowledge of the translocation



site. Thus, the high Trumpeter swan mortality may be due to a higher vulnerability of Trumpeter swans to hunting but may also be due to the translocation itself. Unfortunately, the project was discontinued after one field season so that the vulnerability issue is unresolved.

Hunting may also indirectly threaten the persistence of the Trumpeter swan population because Trumpeter swans may be more vulnerable to lead poisoning. Even though hunting with lead has been illegal since 1980, lead pellets are still present in wetland sediments. This lead, mostly found in deeper sediment, may be ingested by swans. In fact, one out of 10 Trumpeter swans that wintered in Utah in 1996/1997 died from lead poisoning (National Wildlife Health Center unpub. data). Two other Trumpeter swans died of unknown causes. These, too, may have died of lead poisoning. Other cases of lead poisoning in Trumpeter swans have also been documented (Blus et al. 1989)

Banko (1960) mentions hunting as a possible decline of Trumpeter swans in the early 1900's. At the same time wetlands were increasingly lost to agriculture, changes in hydrology, human housing, and industry. Trumpeter swans may not be able to fly from one suitable wetland to the next on a migration to the south because suitable wetlands may now be too far apart. Tundra swans, on the other hand, are smaller and lighter so flying is energetically less expensive for them. Thus, they may be able to fly longer distances than Trumpeter swans. This may be why Tundra swans are able to fly to the Central Valley of California to winter whereas Trumpeter swans may not be able to make the jump across the Great Basin. This also may be why Tundra swans are thriving whereas the persistence of the RMTSP is still questionable. One can speculate forever on the factors threatening

Trumpeter swan persistence. However, the factors threatening Trumpeter swan long-term persistence need to be scientifically identified so that the RMTSP can be managed accordingly and effectively.

#### Criterion 5: The Habitat Is Ecologically Suitable

Before 1900, Trumpeter swans were abundant across the North American continent (Mitchell 1994). Thus, Utah should lie well within the Trumpeter swan range. Additionally, Tundra swans feed extensively at the BRMBR and BRC during fall and spring migrations. Tundra swans are similar to Trumpeter swans, thus, northern Utah should be ecologically suitable to Trumpeter swans as well. To ensure that BRMBR and BRC provide adequate food resources for Trumpeter swans, sago pondweed tuber biomass was quantified (chapter 2). Trumpeter swans should feed exclusively on these tubers because sago pondweed tubers are the only food resource available during the winter and swans appear to prefer the tubers when available (Mitchell 1994). The results of chapter 2 suggest as many as 6.5 million swan-days could potentially be supported by the tuber resource (1.8 million kg) in winter 1996/1997. Approximately 1.5 million swan days (0.5 million kg) were used during winter 1996/1997. Thus, the food resources at BRMBR and BRC should be sufficient to support the translocated Trumpeter swans.

#### Criterion 6: The Habitat Is Not Saturated with Competitors

Even though food resources appear to be abundant at the translocation sites, competition with Tundra swans may eventually prohibit Trumpeter swans from obtaining

enough food resources for survival and reproduction. This is not the case at this time because Tundra swan numbers appear to be below carrying capacity, and 165,000 Trumpeter swan-days could potentially be supported by exclusive resources alone (Table 5). Exclusive resources are tubers unavailable to Tundra swans because they are buried too deep in the sediment for Tundra swans to reach, but available to Trumpeter swans due to their longer necks and bodies.

Chapter 3 suggests that Trumpeter swans may be more efficient in extracting tubers from the sediment. Thus, Tundra swans are unlikely to outcompete Trumpeter swans for resources. Additionally, Trumpeter swans are more aggressive foragers and will actively displace foraging Tundra swans from established foraging holes. In fact, out of 26 interactions between species (categorized as bites, chases, neck threats, and passive displacements, and hisses), only one Tundra swan threatened a Trumpeter swan with a hiss, after which the Trumpeter swan retreated. All other encounters were initiated and successfully completed by Trumpeter swans. Bites were the most frequent interaction (16), followed by passive displacement (7), neck threats (2), and hissing (1). Thus, Trumpeter swans are likely to be competitively superior. Does this mean that the introduction of Trumpeter swans may potentially threaten Tundra swan persistence? At this time Trumpeter swan numbers are too low to be a threat to Tundra swans. Even if Trumpeter swans were more abundant in Utah, Tundra swans are more efficient in traveling between patches of high tuber biomass due to lower traveling costs. The trade-off between foraging efficiency and traveling efficiency as a mechanism for coexistence has been suggested by Brown (1989). Finally, the two species may coexist because tuber

resources may rarely be limited in staging habitats. As resources become limited, foragers move on to the next staging ground.

#### Criterion 7: The Local Community Is Not Impacted

Before Trumpeter swans were released in Utah in 1996, state and federal agencies debated whether the Utah Tundra swan hunt should be continued. Tundra and Trumpeter swans are so similar in appearance that swan hunters generally cannot distinguish between the two species. Thus, some of the translocated Trumpeter swans were predicted to be killed by Tundra swan hunters. However, local Tundra swan hunters would have been negatively impacted by discontinuing the Tundra swan hunt because Tundra swan hunting has been an established tradition for many hunters since 1962. The State of Utah therefore compromised by shortening the Tundra swan season to the end of November instead of the end of December on the basis that Trumpeter swans are likely to migrate through Utah later (i.e., in December) than Tundra swans. BRMBR also imposed a 10-shell limit on all swan hunters to encourage hunters to shoot wisely instead of blindly. Finally, the State of Utah established a Trumpeter swan quota, which legalized the harvesting of 15 Trumpeter swans before the Tundra swan hunt would be discontinued. This quota was intended to encourage hunters to report accidentally shot Trumpeter swans.

#### Criterion 8: Community Support Exists

Community support exists for the translocation program. The local print media (e.g., Deseret News and Standard-Examiner) generally acknowledged that the

introduction of Trumpeter swans to Utah would enrich the community by adding a species to the area. A new species would provide bird watchers with a new bird species to watch and perhaps provide waterfowl hunters with a new species to hunt in the future.

#### Criterion 9: Governmental and Nongovernmental Support Exists

Governmental and nongovernmental support ceased after the first of four years. However, Griffith et al. (1989) surveyed intentional releases of native birds and mammals to the wild between 1973 and 1986 and concluded that translocations were more likely to be successful if multiple releases were carried out over several years. The goal of the Utah Trumpeter swan introduction program was to establish a dispersal/migratory tradition. This goal will probably not be met because a tradition is unlikely to be established after only one release. Thus, the overall success of the Utah reintroduction program probably failed (none of the Utah released Trumpeter swans have yet returned in 1997), even though the 1996 Trumpeter swan release into northern Utah marshes was a success.

Why support ceased after the first year of a 4-year reintroduction program is unclear. Nongovernmental groups (e.g., The Trumpeter Swan Society) were concerned that nine Trumpeter swans were accidentally killed or wounded by Tundra swan hunters even though a high mortality rate was expected and was probably not jeopardizing the entire Trumpeter swan population. Apparently, nongovernmental groups are more concerned about the fate of individuals rather than the fate of the entire population, which needs to learn to disperse and migrate. Swan hunting is a major concern of the State of Utah, and needs to be addressed by scientifically determining whether hunting is indeed

the problem or whether one should focus on other factors threatening Trumpeter swan persistence (i.e., criterion 4).

Governmental agencies (Idaho and Wyoming Fish and Game) were concerned about removing Trumpeter swans from the tristate area because low numbers of wintering Trumpeter swans were counted on Harriman State Park (HSP) in the winter of 1996/97 compared to previous years. Interestingly, the entire population wintering in the tristate area remained relatively stable such that a small population size was not of concern. Rather, agencies were concerned that the Utah translocation effort would remove year-round residents from HSP. Interestingly, the resident population appears to be inbred, judging from abnormally colored feet of some individuals and genetics work performed on the population (Marsolais and White 1997). Wyoming Fish and Game was especially concerned that Trumpeter swans breeding in Yellowstone National Park would accidentally be removed; however, Wyoming insisted that these swans should not be marked to distinguish them from other Trumpeter swans because that would decrease the aesthetic value of the swans (Wyoming Fish and Game 1997). Furthering a nonmigratory tradition is contrary to widely accepted goals for this species. Furthermore, establishing breeding pairs in areas that are traditional staging grounds and that may not be suitable as breeding grounds is also dubious. In fact, in a position paper (Wyoming Fish and Game 1997, p. 1), managers stated that "competition for food resources in limited winter and spring habitats impacts body condition and reproductive potential of resident swans. Ultimately, competition with migratory swans may displace and eliminate the resident breeding population."

Criterion 10: Laws and Regulations Are  
Abided By

All federal and state laws and regulations were abided by.

Criterion 11: Reintroduction Technology Is  
Known or in Development

Trumpeter swans were captured by airboat at night when environmental conditions were unfavorable for swan flight. This method has proven best for capturing Trumpeter swans in the tristate area. Trumpeter swans were transported in crates to northern Utah where they were immediately hard- or soft-released. Hard-release releases translocated animals immediately at the translocation site, whereas soft-release releases the animals into enclosures at the translocation site for a period of time to allow acclimatization to the new environment. Translocated Trumpeter swans have generally been hard-released. I decided to soft-release some swans to determine whether soft-released swans stay at the translocation site longer after the release into the wild than hard-released swans. No significant difference was found between the two release methods.

Criterion 12: Information About Species  
Biology Exists

General information about Trumpeter swan biology exists and has been summarized by Mitchell (1994). Unfortunately, most information about swan biology exists in grey literature and is therefore hard to find.

Criterion 13: Sufficient Resources Exist

Sufficient resources existed for one year. The funding was cut after the first year

because governmental support for the translocation ceased.

### MANAGEMENT CONSIDERATIONS

The State of Utah decided in 1997 that no more Trumpeter swans would be translocated to Utah until the year 2000 (Subcommittee on Rocky Mountain Trumpeter Swans 1997). This decision was made to allow adequate time to resolve political conflicts. However, Trumpeter swans may be translocated to Utah after 2000 such that it would be fruitful to make several management recommendations at this time.

1. The overall goal of any translocation program is to enhance the long-term persistence of the population. Long-term persistence of the RMTSP may be obtained by increasing the breeding population in the tristate area, by encouraging dispersal during the winter and/or by establishing a migratory route. Presently, Idaho is most interested in encouraging dispersal, Utah wants to establish a migratory route, and Wyoming is interested in increasing the local breeding population. Translocations to Utah should not be attempted until all states involved with the RMTSP are ready to adopt a common objective, or are ready to work with and not against each other's objectives.

2. A research program needs to be established to determine whether the RMTSP is genetically distinct from the Pacific Population. This needs to be done to determine appropriate transplanting stock, and whether transplantation programs are even necessary.

3. Environmental factors contributing to low Trumpeter swan use of Harriman State Park need to be determined. This means establishing a rigorous monitoring program, possibly by aircraft and satellite telemetry, to understand dispersal patterns. In addition,



the quality of wintering habitats needs to be determined rigorously. This includes studying abiotic and biotic factors that cause habitat quality to decrease and increase, as well as studying the effects of habitat quality on Trumpeter swan survivorship and population growth.

4. Trumpeter swan vulnerability to hunting needs to be scientifically determined.

This means monitoring the mortality of a sample of Tundra swans and a sample of Trumpeter swans during hunting seasons in Utah, Nevada, and Montana for at least 3 years. In addition, the habitat selection and foraging behavior of the two species needs to be observed to understand why vulnerability might be different between the two species.

5. Nongovernmental and governmental support for the duration of the entire translocation program needs to be secured. This means addressing concerns of all parties involved before the translocation commences.

6. All decisions regarding the RMTSP need to be ecologically sound, i.e., the long-term persistence of the population needs to be emphasized as a goal for enhancing Trumpeter swan long-term persistence; the focus on individual Trumpeter swans, e.g., local breeding flocks, needs to be deemphasized.

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## APPENDICES

## Appendix A. Variograms of Units 1, 2, and 4, and BRC in March and September.

Sediment cores are separated into 5cm sections.

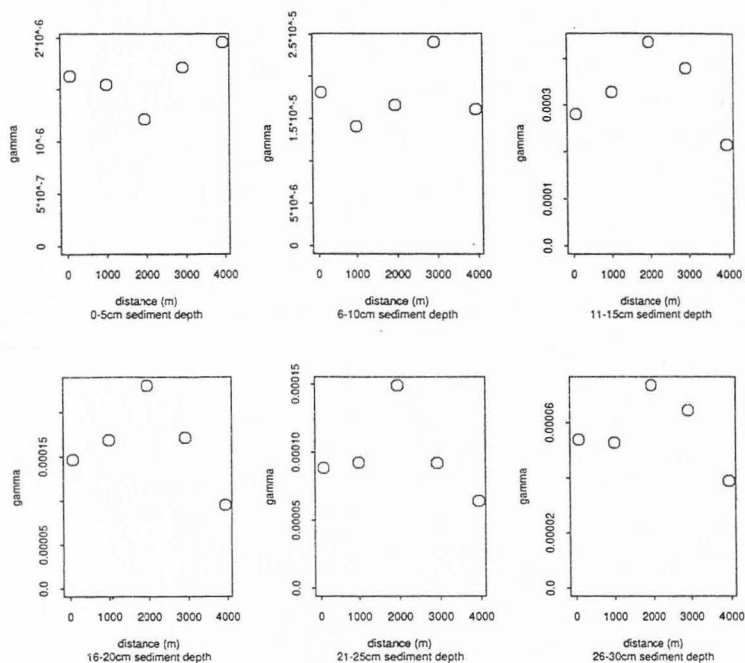


Figure A.1. Variograms of Unit 1 tuber biomass September data separated by sediment sections.

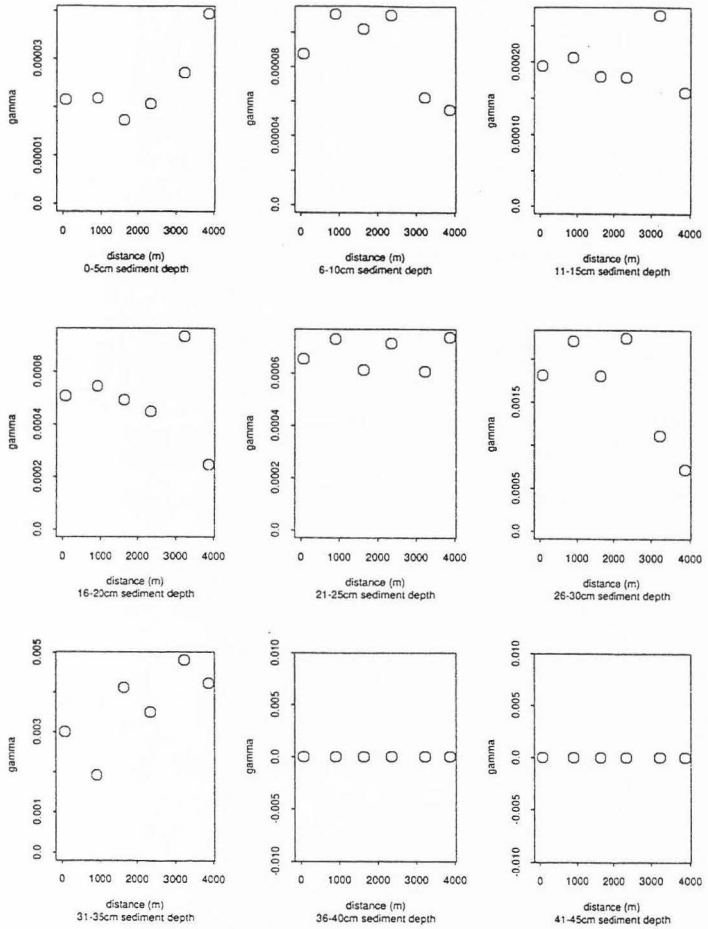


Figure A.2. Variograms of Unit 2 tuber biomass September data separated by sediment sections.

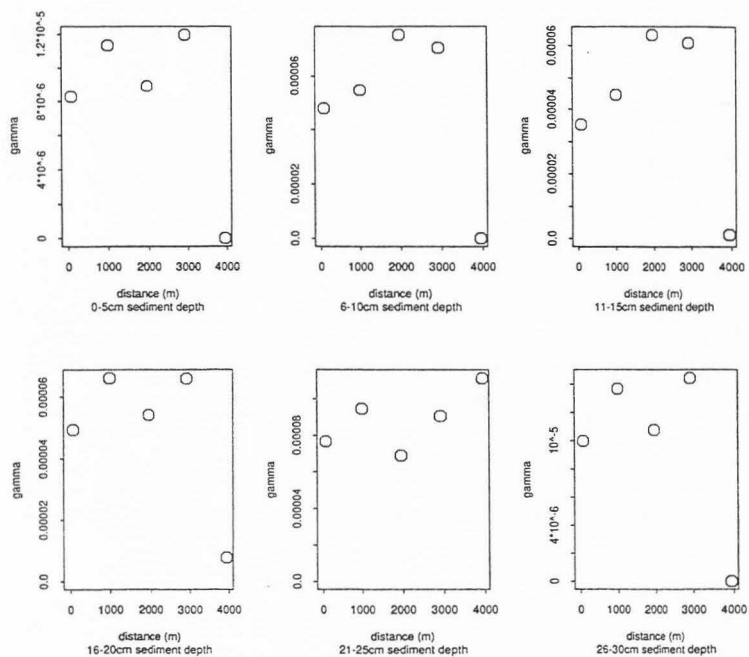


Figure A.3. Variograms of Unit 4 tuber biomass September data separated by sediment sections.

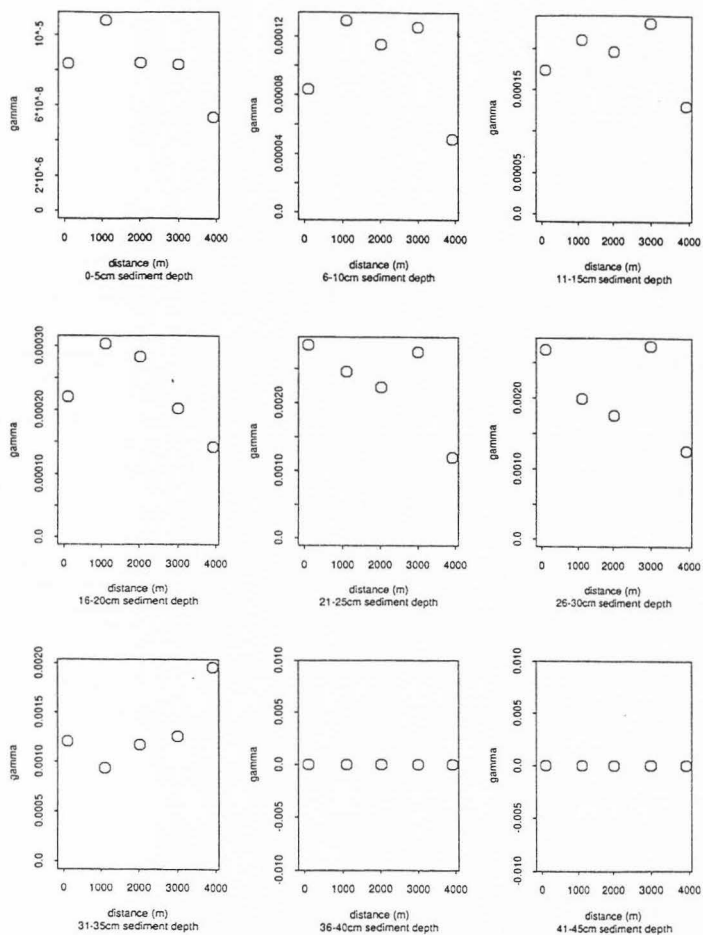


Figure A.4. Variograms of Bear River Club tuber biomass September data separated by sediment sections.

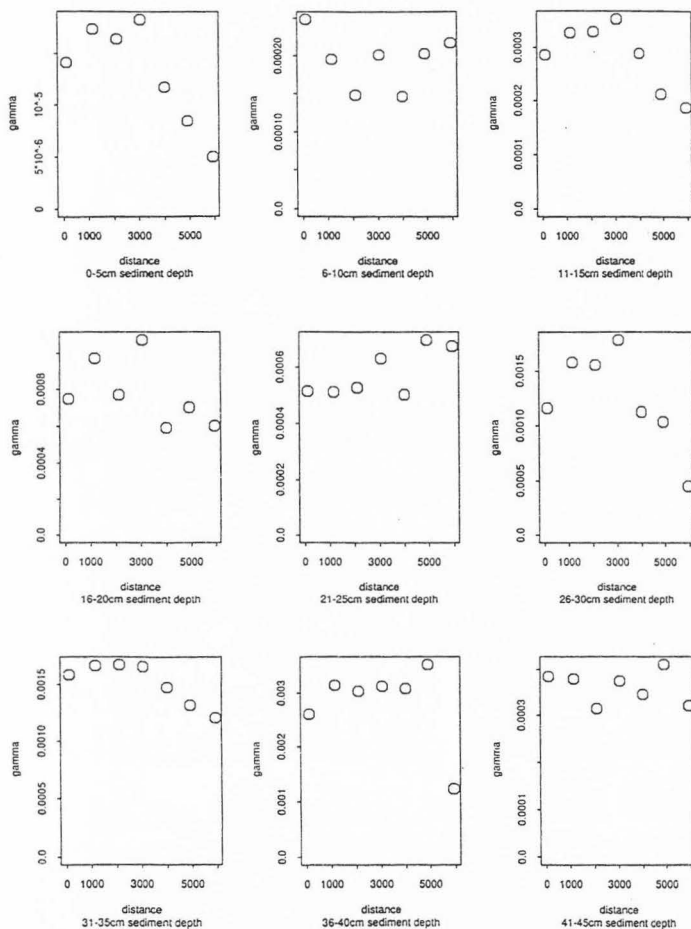


Figure A.5. Variograms of Unit 1 tuber biomass March data separated by sediment sections.



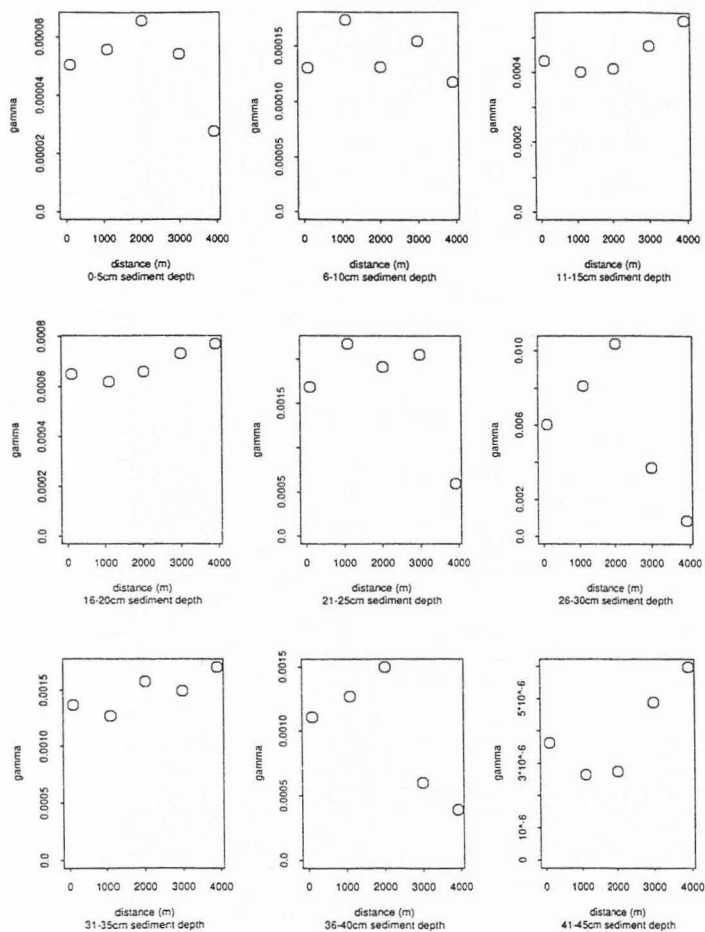


Figure A.6. Variograms of Unit 2 tuber biomass March data separated by sediment sections.

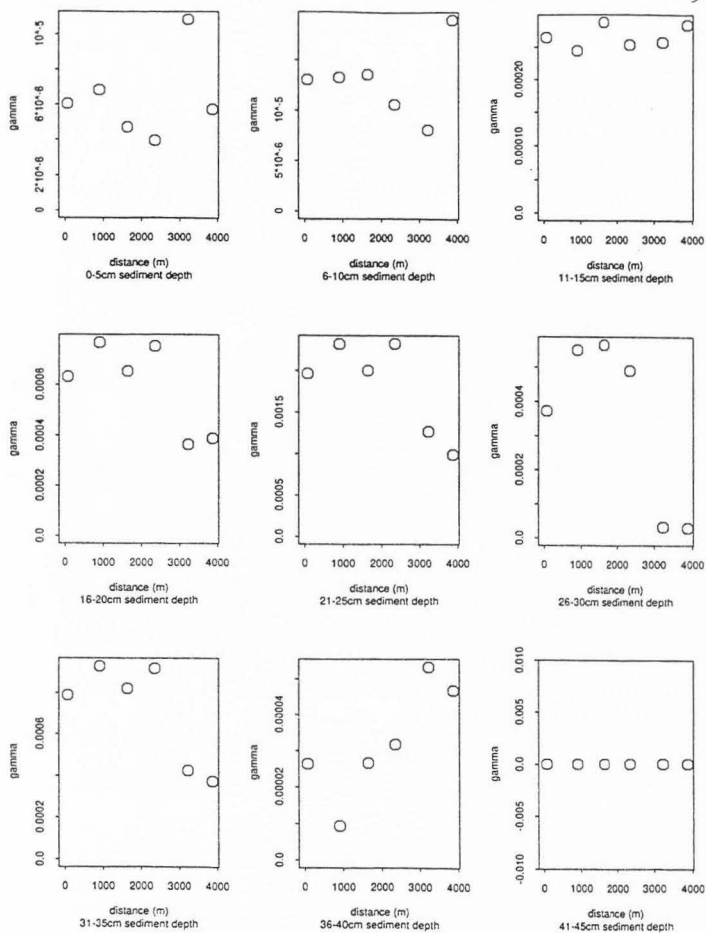


Figure A.7. Variograms of Unit 4 tuber biomass March data separated by sediment sections.

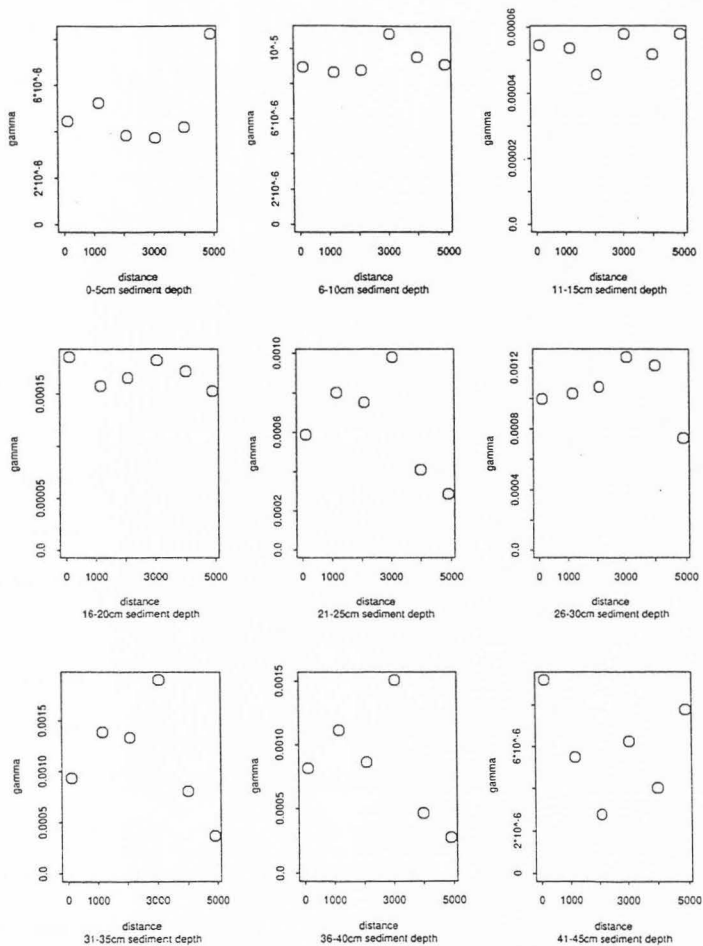


Figure A.8. Variograms of Bear River Club tuber biomass March data separated by sediment sections.

Appendix B. Digging rules for Trumpeter and Tundra swans (Tundra swans in parentheses)

1. If the swan is effective when paddling, then use digging times obtained from the simulations until no depth changes are recorded. Then proceed to item #2.
  
2. If the swan is not effective when paddling but does not have to tip up to reach the sediment, then:
  - a) first 3 (2) sections will take 1 second per bill stab.
  - b) next 1 to 2 sections add 1 second per bill stab until swan has to tip up.
  - c) once swan has to tip up, add 2 seconds per bill stab next 2 (3) sections, then add 3 seconds per bill stab to next 2 (3) sections, etc.
  
3. If the swan has to tip up from the beginning, then:
  - a) first 3 (2) sections will take 2 seconds per bill stab.
  - b) next section add 1 second per bill stab.
  - c) following sections add 2 seconds per bill stab next 2 (3) sections, then add 3 seconds per bill stab to next 2 (3) sections, etc. Appendix 1. Variograms of Unit 1 tuber biomass September data separated by sediment sections.