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Changes in Trumpeter Swan (Cygnus buccinator) Activities from Winter to Spring in the Greater Yellowstone Area

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ABSTRACT.—Trumpeter swans (*Cygnus buccinator*), in the winter, primarily, slept 42% of the time, fed 30%, swam 12%; and preened 7%. Comparisons of swan activities among diel periods during the winter indicated they increased feeding throughout the day into night, when they fed at their highest rate. Swans spent more time sleeping as winter temperatures decreased; feeding mostly ceased when temperatures fell below approximately −17 C. Dominant activities in spring included feeding (45%), sleeping (17%), swimming (13%); and preening (12%). During spring, swans fed at a high rate throughout day and night, suggesting that spring use-areas may be important to swans depositing endogenous reserves before nesting.

INTRODUCTION

The number of wintering trumpeter swans (*Cygnus buccinator*) in the greater Yellowstone ecosystem has increased sharply from approximately 700 birds in 1974 (Gale *et al.*, 1987) to 2,200 in 1992 (Niethammer, 1992). There has also been a sharp increase in the number of people living and recreating near swan wintering areas; this has heightened the need to understand the habitat-use patterns of wintering trumpeter swans (Squires, 1991). Time-activity data are useful for delineating important habitats of nonbreeding waterfowl (Fredrickson and Drobney, 1979). Changes in activity, especially feeding rates, can indicate which seasonal habitats are important to swans when establishing the endogenous reserves that affect reproduction (Reynolds, 1972; Andersen-Harild, 1981; Bacon and Andersen-Harild, 1989; Beekman, 1991). In addition, time budget information may be combined with empirically derived estimates of the energetic costs of the individual activities in order to estimate the population's energetic demands (Weathers *et al.*, 1984).

Our primary objective was to determine whether diel activity patterns of trumpeter swans differed from winter to spring. In addition, we investigated how weather affected swan activity.

STUDY SITES

The study area is located in the western United States near the intersection of Wyoming, Idaho and Montana. This area is bordered by the Yellowstone Plateau to the N, the Teton Range to the S and W, and the Gros Ventre Mountains to the E. Trumpeter swan wintering sites are located in Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, the National Elk Refuge and on private lands near Jackson, Wyoming. Elevation of wintering areas is approximately 2000 m. In December through February, air temperature averages −9.3 C and winter precipitation (mostly snow) averages 7.4 cm per month (30-yr average, NOAA Climatological Data Annual Summary, Moran, Wyoming). In spring (March through May), air temperature averages 0.6 C and precipitation averages 4.8 cm per mo (30-yr average, NOAA Climatological Data Annual Summary, Moran, Wyoming).

During winter, most trumpeter swans feed in low velocity (0.06 m/sec) streams (Squires *et al.*, 1992) on aquatic macrophytes and the subterranean tubers of *Potamogeton pectinatus* (Squires and Anderson, 1995). The most prevalent macrophytes in the winter diet of this population include *Chara* spp. (37% diet composition), *Elodea canadensis* (30%), and *P. pectinatus* tubers (23%); the foliage of *P. pectinatus* senesces by midwinter (Kantrud, 1990) and is unavailable to swans. Macrophytes most prevalent in spring diets include *P. pectinatus* tubers (39%), *Chara* spp. (27%) and *Potamogeton* spp. (16%, Squires and Anderson, 1995).

METHODS

Sampling.—We documented trumpeter swan activities on winter and spring-use areas from December 1989 through May 1990. We defined winter as December through February and spring as March through May. Day and night activities were recorded during 4-h observation periods that were sampled sequentially throughout the winter and spring. We used a night-vision scope for observations on nights with at least a one-quarter phase moon to provide light; reflected light from a ski area was sufficient for observations on 2 moonless nights.

We quantified activities by scan-sampling, using instantaneous sampling procedures (Altmann, 1974). At 10-min intervals, each bird in a flock was observed with a spotting scope for 5 sec to determine its activity. Scans proceeded from left to right until the activities of each bird were recorded. A maximum of 25 birds were observed during a given scan; remaining birds were sampled during the next scan. Swan activities were categorized into nine primary activities: (1) feeding; (2) preening; (3) watchful floating; (4) swimming; (5) standing/walking; (6) sleep; (7) display (fighting, chasing, chest to-chest display, head bob, Banko, 1960); (8) flying, and (9) other (laying, bathing and hiding). Temperature, wind speed, cloud cover (estimated to 10% intervals) and precipitation were also recorded at each scan.

Data analysis.—To test for overall differences between winter and spring activities, we compared the proportion of time spent in each activity as determined from scan samples aggregated throughout each observation day. We assumed the proportion of scores in a given activity represented the time swans actually engaged in that activity. Statistical analyses were conducted on proportions but are reported as percentages in the text and tables for clarity. Variables describing swan activities were nonnormally distributed so we used multiresponse permutation procedures (MRPP) to compare overall seasonal differences (BLOSSOM software, Slauson *et al.*, 1991). MRPP is a distribution-free statistical procedure based on Euclidean distance functions that has greater reliability and power for detecting differences in skewed distributions than variance-based statistics (Zimmerman *et al.*, 1985, Mielke, 1986).

In order to further interpret seasonal differences, activities were grouped into four daily time intervals: (1) morning (sunrise to 2.5 h past sunrise); (2) midday (between 2.5 h past sunrise and 5 h before sunset); (3) late day (5 h before sunset to sunset) and (4) night. The proportion of time swans engaged in activities according to time interval per observation day was the sampling unit. Because a 2-factor extension of MRPP has not been developed, multivariate analyses of variance (MANOVA) were used to simultaneously test for differences of activity among time intervals according to season. If the MANOVA indicated significant seasonal differences among time intervals, the relationship was further explored with analysis of variance (ANOVA) and multiple contrasts (Wilkinson, 1986), re-

TABLE 1.—Mean percent of time trumpeter swans spent in selected activities during winter and spring

	Winter (n = 64 observation days)		Spring (n = 109)		
	Percent	Standard error	Percent	Standard error	
Sleep	42.1	3.7	16.6	1.9	$P < 0.001$
Feed	29.6	2.7	44.5	2.1	$P < 0.001$
Swim	12.0	1.3	13.3	1.3	$P = 0.816$
Preen	7.0	0.6	11.5	0.9	$P < 0.001$
Float	3.0	0.4	3.4	0.4	$P = 0.276$
Stand/walk	1.8	0.5	3.3	0.7	$P = 0.103$
Display	1.6	0.4	2.4	0.7	$P = 0.251$
Fly	0.5	0.1	0.4	0.2	$P = 0.069$
Other[1]	2.4	0.5	4.5	0.7	

[1] = not meaningful statistical test

alizing activities are not independent. Since proportions were not normally distributed, they were arcsine-transformed before MANOVA and ANOVA analyses (Zar, 1984) which normalized distribution data as required by these analyses. Application of MANOVA/ANOVA to transformed proportions provided the appropriate analysis for addressing our objectives. Spearman rank correlations were used to relate activities to weather variables. We used alpha equal to 0.10 for all tests except for correlations, where the alpha equaled 0.01; a more conservative alpha was selected for correlations because of the number of tests.

RESULTS

Trumpeter swans were observed for 153 h during winter and 254 h during spring. In the winter, swans primarily slept (42% percent of time), fed (30%), swam (12%), or preened (7%) (Table 1). In spring, swans engaged in the same dominant activities, but the proportion of time allocated to some activities changed (Table 1). Feeding time increased ($P < 0.001$) from winter (30%) to spring (45%) as the time spent sleeping decreased ($P < 0.001$) from 42% during winter to 17% during spring (Table 1).

During winter the proportion of time allocated to activities differed ($P = 0.006$) among day intervals (Table 2). Feeding activity was periodic ($P = 0.001$). Swans fed least in the morning (17%), then increased feeding throughout the day and into the night when they fed most (49%). Time spent sleeping was inversely related to feeding time, decreasing monotonically from morning (57%) until night (22%). During spring, trumpeter swan activities were not ($P = 0.337$) periodic according to day intervals (Table 2); swans fed at a high rate during all time intervals.

Changes in air temperature during the winter influenced swan activity more than other weather variables (Table 3). Limited evidence suggested that swans fed less and slept more in response to decreasing temperatures. Changes in temperature during spring had little affect on activities.

DISCUSSION

Trumpeter swans wintering in the greater Yellowstone area sharply increased their feeding rate from winter to spring; this activity pattern is similar to other species of waterfowl (Miller, 1984; Paulus, 1988). Although we could not directly measure changes in the body weight of trumpeter swans, we believe the increased feeding rate from winter to spring

Table 2.—Mean percent (se) of time spent by trumpeter swans during winter and spring according to day interval. Sample size equals the number of 4-h observation periods

	Winter				Spring			
	Morning (n = 15)	Midday (n = 22)	Late day (n = 14)	Night (n = 13)	Morning (n = 34)	Midday (n = 50)	Late day (n = 16)	Night (n = 9)
Sleep	57.4 (8.5)A	49.5 (6.1)A	32.5 (6.1)AB	22.4 (5.9)B	12.7 (3.5)A	18.0 (2.4)A	17.1 (5.3)A	22.8 (8.3)A
Feed	16.9 (4.0)A	23.5 (4.4)AB	34.2 (3.9)BC	49.4 (6.5)C	43.3 (4.6)A	42.6 (2.5)A	52.1 (6.4)A	45.8 (7.3)A
Swim	11.4 (3.4)A	9.4 (1.5)A	12.5 (2.0)A	16.8 (3.8)A	16.0 (3.2)A	12.4 (1.6)A	9.9 (1.8)A	13.9 (2.7)A
Preen	6.1 (1.1)A	8.1 (1.0)A	8.4 (1.4)A	4.7 (1.0)A	11.8 (2.0)A	11.4 (1.0)A	11.3 (2.4)A	11.1 (3.2)A
Display	2.2 (1.1)A[1]	1.4 (0.6)A	2.1 (0.7)A	0.9 (0.3)A	3.6 (1.8)A	2.5 (1.0)A	0.3 (0.2)A	0.8 (0.5)A
Stand/walk	2.0 (1.2)A	1.8 (0.7)A	1.7 (0.5)A	1.7 (1.6)A	4.3 (1.7)A	3.2 (0.8)A	3.5 (1.4)A	0.4 (0.2)A
Float	1.9 (0.7)A	2.4 (0.6)AB	4.5 (1.0)B	3.5 (0.8)AB	4.1 (0.9)A	2.9 (0.5)A	2.3 (1.0)A	4.5 (1.3)A
Fly	0.6 (0.4)A	0.5 (0.2)A	0.7 (0.3)A	0.1 (0.1)A	0.8 (0.5)A	0.3 (0.1)A	0.0 (0.0)A	0.1 (0.1)A
Other[2]	1.6 (0.5)	3.4 (1.3)	3.5 (1.1)	0.5 (0.2)	0.3 (1.2)	6.4 (1.1)	3.3 (1.1)	0.7 (0.5)

[1] = like letters across day intervals were statistically similar ($P > 0.10$), each season was considered separately

[2] = not meaningful test

TABLE 3.—Spearman rank correlations among weather variables and trumpeter swan activities

	Temperature		Wind speed		Cloud cover		Precipitation	
	Winter[1]	Spring[1]	Winter	Spring	Winter	Spring	Winter	Spring
Display	0.044	−0.113	0.142	0.004	0.207[2]	0.195[2]	0.092	0.154[2]
Feed	0.290[2]	0.006	0.024	−0.010	0.179	0.151[2]	−0.07	0.147
Float	0.211[2]	−0.173[2]	0.112	0.015	0.096	−0.071	−0.085	0.045
Fly	0.109	−0.06	0.262[2]	0.181[2]	0.089	0.013	−0.001	0.059
Preen	−0.023	0.102	0.035	−0.103	−0.043	−0.004	−0.037	−0.051
Sleep	−0.427[2]	0.038	−0.107	0.032	−0.11	−0.251[2]	0.091	−0.092
Stand	0.277[2]	0.093	0.173	−0.027	−0.006	−0.131	0.064	−0.057
Swim	0.320[2]	−0.064	0.188[2]	0.031	0.236[2]	−0.001	0.099	0.102

[1] n = 187 (winter) and 304 (spring) hourly intervals per observation day

[2] Significant at $P < 0.01$

suggests that spring use-areas may be important for depositing endogenous reserves. Establishing endogenous reserves has been found to affect the productivity of other species of swans (Reynolds, 1972; Andersen-Harild, 1981; Bacon and Andersen-Harild, 1989; Beekman, 1991); we assume trumpeter swans respond similarly. Bortner (1985) found that tundra swans (*Cygnus columbianus*) in North Carolina lost weight throughout winter by reducing lipid reserves, even though he believed food was not limiting. He speculated that spring habitats were used to accumulate endogenous reserves. Several species of arctic geese also depend on spring habitats to establish body reserves (Ankney and MacInnes, 1978; Raveling, 1979; McLandress and Raveling, 1981; Ebbinge *et al.*, 1982). We believe that the quality of spring habitats in the greater Yellowstone ecosystem may affect the productivity of this trumpeter swan population.

In order for trumpeter swans to establish endogenous reserves, energy intake must exceed costs associated with maintenance and other activities. During the winter, the maximum percent of time that swans allocated to feeding was at night (49%); this feeding rate was similar to the highest rates that swans fed during spring. However, during the spring, swans fed at this high rate throughout the day and night. The time that waterfowl allocates to feeding is related to forage type (Paulus, 1988). Trumpeter swans wintering in the greater Yellowstone ecosystem eat primarily *Chara* spp., *Elodea canadensis* and the tubers of *Potamogeton pectinatus* (Squires and Anderson, 1995) and pass these foods quickly through their digestive tract at the expense of digestive efficiency (Squires, 1991). Because swans wintering in the greater Yellowstone ecosystem feed on low-quality forages, they must allocate a large proportion of their time to feeding. White-fronted geese (*Anser albifrons,* Owen, 1972) and barnacle geese (*Branta leucopsis,* Ebbinge *et al.,* 1975) may spend up to 80% of daylight hours feeding when eating foliage, whereas snow geese eating agricultural grains may satisfy their foraging needs in only a few hours (Frederick and Klaas, 1982). Trumpeter swans spending up to 52% of their time foraging is consistent with other species of waterfowl that eat leafy aquatic vegetation (Paulus, 1988).

Trumpeter swans fed at night like many other species of waterfowl (*see* Jorde and Owen, 1988, for review). Trumpeter swans feeding at night may save energy if heat generated from muscular activity and digestion during nocturnal feeding reduces total thermoregulatory costs (Jorde *et al.* 1984). This may be particularly important for swans wintering in a cold environment like the greater Yellowstone area. During the day, solar radiation may help swans thermoregulate even when they are inactive. Walsberg (1983) cites examples of birds either partially or completely substituting waste heat from nonflight activities for their thermostatic demands even at low temperatures (−30 C). We suggest that swans may feed at night as an energy conservation measure, especially since other factors like human disturbance, predator avoidance or hunting do not appear to force night foraging.

Although the relationship was variable, trumpeter swans tended to sleep more and feed less in response to decreasing air temperatures. Waterfowl foraging activity typically increases as temperatures decrease to approximately 0 C (*see* Paulus, 1988, for review). However, at low temperatures, waterfowl may decrease activity as energetic costs exceed the gains from foraging (Brodsky and Weatherhead, 1984; Paulus, 1988). We observed that trumpeter swans tended to decrease their feeding activity when temperatures fell below −17 C. Mallards and black ducks select microclimates in response to cold temperatures (Brodsky and Weatherhead, 1984; Jorde *et al.,* 1984), but our field observations suggest this was not the case for trumpeter swans. Even at low temperatures, swans used open areas such as sand bars or ice that were exposed to wind with their head and feet tucked under their plumage. Below −23 C, swans remained in this tucked posture and rarely fed. We assume that at this temperature the increased thermoregulatory cost associated from exposure during feeding exceeds the energy acquired.

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