

LANDSCAPE-LEVEL HABITAT USE BY TRUMPETER SWANS IN THE SANDHILLS OF NEBRASKA AND SOUTH DAKOTA

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INTRODUCTION

Since initial efforts to restore trumpeter swans (*Cygnus buccinator*) to the northern Great Plains began in the early 1960s (Monnie 1966), the High Plains Flock (HPF) has successfully increased its numbers and expanded its range from the introduction at Lacreek National Wildlife Refuge in southwestern South Dakota into the Sandhills of Nebraska and nearby locales. Trumpeter swans of the Interior Flock, of which the HPF is a component, have been identified as a focal species within the U.S. Fish and Wildlife Service's Focal Species Strategy. The Cooperative Management Plan for this population seeks to increase numbers and distribution of trumpeter swans, specifying "a dispersed population consisting of at least 500 total birds counted during the production survey and 50 successful breeding pairs" (Comeau-Kingfisher and Koerner 2005). Currently the HPF consists of 524 birds and 65 successful nesting pairs with an average growth rate of 4.9% per year during 1990-2010 (Comeau and Vrtiska 2010). However, the objectives of the plan were not based on any empirical information about the use of wetlands and surrounding landscapes by trumpeter swans. Rather, they were based simply on a desired abundance. Without an understanding of the types of habitats used by swans, managers cannot objectively determine the amount of habitat needed to maintain that number of birds.

We used trumpeter swan locations from survey information in conjunction with digital GIS landscape data to investigate relationships between swan use of wetlands and characteristics of those wetlands and surrounding landscapes on their Sandhills breeding grounds. The objectives of this analysis were to (1) synthesize information on numbers and distribution of HPF swans from existing survey databases; (2) compare characteristics of wetlands and landscapes where swans were located to characteristics of wetlands and landscapes where swans were not observed to make inferences about broad-scale habitat use by swans in the region; and (3) use the

results to provide information about other locations within the range of the HPF that are suitable for nesting swans, or could be made suitable with management. We hoped to provide information that would better enable managers to conduct management activities to support numerical and distributional objectives specified in the management plan.

METHODS

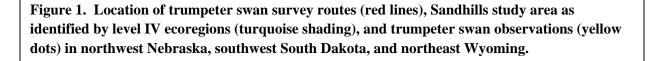
Surveys

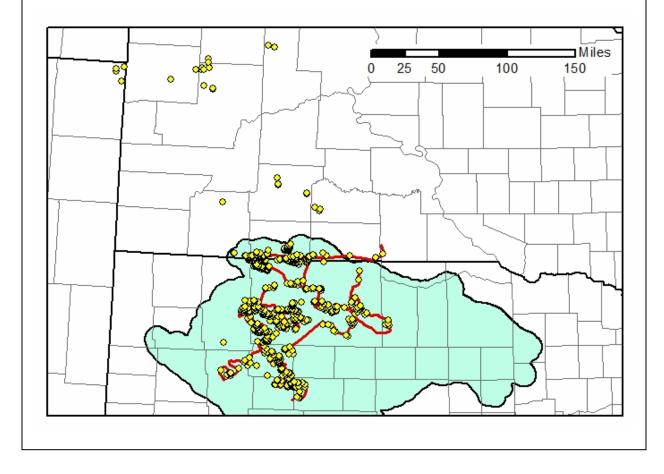
Data from aerial cruise surveys conducted in August were available for 17 years during the period 1979 to 2007. The surveys monitored the location, number, and age class (adults/subadults or cygnets) of trumpeter swans in northeastern Wyoming and the western portions of Nebraska and South Dakota (Figures 1 and 2). Survey routes were non-probabilistic and focused toward sampling areas of known swan use. Swan observations recorded during the surveys were of birds on wetlands and did not include observations of swans in flight. The survey route and swan observations were recorded on U.S. Geological Survey topographic maps each year. During surveys, American white pelicans (*Pelecanus erythrorhynchos*) and trumpeter swans were generally visible up to one mile from the aircraft. When large, white birds were spotted in the distance, surveyors deviated from the survey route to identify the species and record the location, number, and age class of any swans and then returned to the route.

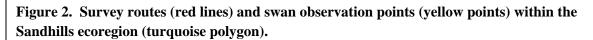
Data assessment

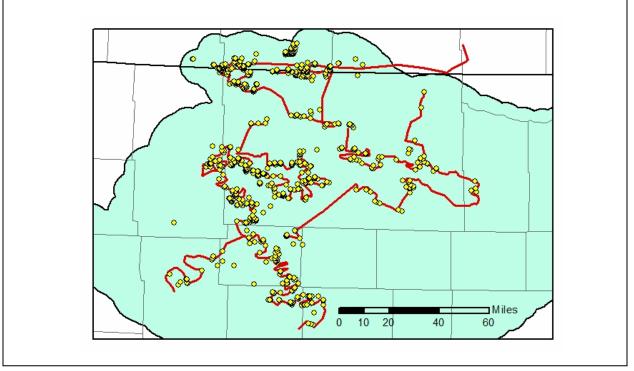
Locations of swans from the topographic maps were integrated into a geodatabase that included 933 swan locations throughout northeastern Wyoming, north-central Nebraska, and south-central South Dakota (Figure 1), which we assessed for quality and relevance. Because of

limited observations and lack of consistent land cover data outside of the Sandhills ecoregion, analysis was limited to the Sandhills of Nebraska and South Dakota and a 10-km buffer surrounding the area, which reduced the number of points for analysis to 728. An additional two observation points within the Sandhills boundary were removed because they contained no data on the number of birds at that location, further reducing the number of points for analysis to 726. Although biologists typically flew similar survey routes each year, the same path was not followed in all years and we did not quantify any differences or deviation in routes across years.









Part of our analysis involved comparing characteristics of wetlands where swans were observed with wetlands that were available but swans were not observed. Given the one-mile detection distance, we defined available and nominally unused wetlands as those wetlands where swans were not recorded within one mile on each side of survey routes. Wetlands along the borders of the buffer were included if more than 50% of their area fell within the buffer zone. Because the pool of available wetlands was constrained to this two-mile-wide swath, we did not assess wetlands where swans were observed that were outside of the buffer. We assumed that wetlands where swans were observed outside of the survey routes and buffer were not sampled regularly.

Processing of wetland data

We used National Wetlands Inventory (NWI; Wilen and Bates 1995) data to characterize wetlands on which swans were observed and wetlands within the one-mile detection buffer where swans were not observed. As depicted by NWI data, individual wetlands are often comprised of several polygons that represent different substrate, permanency, and vegetation zones. We combined contiguous polygons into individual wetland basins classified by the most permanent water regime associated with each basin (Figure 3 and Table 1; Cowardin et al. 1995, Johnson and Higgins 1997).

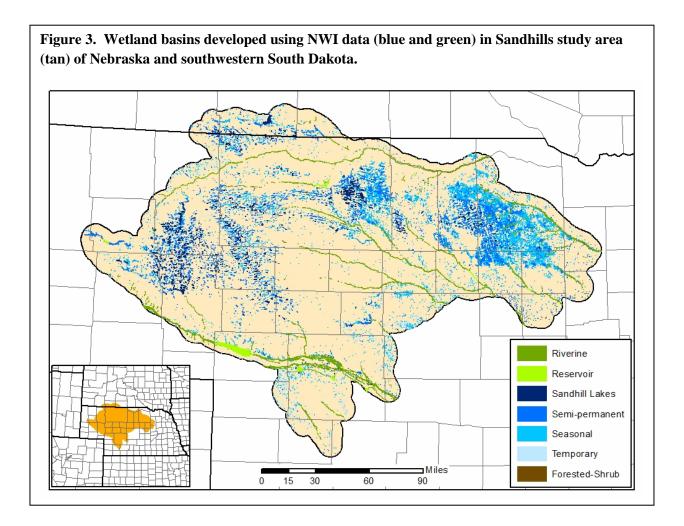


Table 1. Wetland basin classes and definitions of associated water regime modifiers from Cowardin et al. (1979) used in integration of adjoining wetland zones into basins classified by the most permanent water regime identified by the National Wetlands Inventory.

Basin class	Definition					
Temporary	Surface water is present for brief periods during the growing season, but the					
	water table usually lies well below the soil surface for most of the season.					
	Plants that grow both in uplands and wetland are present. Also includes					
	saturated soils where surface water is seldom present.					
Seasonal	Surface water is present for extended periods especially early in the growing					
	season, but is absent by the end of the season in most years. When surface					
	water is absent, the water table is often near the land surface.					
Semi-	Surface water persists throughout the growing season in most years. When					
permanent	surface water is absent, the water table is usually at or very near the land					
	surface. Also includes intermittently exposed and permanently flooded					
	palustrine wetlands.					
Lake	Surface water is present throughout the year except in years of extreme					
	drought. Includes both limnetic and littoral zones.					
Forested/Shrub	Any type of palustrine system with a FO (forested) or SS (shrub/scrub) class.					
	Given the ranking of the classification, these wetlands were completely					
	forested or covered with scrub/shrub.					
Riverine	Any water body identified as riverine by NWI, except for reservoirs, from					
	which limnetic or littoral polygons were classified as lakes. The emergent					
	area around reservoirs remained classified as riverine.					

UTM coordinates for 349 of 726 swan observations in the database did not coincide with a wetland basin; we assigned those points to the nearest wetland within the one-mile detection buffer. Distance to nearest wetland was <500m for 318 (91%) of the 349 points whose coordinates did not coincide with a wetland basin (Table 2). A random point was assigned to each available wetland where swans were not observed within the two-mile-wide window along the flight path. The resulting dataset contained 9,411 total points on wetlands, of which 726 represented wetlands where swans were observed and 8,685 represented available wetlands where swans were not observed and 5).

Table 2. Number of swan observations, by distance from nearest wetland basin, that did not coincide with a wetland basin.

Distance	0-50	50-	100-	150-	200-	250-	300-	350-	400-	450-	>500
category (m)		100	150	200	250	300	350	400	450	500	
n	69	55	58	43	30	17	25	7	9	5	31

Figure 4. Example of trumpeter swan observation points in relation to wetland basins developed using NWI data (blue and green) within one-mile buffer (orange lines) on either side of trumpeter swan survey route (red line) in Grant County, Nebraska.

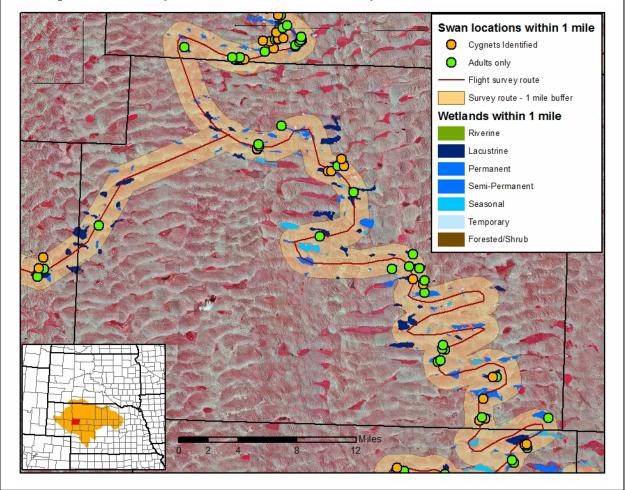
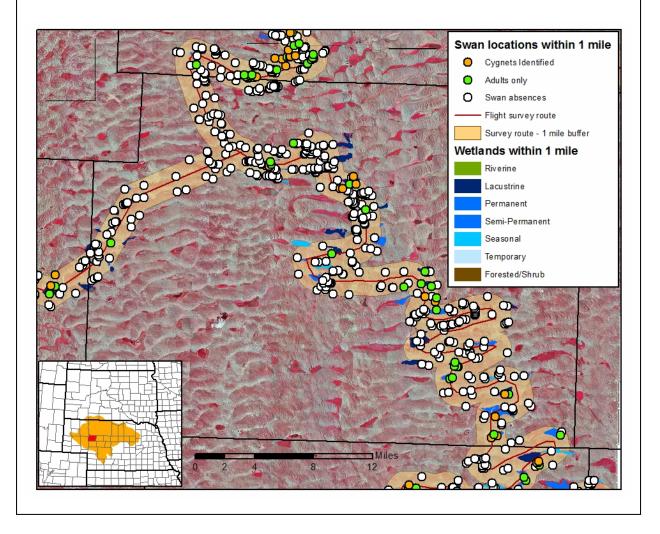


Figure 5. Example of trumpeter swan observation points and available points in relation to wetland basins developed using NWI data (blue and green) within one-mile buffer (orange lines) on either side of trumpeter swan survey route (red line) in Grant County, Nebraska.



We used digital landcover data with hierarchical classes to characterize landscape characteristics surrounding used and available wetlands (Table 3, Figure 6). Landcover data were created by the Great Plains GIS Partnership by integrating and processing multiple existing spatial data layers including Nebraska ecosystems; cropping data derived from National Agriculture Statistics Service data; Farm Service Agency Conservation Reserve Program (CRP) data; wet meadow, forest/woodland, and developed lands data; and roads data (Bishop et al. 2009). After processing, data were joined and clipped to the extent of the Sandhills ecoregion plus the aforementioned 10-km buffer.

Because many bird species are influenced by the landscape beyond the immediate observation point, we sampled landscape and NWI data at eight scales using circular moving window analysis, which summarizes data within a "window" of a selected size around each cell in a GIS data layer. Landscape data were in raster format and the area within each moving window was 0.5, 2.0, 3.1, 8.0, 12.5, 28.3, 50.2, and 78.5 km², respectively, for circles with radii approximating 0.4, 0.8, 1.0, 1.6, 2.0, 3.0, 4.0, and 5.0 km. Moving windows calculated the percentage of each land cover class (Table 2) or NWI basin water regime within the respective radii. Percentage outputs were then attached to the swan location point files using the intersect points function within the Hawth's tools ArcGIS extension (Beyer 2004). Moving windows were also used to count the total number of wetland basins within the 400m-5km radii.

Table 3. Landcover classes used to characterize landscapes around swan observations and available wetland points in the Sandhills of Nebraska and South Dakota. Numbers in description represent specific classes from Bishop et al. (2009).

Variable	Description					
Grassland	CRP grass (31), CRP (39), Mixed Grass (71), Sandhills Grasslands (73),					
	Shortgrass (75), Tallgrass (77), Wetmeadow (247)					
Woodland	CRP upland trees (32), CRP riparian trees (33), Eastern Red Cedar (59),					
	Ponderosa Pine-many trees/little grassy understory (60), Upland Woodland					
	(61), Ponderosa Pine (63), Juniper (66), Ponderosa Pine-few trees/grassy					
	understory (69), Riparian Canopy (241), Exotic Riparian Shrubland (242),					
	Native Riparian Shrubland (243)					
Cropland	Alfalfa (201), Corn (202), Fallow (203), Sorghum (206), Soybeans (207),					
	Sunflowers (208), Wheat (209), Other Ag (211)					
Developed	Other Roads (41), Rural Developed (42), 4-Lane Roads (44),					
	Urban/Suburban (46)					
All wetland	Playas (12), Sandhills Wetlands (13), CRP wetlands (34), Canals (48),					
	Freshwater Lake/Sandhill Lake (101), Sand Pit/Irrigation reuse pit (103),					
	Reservoir (104), Stock Pond (106), Emergent Marsh (152), Saline Marsh					
	(153), River Channel (244), Wet Meadow (247), Floodplain Marsh (248)					
Roads	Other Roads (41), 4-lane Roads (44)					

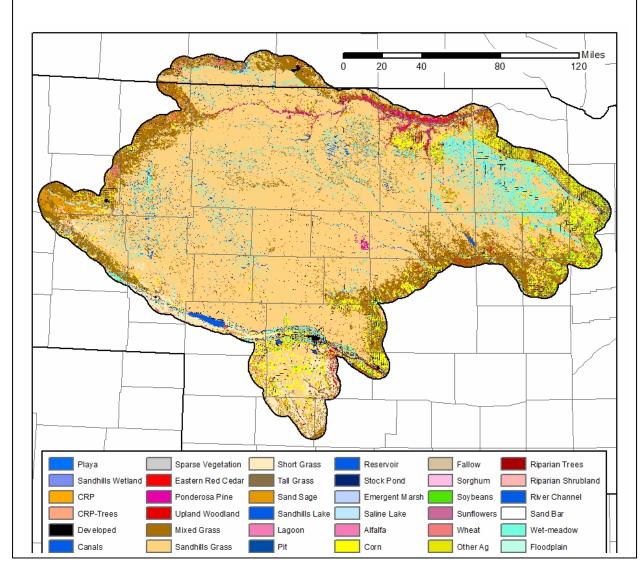


Figure 6. Distribution of land cover classes used in characterization of landscapes surrounding wetlands used by swans and wetlands available to swans.

Statistical analysis

Because of the non-probabilistic manner in which swan location data were collected, we used descriptive analyses to show patterns in the data and do not make inferences about a larger population. Also, swans generally used the same wetlands each year and changes in land cover over time were negligible. Changes in land cover over time were considered negligible since the land cover has only changed 4.2 % since 1973 and much of that has been around the periphery of

the ecoregion where topography and soil constraints are more easily overcome (Drummond and Auch 2011). Consequently, we did not analyze data by year as observations were not independent, sample sizes would have been inflated, and there was no variation in landscape variables over time. Instead, we analyzed relationships between swans and land cover using data from 2002, which was from the midpoint of the time series, had the greatest number of swan observations on individual wetlands (85), and included sites used in other years. We analyzed data at two levels of response. First, we compared characteristics of wetlands and surrounding landscapes for wetlands at which adult or subadult swans (observers are unable to distinguish between the two age groups) were observed to wetlands that we considered available (i.e., within one mile of the survey transect) where no swans were observed. Second, for wetlands at which adult/subadult swans were present, we compared characteristics of wetlands and their surrounding landscapes for wetlands at which swans with cygnets were observed relative to wetlands at which adult swans without cygnets were observed.

RESULTS

Swan Observations

The number of points at which trumpeter swans were observed increased from 1979 to 1991 but showed little increase from 1991 to 2007; the number of adults/subadults and cygnets varied among years, with adult/subadult numbers generally increasing from 1979-2007 (Figure 7). The number of points, adults/subadults, and cygnets within the one-mile buffer were all slightly lower, but followed a similar pattern (Figure 8). The proportion of all observations that occurred within the one-mile buffer varied over time (Figure 9). Figure 7. The number of points at which trumpeter swans were observed (red), number of adults/subadults (blue), and cygnets (black) observed in the sandhills study area varied among years, with number of adults increasing over time.

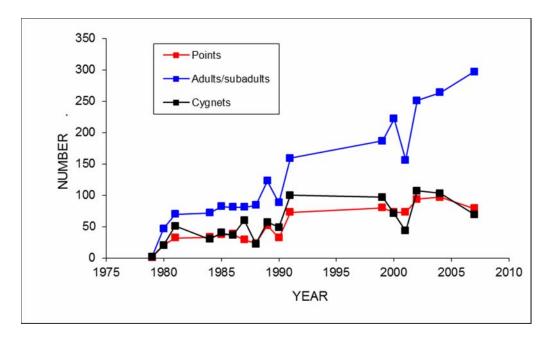


Figure 8. The number of points at which trumpeter swans were observed (red), number of adults/subadults (blue), and cygnets (black) observed within one mile of the survey routes was similar but generally lower than the total number observed within the sandhills study area.

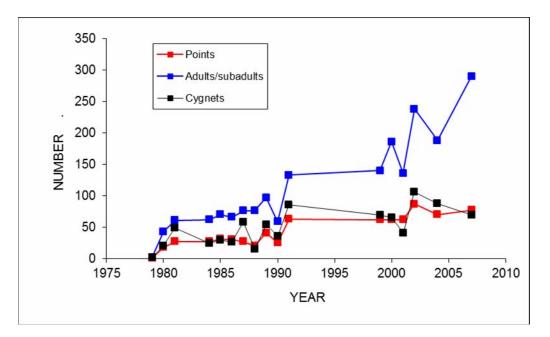
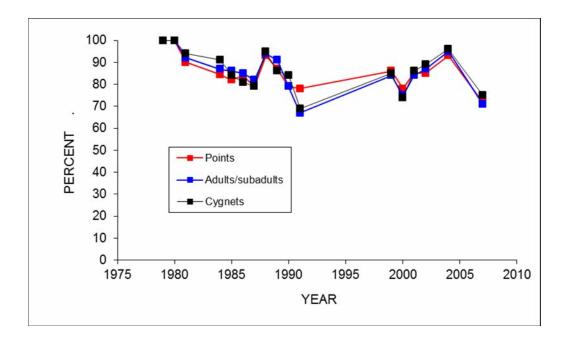


Figure 9. The percentage of points at which trumpeter swans were observed (red), percentage of adults/subadults (blue) observed, and percentage of cygnets (black) observed within one mile of the survey routes varied among years.



Characteristics of wetlands and landscapes where adult swans were observed

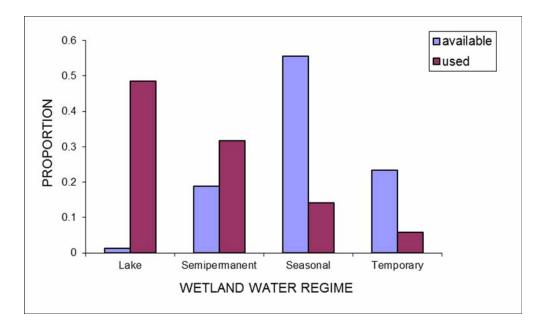
The majority (79%) of wetland basins available to swans had temporary or seasonal water regimes. However, swans did not use wetlands in proportion to their availability, instead showing strong selection for lake and semipermanent wetlands and avoidance of temporary and seasonal wetlands (Table 4, Figure 10). No use of forested/shrub, reservoir, and riverine wetlands was observed, but these types of wetlands were rare in the sample. Even within the lake and semipermanent water regime classes swans showed selection for size, as lakes used by swans were significantly larger than wetlands that were available (\bar{x} [SE] = 83.8 [9.6] and 52.3 [6.7] ha, respectively). Swans showed similar selection for size on semipermanent wetlands, as semipermanent wetlands used were significantly larger than wetlands that were available (\bar{x} [SE] = 37.1 [8.4] and 3.9 [0.3] ha, respectively). Swans showed no statistically discernable selection

for size of the few wetlands with temporary or seasonal water regimes that were used by adult/subadult swans.

Table 4. Number of wetlands available within one-mile buffer of swan survey routes and number
of wetlands with observed use by adult/subadult swans, by water regime, 1999-2007.

	Available	1999	2000	2001	2002	2004	2007
Forested/shrub	61	0	0	0	0	0	0
Lacustrine	114	33	33	34	41	42	22
Reservoir	1	0	0	0	0	0	0
Riverine	5	0	0	0	0	0	0
Seasonal	4834	4	1	3	12	3	18
Semipermanent	1640	22	23	20	27	23	23
Temporary	2031	3	4	3	5	2	13
Total	8686	62	61	60	85	70	76

Figure 10. Water regimes of wetlands used by swans in 2002 differed from water regimes that were available for use, with swans using more lake and semipermanent wetlands and fewer seasonal and temporary wetlands than were available.



Landscapes around wetlands at which swans were observed and available wetlands where swans were not observed were both dominated by grasslands and wetlands, particularly lakes and semipermanent wetlands (Figure 11). Landscapes surrounding used wetlands generally had lower densities of wetlands relative to what was available (Figure 11). Cropland, developed land, and woodland were uncommon, with swans showing a tendency to use wetlands in areas with lower amounts of cropland and woodland relative to what was available (Figure 11).

Figure 11. Means and standard errors of amount of land or water (as percentage of landscape) and number of wetlands at multiple radii around 8,619 available wetlands (solid circles) and 85 wetlands at which adults were observed (white circles) in 2002. Land cover classes are defined in Tables 1 and 2.

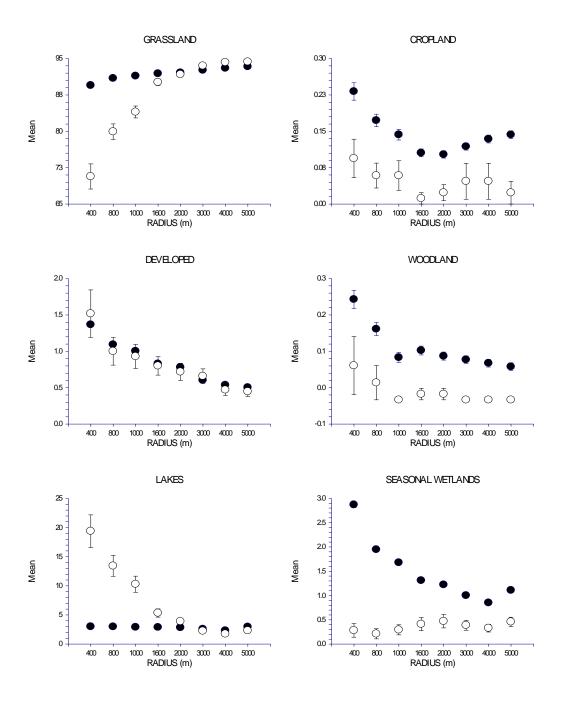
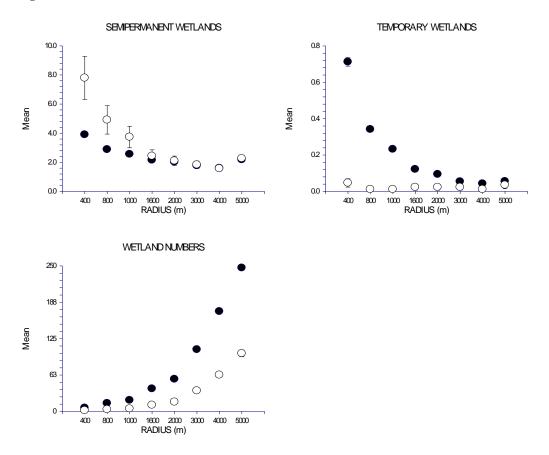


Figure 11, continued.

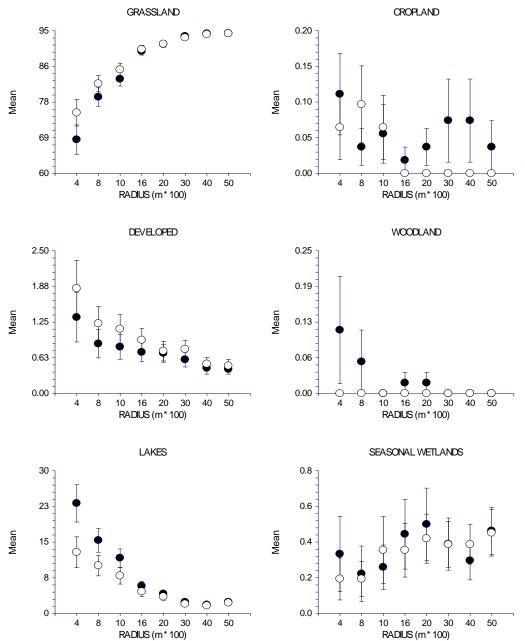


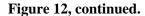
Characteristics of wetlands and landscapes where cygnets were observed

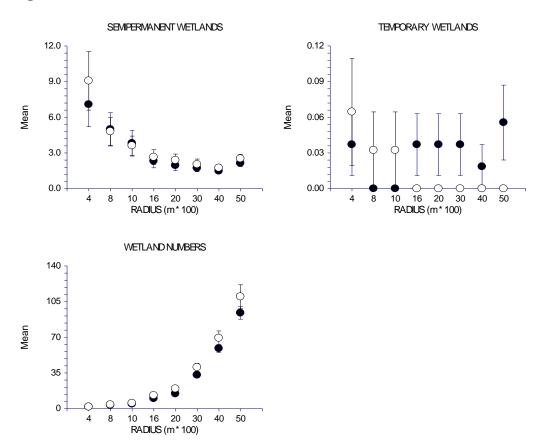
Lakes at which adults/subadults and cygnets were observed in 2002 were nominally larger than lakes at which adults/subadults but no cygnets were observed, but the difference was not statistically significant (\bar{x} [SE] = 88.8 [12.8] and 72.4 [14.7] ha, respectively, p = 0.38). Semipermanent wetlands showed a similar pattern (\bar{x} [SE] = 42.3 [12.9] and 28.2 [6.0] ha, respectively, p = 0.35).

Landscapes around wetlands at which cygnet and adult/subadult swans were observed had slightly greater amounts of grassland and developed land, lower amounts of woodland and lakes, and slightly more wetlands than landscapes around wetlands at which adults/subadults only were observed (Figure 12).

Figure 12. Means and standard errors of amount of land or water (as percentage of landscape) and number of wetlands at multiple radii around 54 wetlands at which adults but no cygnets were observed (solid circles) and 31 wetlands at which adults and cygnets were observed (white circles) in 2002. Land cover classes are defined in Tables 1 and 2.







DISCUSSION

Our ability to make inferences about broad-scale habitat selection by trumpeter swans in the High Plains Flock in this analysis is limited by several factors. First, the Sandhills ecoregion is comprised primarily of grass and water. Consequently, there is relatively little variation in landscape characteristics for which trumpeter swans can select. This limited range of variation in landscape composition also influences the appearance of selection, along with the scale that is used to assess habitat. For example, adult/subadult swans appear to select for low-grass landscapes at 400-1600-m scales. However, this apparent selection is a function of the large wetlands used by trumpeter swans in the study area, as the percentage of the landscape covered by lakes declined while the percentage of the landscape covered by grassland increased as the radius of the sampling window increased.

Nevertheless, some of our findings are consistent with results of trumpeter swan habitat selection studies in other locations. For example, swans with broods in Alaska also selected larger lacustrine, palustrine aquatic bed, and palustrine unconsolidated wetlands over smaller wetlands, particularly forested or riverine wetlands (Schmidt et al. 2009). Interestingly, swans, which are often sensitive to human disturbance (summarized in Mitchell and Eichholz 2010), did not show an avoidance of developed lands in our study, which included rural developed sites and roads. In fact, wetlands where swans with broods were present generally were surrounded by more developed lands than available wetlands. This seeming discrepancy may be explained by the nature of human activity on developed lands in our study area, as trumpeter swans react more strongly to loud, sporadic disturbances or those where humans are readily visible than they do to vehicles passing by or airplanes passing overhead (Henson and Grant 1991).

The composition of landscapes surrounding wetlands with adults and cygnets relative to wetlands with adults/subadults with no cygnets shows patterns that differ from those of landscapes surrounding wetlands used by adults/subadults relative to what was available (see multiple-radii plots for area of grassland, area of lakes, and wetland numbers for examples). This complicates management recommendations, as characteristics of landscapes for which unsuccessful adults and subadults appear to be selecting differ from landscapes in which successful breeding occurred. However, these relationships are poorly defined because of the large amount of uncertainty associated with the data. For example, wetlands with adults/subadults but no cygnets may represent non-breeders or failed breeders; distinguishing between the two groups will be necessary to make more reliable inferences about landscape

characteristics associated with successful breeding. Population growth of trumpeter swans is often slow because of their long life, delayed maturation, and single broods (Mitchell and Eichholz 2010). Consequently, detecting changes in populations over time may be difficult.

Many of the shortcomings associated with these data can be resolved by altering the survey design and data collection methods to meet specific, identified purposes. Historically, the survey has been used solely to assess the abundance and production of swans in the HPF. However, to better understand landscape-level habitat selection and develop models that can be applied to spatial data to create "thunderstorm" maps (e.g., Reynolds et al. 2006, Niemuth et al. 2008), data should be collected using a probabilistic sampling framework that encompasses the geographic area of interest and a wide range of landscape characteristics. Present survey routes, which focus on known nesting sites, do not allow reliable inferences about what is used relative to what is available across the landscape. To identify types of landscapes associated with successful nesting, it might be necessary to make multiple flights (i.e., during incubation as well as in August) to determine which wetlands hosted breeding pairs and which hosted non-breeders. Multiple surveys would also increase certainty of determining use versus non-use of wetlands. However, such design modifications could impact the original intent of the survey, to estimate overall swan abundance. If the survey is re-designed to meet multiple objectives, managers should consult with a statistician to ensure that data collected on the surveys are able to answer key questions. Modifying the survey could also help address issues related to the original intent of the survey. For example, a probability-based sample, as opposed to the present sample where known sites are monitored, would allow inferences about changes in selection over time as swans occupy and "fill in" lower-quality territories (see Banko 1960 and Corace et al. 2006). More simply, a probability-based sample over a broader spatial extent would better enable

managers to quantify increases in the number of swans in the High Plains Flock and their distribution.

Results of this analysis suggest several possible management recommendations for trumpeter swans in the HPF. Use of large semipermanent and lacustrine wetlands by trumpeter swans suggests the value of these sites to swan populations. The presence of cygnets, and by extension, successful nesting, appears to be higher in areas with few trees and much grass, suggesting the maintenance or restoration of grass in areas with breeding swans and perhaps tree removal as potential management options for swans in the High Plains flock. Finally, relatively high wetland densities in landscapes surrounding wetlands where cygnets were observed suggest the importance of wetland complexes around large semipermanent and lake wetlands. However, because the nature of the data used in this analysis limits inferences that can be made, any changes in management should be supported by results of other studies or insights gained from the biology of trumpeter swans in the High Plains Flock.

LITERATURE CITED

- Banko, W. E. 1960. The trumpeter swan. North American Fauna 63. U.S. Fish and Wildlife Service, Washington, DC.
- Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.
- Bishop, A., J. Liske-Clark, and R. Grosse. 2009. Nebraska land cover development. Unpublished report. Great Plains GIS Partnership, Grand Island, Nebraska. 33pp.

- Comeau-Kingfisher, S., and T. Koerner. 2005. Management plan for the High Plains Trumpeter Swan Flock. U.S. Fish and Wildlife Service, Lacreek National Wildlife Refuge. Martin, SD. 19pp.
- Comeau, S., and M. Vrtiska. 2010. Fall trumpeter swan survey of the High Plains Flock. U.S. Fish and Wildlife Service, Lacreek National Wildlife Refuge, Martin, SD. 7pp.
- Corace, R. G., D. L. McCormick, and V. Cavalieri. 2006. Population growth parameters of a reintroduced trumpeter swan flock, Seney National Wildlife Refuge, Michigan, USA (1991-2004). Waterbirds 29:38-42.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service FWS/OBS/-79/31. Washington, D.C., USA.
- Cowardin, L. M., T. L. Shaffer, and P. M. Arnold. 1995. Evaluation of duck habitat and estimation of duck population sizes with a remote-sensing based system. National Biological Service, Biological Science Report 2, US Department of the Interior, Washington, DC.
- Drummond, M. A., and R. Auch. 2011. Land-cover change in the United States Great Plains. Land Cover Trends Project. U.S. Geological Survey. Available at http://landcovertrends.usgs.gov/gp/regionalSummary.html.
- Henson, P., and T. A. Grant. 1991. The effects of human disturbance on trumpeter swan breeding behavior. Wildlife Society Bulletin 19:248-257.
- Johnson, R. R., and K. F. Higgins. 1997. Wetland resources of eastern South Dakota. South Dakota State University, Brookings.

- Mitchell, C. D., and M. W. Eichholz. 2010. Trumpeter Swan (Cygnus buccinator). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <u>http://bna.birds.cornell.edu/bna/species/105</u>
- Monnie, J. B. 1966. Reintroduction of the trumpeter swan to its former prairie breeding range. Journal of Wildlife Management 30:691-696.
- Niemuth, N. D., R. E. Reynolds, D. A. Granfors, R. R. Johnson, B. Wangler, and M. E. Estey.
 2008. Landscape-level planning for conservation of wetland birds in the US Prairie
 Pothole Region. Pages 533-560 *in* J. J. Millspaugh and F. R. Thompson, eds. Models for
 planning wildlife conservation in large landscapes. Elsevier Science, Burlington.
- Reynolds, R. E., T. L. Shaffer, C. R. Loesch, and R. R. Cox, Jr. 2006. The Farm Bill and duck production in the Prairie Pothole Region: increasing the benefits. Wildlife Society Bulletin 34:963–974.
- Schmidt, J. H., M. S. Lindberg, D. S. Johnson, and J. A. Schmutz. 2009. Environmental and human influences on trumpeter swan habitat occupancy in Alaska. The Condor 111:266-275.
- Wilen, B. O., and M. K. Bates. 1995. The US Fish and Wildlife Service's National Wetlands Inventory project. Vegetation 118:153-169.