

# Trumpeter Swan Abundance and Growth Rates in Yellowstone National Park

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**ABSTRACT** Decreasing abundance of resident, nonmigratory trumpeter swans (*Cygnus buccinator*) in Yellowstone National Park (YNP), USA, raised concern that this population, which helped facilitate the restoration of the species across North America, may disappear. We quantified trends in abundance of resident and migratory trumpeter swans in YNP from 1967 to 2007 and investigated the potential mechanisms for declining population trends, including cessation of the supplemental feeding program and relocation programs outside of YNP, density dependence, and annual variations in environmental conditions. Estimated abundance of resident trumpeter swans in YNP ranged from 59 individuals in 1968 to 10 individuals in 2007. Using log-linear modeling, the best approximating model chosen from an a priori set of competing models estimated the annual growth rate ( $r$ ) of resident swans from 1967 to 2007 was  $-0.036$  (95% CI =  $-0.042$  to  $-0.030$ , Akaike wt [ $w_i$ ] = 0.44). A competing model provided evidence that decreases in abundance became more dramatic after supplemental feeding of grain outside of YNP was terminated in winter 1992–1993 ( $\hat{r}_{1967-1992} = -0.027$ , 95% CI =  $-0.039$  to  $-0.015$ ;  $\hat{r}_{1993-2007} = -0.053$ , 95% CI =  $-0.029$  to  $-0.080$ ;  $w_i = 0.42$ ). There was little evidence of density-dependent effects on the resident population growth rates ( $\hat{\beta}_{YNPpop} = 0.006$ , 95% CI =  $-0.017$  to  $0.007$ ), but rates were lower following severe winters, wetter springs, and warmer summers. Our results indicate that the YNP population of trumpeter swans is decreasing and may act as a sink to surrounding populations. Thus, population levels of YNP trumpeter swans may depend on management outside the Park and we recommend the National Park Service collaborate with surrounding agencies in managing trumpeter swans throughout the Tri-state region where more productive habitats may exist. (JOURNAL OF WILDLIFE MANAGEMENT 73(5):728–736; 2009)

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Trumpeter swans (*Cygnus buccinator*) were nearly extirpated in North America due to overharvest and habitat destruction (Banko 1960). Conservation measures, including harvest regulations and habitat protection, were enacted nationally and trumpeter swan populations across North America (Fig. 1) have increased over the past 40 years. The Pacific Coast Population increased from 2,847 to 24,928 trumpeter swans between 1968 and 2000, with most growth occurring in the Alaskan flocks (Conant et al. 2002, U.S. Fish and Wildlife Service [USFWS] 2006). The Interior Population increased from 64 to 4,647 trumpeter swans during the same time period (USFWS 2006). The Rocky Mountain Population (RMP) increased from 811 to 5,228 trumpeter swans from 1968 to 2005, but decreasing abundance was observed in some subpopulations (USFWS 2006).

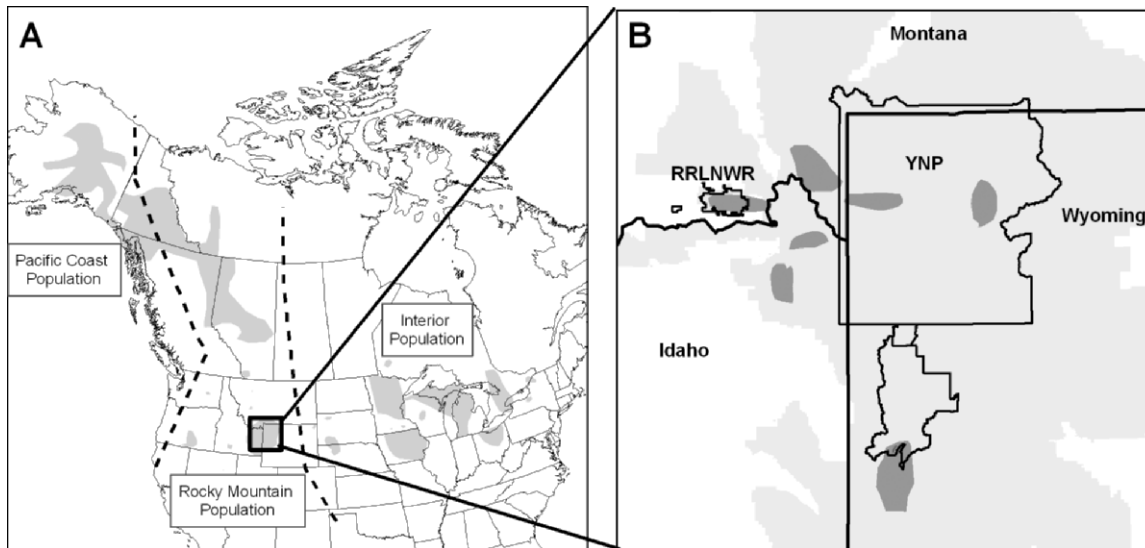
The RMP of trumpeter swans is comprised of several genetically similar subpopulations (Oyler-McCance et al. 2007) that breed in different locations (Fig. 1). Breeding areas for the Canadian subpopulation extend from southeastern Yukon territories to eastern Alberta, whereas breeding areas for the Tri-state subpopulation include the greater Yellowstone region of Montana, Wyoming, and Idaho (USA). Both subpopulations use common wintering sites in the Tri-state region. Most growth in the RMP has occurred in the Canadian subpopulation (Fig. 2). The overall Tri-state subpopulation size has remained stable during the past 40 years; however, declines have been

observed in some areas, including Yellowstone National Park (YNP).

Decreases in the YNP population may be partly attributed to the termination of supplemental feeding, which occurred during winter on Red Rock Lakes National Wildlife Refuge, Montana, from 1936 to 1992. Additionally, in the late 1980s and early 1990s, trumpeter swans were translocated to other regions, wintering ponds were drained, and swans were hazed during winter in the Tri-state region to reduce bird concentrations and establish new populations outside the Tri-state region (USFWS 2003). Despite these activities, overall the number of swans wintering in the Tri-state area continued to increase, probably due to the growth of the Canadian subpopulation (USFWS 2007).

The segment of the Tri-state subpopulation that resides and nests in YNP has experienced a steady decrease in abundance during the past 40 years, raising concern that resident trumpeter swans may disappear from this portion of their native range. Although a long-term population-monitoring program has been conducted in YNP since the late 1960s, no previous studies have quantified trends in population abundance or investigated potential mechanisms for declining trends. We hypothesized that mechanisms could have included cessation of the supplemental feeding program, increasing competition with migratory swans, and changes in environmental conditions in the YNP. Thus, our first objective was to quantify trends in trumpeter swan abundance in YNP from 1967 to 2007, which we divided into 2 periods: 1967–1992 and 1993–2007. The first period

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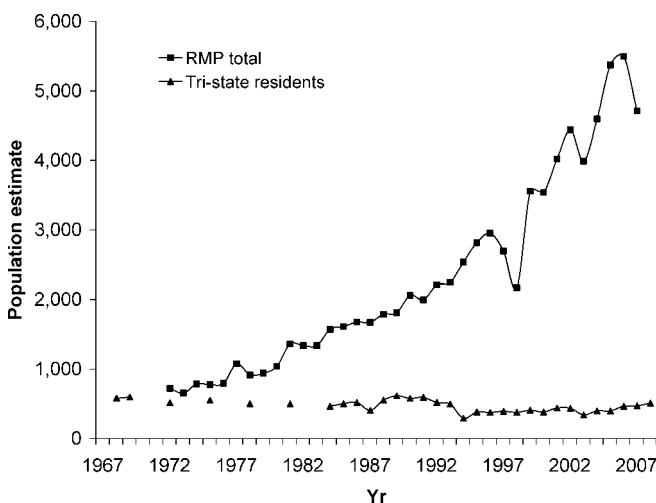


**Figure 1.** Approximate ranges (light grey) of the Pacific Coast, Rocky Mountain, and Interior trumpeter swan populations (Panel A), 1967–2007. The study area, Yellowstone National Park (YNP), USA, was located within the greater Yellowstone area (light grey) to the east of Red Rocks Lake National Wildlife Refuge (RRLNWR) and provided important wintering range (dark grey) for Rocky Mountain trumpeter swans that aggregated in the greater Yellowstone area over winter (Panel B).

was characterized by supplemental feeding of swans for the entire duration and swan translocation and draining of wintering ponds during the later years. The second period was characterized by no supplemental feeding and no active translocation programs or pond draining. Our second objective was to investigate potential impacts of these management actions, density dependence, and annual environmental conditions on the population growth rates of trumpeter swans in YNP.

## STUDY AREA

Yellowstone National Park encompassed approximately 8,991 km<sup>2</sup> in northwestern Wyoming and adjacent portions of Montana and Idaho (44°N, 110°W; Fig. 1). Elevations varied from 1,500 m in the river drainages to 3,400 m on



**Figure 2.** Population estimates for the Rocky Mountain population of trumpeter swans (squares) and the year-round Tri-state flock residents (triangles) during 1971–2007 (U.S. Fish and Wildlife Service 2007).

mountaintops. The climate was characterized by short, cool summers and long, cold winters (Despain 1990). Mean annual precipitation at lower elevations was 25 cm, of which 30–35% was snow. At higher elevations, mean annual precipitation was 180 cm, with most (70%) being snow (Farnes et al. 1999).

During spring and summer, swans occupied small lake, river, and wetland habitats throughout YNP. Approximately 10% of YNP was classified as wetlands (Elliot and Hektner 2000), with areas varying substantially in size, depth, persistence, and availability of water. However, most areas were unsuitable for nesting by trumpeter swans due to high elevation, oligotrophic conditions, fluctuating water levels, or unusual water chemistry due to geothermal influences. Nesting habitat used by trumpeter swans in YNP was considered marginal because nesting lakes were small, shoreline complexity was low, shorelines were commonly timbered, habitat for feeding and nesting was often discontinuous, and feeding areas were generally only at the periphery of wetlands due to deeper water at the center of lakes (Gale et al. 1987). During winter, aggregations of trumpeter swans within YNP occupied ice-free waters on the north and west shores of Yellowstone Lake and along the Yellowstone, Madison, and Firehole rivers. Smaller groups were located in areas where warm springs created ice-free feeding areas on Indian, Squaw, Shoshone, Heart, Beula, and Lewis lakes. Availability of ice-free areas varied annually, and as open-water areas diminished, migrant trumpeter swans left for lower elevations outside YNP.

The degree of interaction among resident trumpeter swans in YNP and other segments of the Tri-state subpopulation was unknown but likely occurred. The Red Rock Lakes–Centennial Valley, Paradise Valley, and Grand Teton National Park segments were located 120 km west, 15 km north, and immediately south of YNP. Some evidence that

trumpeter swans originally banded at Red Rocks Lakes National Wildlife Refuge dispersed to YNP and established nesting territories exists (McEneaney 1986); however, opportunistic banding and marking programs and sampling designs prevent strong inferences regarding patterns of movement and dispersal among Tri-state trumpeter swans (USFWS 2002).

## METHODS

Trumpeter swan surveys were conducted throughout YNP as part of a cooperative interagency effort to count and document distribution of the Tri-state subpopulation of trumpeter swans. Autumn counts to estimate abundance of resident trumpeter swans in YNP occurred each year from 1967 to 2007, except in 1969, 1970, 1972, 1973, 1975, 1981, and 1982 due to insufficient funding. Winter counts to estimate abundance of resident and migratory trumpeter swans in YNP occurred each year from 1974 to 2007. The autumn survey occurred during the second or third week in September and the winter survey occurred during late January or early February. Surveys were conducted aurally along established transects across the park, with one observer and one pilot counting birds from approximately 60 m above ground level. Birds were classified based on size as either adults–subadults or cygnets. Counts were not adjusted for detection probability; however, high continuity among pilots and observers combined with high visibility of trumpeter swans likely resulted in high detection probability and consistency across years (Bart et al. 2007). We excluded surveys conducted prior to 1967 to be consistent with population assessments by the USFWS and because methodologies and survey areas may have changed prior to this time (USFWS 2008).

We first investigated trends in the abundance of trumpeter swans in YNP and potential changes in abundance associated with 2 periods: 1967–1992 and 1993–2007. The primary difference between these periods was supplemental feeding during the former. Also, from 1988 to 1992, swans were translocated from the region for population restoration efforts elsewhere and hazing occurred outside of YNP. Using a log-linear modeling approach, we estimated trends in the rates of change in trumpeter swan abundance for resident and wintering populations. Log-linear models estimate an average rate of population change over a time period (Eberhardt 1987). We tested the hypothesis that rates of change in abundance differed between management periods by comparing a continuous model that estimated one rate for 1967–2007 with a 2-time-period model estimating rates separately for 1967–1992 and 1993–2007. The fit of log-linear models may be poor if the true pattern of change is nonlinear; however, there were no obvious nonlinear trends in our dataset. We assessed log-linear models goodness-of-fit using adjusted coefficient of determination values.

We evaluated abiotic and biotic factors potentially affecting the annual growth rate of resident trumpeter swans in YNP using data from 1983 to 2007. We did not

include data from 1967 to 1982 because data were missing from some of the years. We estimated the annual growth rate for year  $t$  ( $r_t$ ) directly from the abundance data as

$$r_t = \log_e(n_t) - \log_e(n_{t-1})$$

where  $n$  refers to the number of swans counted during autumn surveys. We hypothesized that the growth rate of resident trumpeter swans in YNP may be limited by competition with resident trumpeter swans in YNP or by competition with migratory wintering trumpeter swans. Therefore, we evaluated 3 covariates representing density dependence: number of resident trumpeter swans in YNP, number of trumpeter swans wintering in YNP, and number of trumpeter swans wintering in the Tri-state area.

We evaluated 2 types of density-dependent models, Ricker and Gompertz. The Ricker model assumed linear density dependence,

$$r_t = a + b(n_{t-1}) + \varepsilon$$

whereas the Gompertz model assumed a decrease in growth rate with log counts:

$$r_t = a + b[\log_e(n_{t-1})] + \varepsilon$$

We also evaluated 2 density-independent models, a perturbed exponential-growth model,

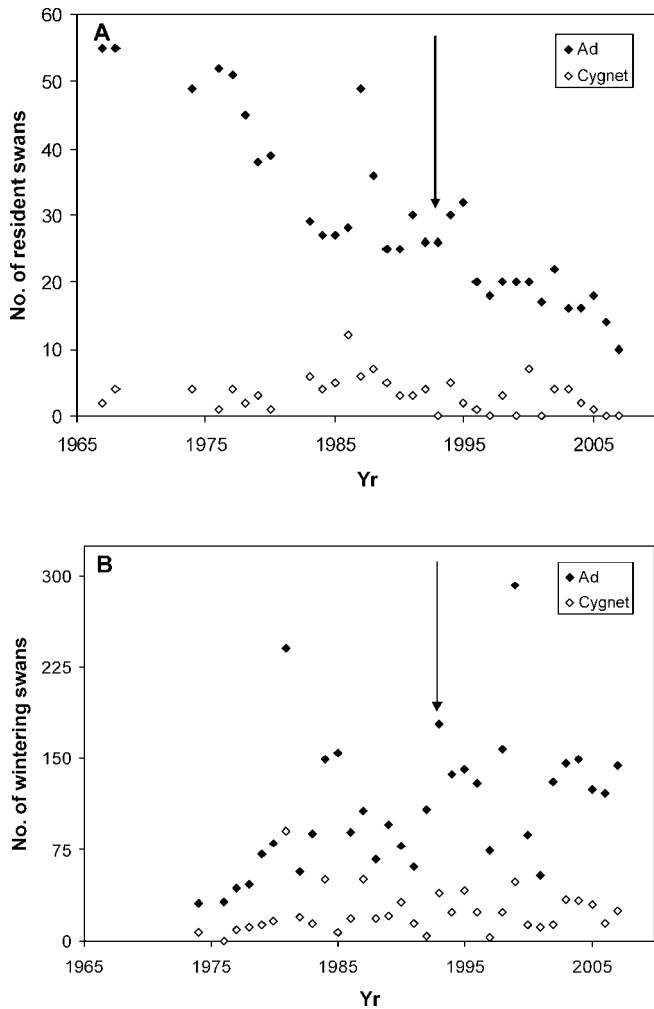
$$r_t = a + \varepsilon$$

where  $a$  represented growth rate in the absence of density dependence, and a random walk model,

$$r_t = \varepsilon$$

where population growth was uncorrelated with population size. Additionally, by adding an indicator variable for management period to our models, we evaluated if management practices outside YNP affected growth rates of resident trumpeter swans inside the park. Prior to constructing our a priori model list, we used partial-rate correlation functions (Berryman and Turchin 2001) to investigate time-delayed dynamics within the trumpeter swan abundance data. We found no evidence of time lags and, therefore, included only density-dependent covariates from the prior year into analyses. Measurement error in the abundance data may inflate Type I error rates, resulting in detecting density dependence when it does not exist (Shenk et al. 1998). However, we assumed this would not be problematic because of consistently high detection rates. Traditional regression models assume error terms are uncorrelated, but this assumption may be violated in time-series modeling if population size and residual errors in one year are correlated with values from the previous year (Cryer and Chan 2008); therefore, we fit each model with and without a first-order autocorrelation parameter. Model performance using adjusted coefficient of determination values.

After determining the most appropriate density-dependent or density-independent model for representing population growth rate based on model selection criteria, we



**Figure 3.** Estimated number of year-round resident (Panel A) and wintering (Panel B) trumpeter swans in Yellowstone National Park, USA, 1967–2007. The arrow denotes implementation of new trumpeter swan management practices, including cessation of supplemental feeding of grain and relocation programs, throughout the Rocky Mountain region.

evaluated effects of annual environmental conditions including temperature, precipitation, North Atlantic Oscillation, and winter severity on annual growth rates of the resident trumpeter swan population in YNP. We evaluated effects of cumulative precipitation during spring (Mar–May) and average temperatures during summer, autumn, and winter (Temp<sub>Sum</sub>: Jun–Aug; Temp<sub>Fall</sub>: Sep–Nov; Temp<sub>Win</sub>: Dec–Feb). We also evaluated effects of spring and autumn

states of the North Atlantic Oscillation (NAO<sub>Spr</sub>: Apr–Jun; NAO<sub>Fall</sub>: Aug–Oct). We used accumulated snow-water equivalent (SWE) measured at Canyon snowpack telemetry (SNOTEL) site during October through April as a metric that integrated severity and duration of winter snow pack. In total, we constructed 9 models. To test for collinearity between predictor variables, we calculated variance inflation factors and we discarded from the analysis any model containing variables with a factor  $\geq 5$ . Based on results of the a priori analysis, we conducted an exploratory analysis of environmental effects on growth rate. In the exploratory analysis, we evaluated new combinations of the original environmental covariates that received support in the a priori analysis, and we evaluated 4 exploratory models.

We developed and assessed hypotheses representing relationships between response variables, resident trumpeter swan abundance, wintering swan abundance, and annual growth rate, and model covariates as a set of a priori competing models. We used Akaike’s Information Criterion corrected for sample size (AIC<sub>c</sub>) and Akaike model weights ( $w_i$ ) to quantify the strength of evidence in the data for each of our hypothesized models and address model-selection uncertainty (Burnham and Anderson 2002). The best model received the lowest AIC<sub>c</sub> score and  $w_i$  provided the weight of evidence in favor of model  $i$  being the actual best model, given one of the candidate models must be the best of the set of candidate models.

## RESULTS

### Population Abundance Data, 1967–2007

We found that abundance of resident trumpeter swans in YNP decreased from 1967 to 2007 (Fig. 3A), and we found support for our hypothesis that rate of decrease was more rapid following changes in management and termination of supplemental feeding outside the park. The 1-period and 2-period models received approximately equal support from the data ( $w_i = 0.44$  and  $w_i = 0.42$ , respectively; Table 1). The continuous-model estimated population abundance declined steadily throughout the entire period ( $\hat{r} = -0.036$ , 95% CI =  $-0.042$  to  $-0.030$ ; Fig. 4A), whereas the 2-period model estimated population abundance declined slowly from 1967 to 1992 ( $\hat{r} = -0.027$ , 95% CI =  $-0.039$  to  $-0.015$ ) and declines accelerated from 1993 to 2007 ( $\hat{r} = -0.053$ , 95% CI =  $-0.029$  to  $-0.080$ ; Fig. 4B).

In contrast, abundance of wintering trumpeter swans in

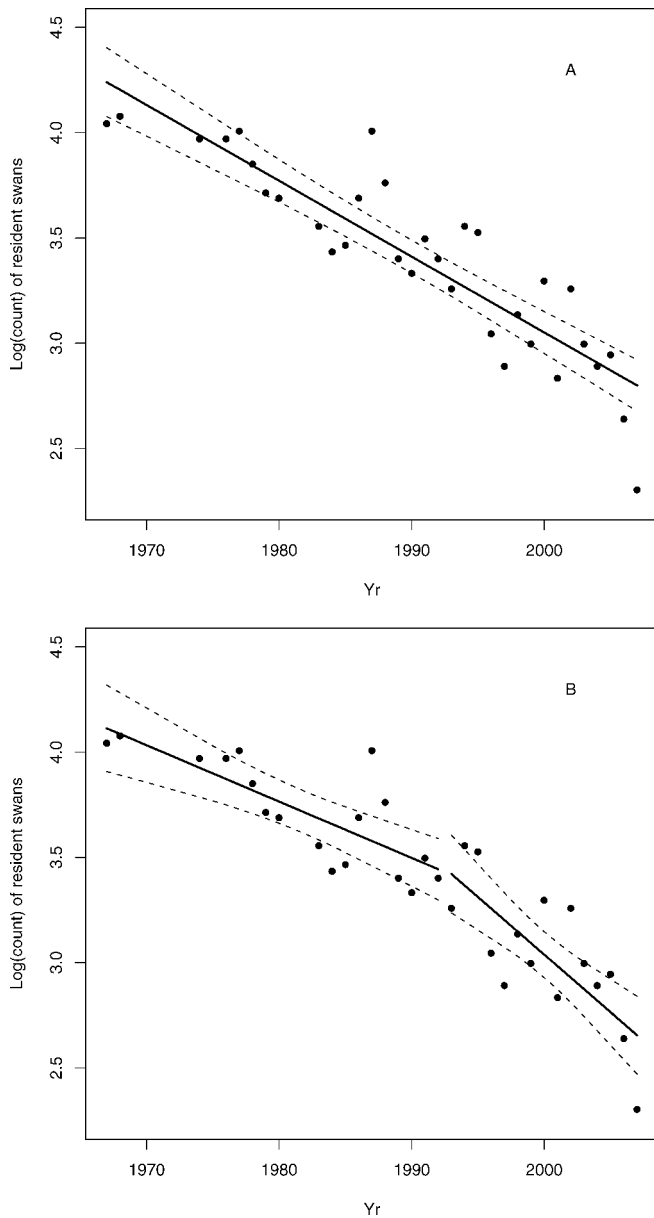
**Table 1.** Model selection results for a priori models examining effects of swan management practices on variations in the log<sub>e</sub> count of resident trumpeter swans in Yellowstone National Park, USA, from 1967 to 2007.

Model <sup>a</sup>	$\Delta AIC_c^b$	$w_i^c$	$R^2_{adj}$
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \varepsilon$	0.00	0.44	0.80
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \beta_3(P \times Y) + \varepsilon$	0.10	0.42	0.81
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \varepsilon$	2.17	0.15	0.80
$\log_e(n_t) = \beta_0 + \varepsilon$	51.09	0.00	

<sup>a</sup> Covariates evaluated included yr (Y) and management period (P). P is an indicator variable in the 2-period model denoting the supplemental feeding period (1967–1992) and the subsequent period with no supplemental feeding (1993–2007).

<sup>b</sup> Akaike’s Information Criterion (AIC<sub>c</sub>) value for the top model was  $-7.45$ .

<sup>c</sup> Akaike model wt ( $w_i$ ).



**Figure 4.** The  $\log_e$  count (solid circles) and predicted rate of change in abundance (solid line) and 95% confidence interval (dashed lines) of resident trumpeter swans in Yellowstone National Park, USA, during 2 periods of swan management. Panel A shows the predicted rate of change estimated over the entire period (1967–2007) and Panel B shows the rate estimated separately for periods of supplemental feeding (1967–1988) and no supplemental feeding (1993–2007).

YNP increased over the study period (Fig. 3B). However, there was some evidence that the number of wintering trumpeter swans leveled off following termination of supplemental feeding (Table 2). The 1-period model received the most support from the data, and estimated population abundance declined steadily ( $\hat{r} = 0.033$ , 95% CI = 0.016–0.050,  $w_i = 0.52$ ; Fig. 5A). The 2-period model also received some support ( $w_i = 0.32$ ), and estimated population abundance increased during the first period ( $\hat{r} = 0.061$ , 95% CI = 0.022–0.101) and remained stable or declined after supplemental feeding was terminated ( $\hat{r} = -0.009$ , 95% CI = -0.078–0.060; Fig. 5B). Overall, there was higher annual variability in wintering counts than in resident counts ( $CV_{\text{resident}} = 0.34$ ,  $CV_{\text{wintering}} = 0.54$ ).

#### Growth Rates, 1983–2007

Annual growth rates of resident trumpeter swans in YNP during 1983–2007 ranged from -0.48 to 0.42 and environmental conditions were variable (Table 3). Density-independent models were most supported (Table 4). The 1-period exponential growth model estimated an annual growth rate declined from 1983 to 2007 at  $\hat{r} = -0.05$  (95% CI = -0.16–0.05,  $w_i = 0.16$ ). Models including density-dependent effects received low support from the data, with the most supported density-dependent model having a weight of 0.07. Of the models containing density-dependent covariates, models including number of resident trumpeter swans and number of wintering trumpeter swans in the Tri-state area received the most support ( $w_i = 0.07$  each); however, neither of these models explained substantial variation in annual growth rates ( $R^2_{\text{adj}} < 0.01$  each). There was little evidence that annual growth rates varied between management periods. Inclusion of an autocorrelation parameter into the top model with covariates (i.e., the 1-period exponential model) did not improve model fit considerably ( $\Delta AIC_c = 1.41$ ). In addition the autocorrelation model estimated annual growth rate ( $\hat{r} = -0.05$ , 95% CI = -0.13–0.03) similar to the 1-period exponential model.

We added environmental covariates to the 1-period exponential growth model and found that environmental covariates improved model fit (Table 5). The top-ranked a priori model included the covariate average summer temperature, with a tendency of higher growth rates following summers with cooler temperatures ( $\beta_{\text{TempSum}} = -0.100$ , 95% CI = -0.197 to -0.005). Models containing no environmental covariates and covariates for winter severity

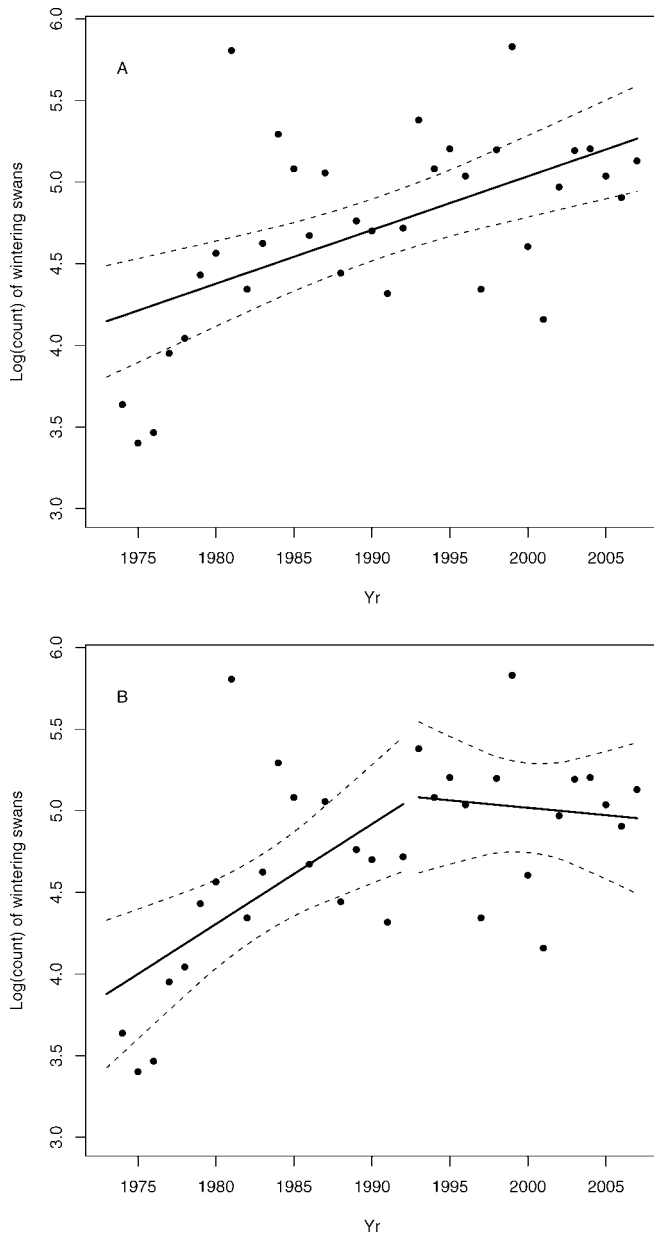
**Table 2.** Model selection results for a priori models examining effects of swan management practices on variations in the  $\log_e$  count of wintering trumpeter swans in Yellowstone National Park, USA, from 1967 to 2007.

Model <sup>a</sup>	$\Delta AIC_c^b$	$w_i^c$	$R^2_{\text{adj}}$
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \varepsilon$	0.00	0.52	0.29
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \beta_3(P \times Y) + \varepsilon$	0.94	0.32	0.33
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \varepsilon$	2.45	0.15	0.31
$\log_e(n_t) = \beta_0 + \varepsilon$	10.18	0.00	

<sup>a</sup> Covariates evaluated included yr (Y) and management period (P). P is an indicator variable in the 2-period model denoting the supplemental feeding period (1967–1992) and subsequent period with no supplemental feeding (1993–2007).

<sup>b</sup> Akaike's Information Criterion (AIC<sub>c</sub>) value for the top model was 53.65.

<sup>c</sup> Akaike model wt ( $w_i$ ).



**Figure 5.** The  $\log_e$  count (solid circles) and predicted rate of change in abundance (solid line) and 95% confidence interval (dashed lines) of the wintering trumpeter swan population in Yellowstone National Park, USA, during 2 periods of swan management. Panel A shows the predicted rate of change estimated over the entire period (1967–2007) and Panel B shows the predicted rate of change estimated separately for periods of supplemental feeding (1967–1988) and no supplemental feeding (1993–2007).

and cumulative spring precipitation also received some support ( $w_i = 0.12$  each). Growth rates tended to be higher following milder winters and springs with low precipitation ( $\hat{\beta}_{SWE} = -0.005$ , 95% CI =  $-0.011$  to  $-0.002$ ;  $\hat{\beta}_{CumulativePrecip} = -0.001$ , 95% CI =  $-0.002$  to  $-0.000$ ). In the exploratory analysis, we found strong support for the model that contained the covariates average summer temperature and cumulative spring precipitation ( $\hat{\beta}_{TempSum} = -0.122$ , 95% CI =  $-0.211$  to  $-0.033$ ;  $\hat{\beta}_{CumulativePrecip} = -0.001$ , 95% CI =  $-0.002$  to  $-0.000$ ). Overall, models explaining variations in annual growth rates for resident trumpeter swans in YNP

**Table 3.** Average annual values and standard deviation, and minimum and maximum annual values for each environmental covariate included in models explaining variation in Yellowstone National Park (USA) trumpeter swan growth rate, 1983–2007.

Covariate <sup>a</sup>	$\bar{x}$	SD	Min.	Max.
SWE (cm)	126.6	44.5	59.2	255.3
Temp <sub>Sum</sub> (° C)	13.6	1.1	10.8	16.0
Temp <sub>Fall</sub> (° C)	2.6	1.3	-0.1	5.1
Temp <sub>Win</sub> (° C)	-7.6	1.4	-11.3	-5.6
NAO <sub>Spr</sub>	0.03	0.60	-1.57	1.56
NAO <sub>Fall</sub>	-0.16	0.59	-1.86	0.34
NAO <sub>Win</sub>	0.49	0.56	-0.63	1.67
Precip (cm)	10.4	3.5	3.9	18.3

<sup>a</sup> SWE = snow-water equivalent, NAO = North Atlantic Oscillation, Precip = precipitation, Sum = Jun–Aug, Fall = Sep–Nov, Win = Dec–Feb, Spr = Mar–May.

that contained environmental covariates received more support from the data than models containing density-dependent or management effects.

## DISCUSSION

Abundance of resident trumpeter swans in YNP decreased substantially over the past 40 years, in contrast to increasing trends in the RMP and stable trends in the Tri-state subpopulation. From 1968 to 2005, the growth rate of the RMP of trumpeter swans averaged 0.054 (Moser 2006), whereas the Tri-state subpopulation growth rate averaged  $-0.008$  (Moser 2006) and the growth rate for resident trumpeter swans in YNP averaged  $-0.036$  (95% CI =  $-0.042$  to  $-0.030$  from 1967 to 2007). Causes of this consistent decrease in YNP are unknown, but tentative explanations include decreased immigration, competition with wintering migrants, and effects of sustained drought and predation on productivity (Gale et al. 1987, USFWS 1998, McEneaney 2006).

We found evidence that decreases in abundance of resident trumpeter swans in YNP were more rapid following cessation of the supplemental feeding program and draining of winter ponds outside of YNP in 1992–1993, suggesting that the dynamics of resident trumpeter swans in YNP may be influenced by larger subpopulations and management actions in the greater Yellowstone area and elsewhere. For example, trumpeter swan dispersal from the nearby Red Rock Lakes–Centennial Valley segment could be an important factor for maintaining resident trumpeter swans in Yellowstone by filling vacant territories or pairing with single adult birds (McEneaney 2006). Banko (1960) suggested that trumpeter swans from the Centennial Valley moved into YNP when numbers were high. Likewise, Gale et al. (1987) concluded that maintenance of nesting residents in YNP in recent decades depended on immigration, most likely of birds dispersing from the Centennial Valley. Thus, when numbers of trumpeter swans in the Centennial Valley decreased by 50% during 1978–1986, the resident flock in YNP began a decrease to its current low numbers (Gale et al. 1987). There are sparse records and few recorded observations to support hypotheses that trumpeter swans banded in the Centennial Valley repeatedly nested in

**Table 4.** Model selection results for a priori density-dependent and density-independent models evaluating effects of management period and density covariates on variations in growth rates of resident trumpeter swans in Yellowstone National Park (YNP), USA, 1967–2007.

Model	Covariates <sup>a</sup>	<i>K</i> <sup>b</sup>	$\Delta AIC_c^b$	$w_i^b$
Random	$r_t = \epsilon$	1	0.00	0.33
Exponential 1-period	$r_t = a + \epsilon$	2	1.40	0.16
Exponential 1-period AR1 <sup>c</sup>	$r_t = a + \epsilon$	3	2.65	0.09
Ricker 1-period	$r_t = a + b(YNPpop) + \epsilon$	3	3.03	0.07
Gompertz 1-period	$r_t = a_1 + b_1[\log_e(TSWinPop)] + \epsilon$	3	3.06	0.07
Ricker 1-period	$r_t = a_1 + b_1(TSWinPop) + \epsilon$	3	3.16	0.07
Gompertz 1-period	$r_t = a + b[\log_e(YNPpop)] + \epsilon$	3	3.20	0.07
Exponential 2-period	$r_t = a + b_2(P) + \epsilon$	3	3.76	0.05
Gompertz 1-period	$r_t = a + b[\log_e(YNPWinPop)] + \epsilon$	3	3.95	0.05
Ricker 1-period	$r_t = a + b(YNPWinPop) + \epsilon$	3	4.03	0.04
Exponential 2-period AR1	$r_t = a + b_2(P) + \epsilon$	4	5.13	0.03
Ricker 1-period AR1	$r_t = a_1 + b_1(TSWinPop) + \epsilon$	4	6.06	0.02
Ricker 2-period	$r_t = a_1 + b_1(YNPpop) + b_2(P) + b_3(YNPpop \times P) + \epsilon$	5	6.20	0.01
Gompertz 2-period	$r_t = a_1 + b_1[\log_e(YNPpop)] + b_2(P) + b_3[\log_e(YNPpop) \times P] + \epsilon$	5	6.52	0.01

<sup>a</sup> Covariates representing density-dependent effects included the no. of resident swans in YNP the previous yr (*YNPpop*), no. of swans wintering in YNP the previous winter (*YNPWinPop*), and no. of swans wintering in the Tri-state area the previous winter (*TSWinPop*). Period (*P*) is an indicator variable in the 2-period model denoting the supplemental feeding period (1983–1992) and subsequent period with no supplemental feeding (1993–2007).

<sup>b</sup> Column headings denote no. of parameters (*K*), Akaike's Information Criterion value corrected for small sample size (*AIC<sub>c</sub>*), and Akaike model wt ( $w_i$ ).

<sup>c</sup> Autoregression (AR1) models include a parameter estimating the autocorrelation coeff. for a lag of 1 yr.

YNP (McEneaney and Sjoström 1983, 1986; McEneaney 1986); however, given the low abundance of YNP swans, only few immigrants would be needed to affect YNP trumpeter swan abundance.

Another explanation for the decrease in YNP trumpeter swan abundance is that increases in the number of Canadian migrants to YNP during winter over the last several decades reduced food resources for resident trumpeter swans during breeding (USFWS 1998). Changes in management of the RMP of trumpeter swans were implemented outside of YNP during 1988–1992, which sought to disperse wintering swans and establish traditions of wintering in new areas. Effects of these management actions on the wintering population in YNP are difficult to assess, and the degree of interchange and

movement among wintering and migratory trumpeter swans inside and outside of YNP is not well-known (McEneaney and Sjoström 1983, 1986; McEneaney 1986). However, we found evidence that the number of trumpeter swans wintering in YNP stabilized after cessation of supplemental feeding, draining of winter ponds, and hazing operations outside the park by winter 1992. Despite the stabilizing abundance of wintering swans, the resident trumpeter swan population continued to decrease and we found little evidence that variations in annual growth rates of resident swans in YNP were affected by the number of migratory wintering swans. These findings suggest that the decrease in resident trumpeter swans in YNP was not primarily attributable to competition with wintering trumpeter swans.

**Table 5.** Model selection results for a priori and exploratory models evaluating effects of environmental conditions on the growth rates of resident trumpeter swans in Yellowstone National Park, USA, from 1983 to 2007.

Model	<i>K</i> <sup>a</sup>	<i>AIC<sub>c</sub></i>	Within-suite		Overall		<i>R</i> <sup>2</sup> <sub>adj</sub>
			$\Delta AIC_c$	$w_i$	$\Delta AIC_c$	$w_i$	
A priori environmental suite <sup>b</sup>							
$r_t = a + b_1(Temp_{Sum}) + \epsilon$	3	5.43	6.57	0.33	2.22	0.14	0.09
$r_t = a + \epsilon$	2	7.67	8.22	0.14	3.87	0.06	0.06
$r_t = a + b_1(SWE) + \epsilon$	3	7.40	8.55	0.12	4.20	0.05	0.05
$r_t = a + b_1(Precip_{Spring}) + \epsilon$	3	7.46	8.60	0.12	4.25	0.05	0.02
$r_t = a + b_1(Temp_{Fall}) + \epsilon$	3	8.21	9.35	0.08	5.00	0.03	0.05
$r_t = a + b_1(NAO_{Win}) + \epsilon$	3	8.58	9.72	0.07	5.37	0.03	0.00
$r_t = a + b_1(NAO_{Spr}) + \epsilon$	3	9.02	10.17	0.05	5.82	0.02	0.00
$r_t = a + b_1(NAO_{Fall}) + \epsilon$	3	9.44	10.59	0.04	6.24	0.02	0.00
$r_t = a + b_1(Temp_{Win}) + \epsilon$	3	9.64	10.78	0.04	6.43	0.02	0.00
Exploratory environmental suite							
$r_t = a + b_1(Temp_{Sum}) + b_2(Precip_{Spring}) + \epsilon$	4	4.35	0.00	0.72	0.00	0.42	0.16
$r_t = a + b_1(Temp_{Sum}) + b_2(SWE) + \epsilon$	4	7.22	2.87	0.17	2.87	0.10	0.13
$r_t = a + b_1(Temp_{Sum}) + b_2(Temp_{Fall}) + \epsilon$	4	9.00	4.65	0.07	4.65	0.04	0.09
$r_t = a + b_1(SWE) + b_2(Precip_{Spring}) + \epsilon$	4	10.01	5.66	0.04	5.66	0.02	0.05

<sup>a</sup> Column headings denote no. of parameters (*K*), Akaike's Information Criterion value corrected for small sample size (*AIC<sub>c</sub>*), and Akaike model wt ( $w_i$ ).

<sup>b</sup> Environmental covariates included winter severity (*SWE*), average summer temperatures (*Temp<sub>Sum</sub>*), average autumn temperatures (*Temp<sub>Fall</sub>*), average winter temperatures (*Temp<sub>Win</sub>*), spring North Atlantic Oscillation (*NAO<sub>Spr</sub>*), autumn North Atlantic Oscillation (*NAO<sub>Fall</sub>*), winter North Atlantic Oscillation (*NAO<sub>Win</sub>*), and cumulative spring precipitation (*Precip<sub>Spring</sub>*).

There was strong support in the data that decreases in abundance of resident trumpeter swans in YNP were influenced by annual variations in environmental conditions and naturally occurring events such as severe winter weather and droughts. Growth rates of trumpeter swans in YNP increased following summers with cooler temperatures and drier springs. Decreased spring precipitation may result in warmer spring water temperatures and increased aquatic vegetation growth or may reduce nest failures due to flooding (Gale et al. 1987). Cooler summers may create favorable conditions in wetland complexes used for foraging and nesting by preventing wetlands from drying until later in the season and increasing aquatic plant production. Additionally, molting adult trumpeter swans and cygnets are flightless during much of the summer and rely on ponds for protection from predators. Therefore, cooler summers may prevent or delay ponds from drying and provide refuge areas for trumpeter swans.

Other possible mechanisms influencing YNP trumpeter swan abundance include changes in reproductive performance related to changes in wetland habitats, human disturbance, or rates of predation, increased mortalities associated with lead poisoning, or reduced foraging success associated with increasing YNP ungulate populations. Long-term changes or reductions in wetland habitat may reduce suitable nesting habitat within YNP, thereby leading to decreases in reproductive performance. In YNP, productivity of wetlands used for nesting varies widely with <20% of nesting sites contributing >60% of all fledged offspring (P. White, National Park Service, unpublished data). Therefore, alteration or disturbance at these important nesting sites, which occur within a landscape of likely marginal trumpeter swan habitat, may lead to substantial changes in YNP swan reproductive success and, ultimately, changes in abundance. Predation by grizzly bears (*Ursus arctos*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), ravens (*Corvus corax*), eagles (*Haliaeetus leucocephalus*, *Aquila chrysaetos*), and wolves (*Canis lupus*) has been documented to cause reproductive failure or mortality for trumpeter swans in YNP (McEneaney 2006) and over the past 40 years overall abundance of these predators has increased substantially (Stahler et al. 2002, Smith 2005, Schwartz et al. 2006), potentially leading to lower reproductive success or increased trumpeter swan mortality. Additionally, increases in bison (*Bison bison*) or elk (*Cervus elaphus*) populations (Taper and Gogan 2002, White and Garrott 2005, Fuller et al. 2007) may have increased competition with trumpeter swans for early spring emergent vegetations, altering habitat quality and trumpeter swan foraging success. Lead poisoning is an important cause of trumpeter swan mortality in the Tri-state area and other portions of their range (Blus et al. 1989, Degernes et al. 2006). Though there is no waterfowl hunting within YNP, trumpeter swans that breed within YNP may forage outside of the park during other portions of the year (where they may be exposed to lead), or trumpeter swans immigrating into YNP from more

productive portions of the Tri-state area may be exposed to lead during dispersal (Whitman and Mitchell 2004).

The National Park Service is committed to the conservation of resident trumpeter swans and preserving habitat for winter migrants in YNP because trumpeter swans are part of the natural biota and a symbolic species with considerable historical significance. Thus, managers at YNP have identified the trumpeter swan as a Native Species of Special Concern, listed them as a high priority in the park's Strategic Plan, and established a goal to improve or stabilize the status of trumpeter swans from the 20 resident adults, 7 nesting pairs, and 2 fledglings produced in 2000 (National Park Service 2000). Actions taken to facilitate this goal included 1) implementing a monitoring protocol that increased survey frequency, 2) identifying the most productive nesting areas, 3) managing human access at important wetland areas, and 4) prohibiting the use of leaded split-shot sinkers, weighted jigs, and soft lead-weighted ribbon. Additionally, outside of YNP, efforts to eliminate introduced mute swans (*Cygnus olor*) were initiated in 1987 and an expansion flock of trumpeter swans in the nearby Paradise Valley of Montana was established in 1989 (McEneaney 2006). Despite these actions, only 10 trumpeter swans resided in YNP during 2007. Thus, barring aggressive interventions (e.g., predator-proof fencing of wetlands, manipulations of hydrology) that are not aligned with National Park Service guidelines to minimize human intervention, trumpeter swan presence in YNP may be primarily limited to occasional residents and wintering aggregations of migrants from outside the park.

## MANAGEMENT IMPLICATIONS

The best available scientific evidence suggests that YNP provides marginal conditions for nesting and acts as a sink for swans dispersing from more productive areas within the Tri-state range. This effect has been compounded over the last several decades by natural changes in habitat (e.g., decreased wetlands due to long-term drought or chronic warming) and community dynamics (e.g., recovery of predator populations). Thus, current management goals (i.e., 20 resident ad, 7 nesting pairs, and 2 fledglings) may be unattainable and need revision given the persistent, limited recruitment and interchange that will ultimately lead to a transient presence of resident trumpeter swans in YNP. The National Park Service should pursue a vision and agenda for the cooperative, integrated management of Tri-state trumpeter swans with agencies controlling more productive areas within the Tri-state range.

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## LITERATURE CITED

- Banko, W. E. 1960. The trumpeter swan, its history, habits, and population in the United States. *North American Fauna* 63. U.S. Department of Interior, Bureau of Sport Fish and Wildlife, Washington, D.C., USA.
- Bart, J., C. D. Mitchell, M. N. Fisher, and J. A. Dubovsky. 2007. Detection ratios on winter surveys of Rocky Mountain trumpeter swans *Cygnus buccinator*. *Wildfowl* 57:21–28.
- Berryman, A., and P. Turchin. 2001. Identifying the density-dependent structure underlying ecological time series. *Oikos* 92:265–270.
- Blus, L. J., R. K. Stroud, B. Reiswig, and T. McEneaney. 1989. Lead poisoning and other mortality factors in trumpeter swans. *Environmental Toxicology and Chemistry* 8:263–271.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference*. Springer-Verlag, New York, New York, USA.
- Conant, B., J. Hodges, D. Groves, and J. King. 2002. Census of trumpeter swans on Alaskan nesting habitats, 1968–2000. *Waterbirds* 25:3–7.
- Cryer, J. D., and K. Chan. 2008. *Time series analysis with applications in R*. Springer Science and Business Media, New York, New York, USA.
- Degernes, L., S. Heilman, M. Trogon, M. Jordan, M. Davison, D. Kraege, M. Correa, and P. Cowen. 2006. Epidemiologic investigation of lead poisoning in trumpeter and tundra swans in Washington State, USA, 2000–2002. *Journal of Wildlife Diseases* 42:345–358.
- Despain, D. G. 1990. *Yellowstone vegetation*. Robert Rinehart, Boulder, Colorado, USA.
- Eberhardt, L. L. 1987. Population projections from simple models. *Journal of Applied Ecology* 24:103–118.
- Elliot, C. R., and M. M. Hektner. 2000. *Wetland resources in Yellowstone National Park*. Yellowstone National Park, Wyoming, USA.
- Farnes, P., C. Heydon, and K. Hansen. 1999. *Snowpack distribution across Yellowstone National Park*. Montana State University, Bozeman, USA.
- Fuller, J., R. A. Garrott, and P. J. White. 2007. Emigration and density dependence in Yellowstone bison. *Journal of Wildlife Management* 71:1924–1933.
- Gale, R. S., E. O. Garton, and I. J. Ball. 1987. *The history, ecology and management of the Rocky Mountain population of trumpeter swans*. U.S. Fish and Wildlife Service, Montana Cooperative Wildlife Research Unit, Missoula, USA.
- McEneaney, T. 1986. *Movements and habitat use patterns of the Centennial Valley trumpeter swan population (Montana) as determined by radio telemetry data*. Red Rock Lakes National Wildlife Refuge, Lima, Montana, USA.
- McEneaney, T. 2006. *Yellowstone bird report, 2005*. National Park Service, YCR-2006–2, Yellowstone National Park, Wyoming, USA.
- McEneaney, T., and R. Sjöstrom. 1983. *Migration and movement of the Tri-state trumpeter swan population—an analysis of neck-banding data*. Red Rock Lakes National Wildlife Refuge, Wildlife Management Study no. 9, Lima, Montana, USA.
- McEneaney, T., and R. Sjöstrom. 1986. *Trumpeter swan movements and seasonal use, Centennial Valley (Montana)—an analysis of neck-banding data*. Red Rock Lakes National Wildlife Refuge, Lima, Montana, USA.
- Moser, T. J. 2006. *The 2005 North American trumpeter swan survey*. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Denver, Colorado, USA.
- National Park Service. 2000. *Strategic plan, FY 2001–2005*. Yellowstone National Park, Mammoth, Wyoming, USA.
- Oyler-McCance, S. J., F. A. Ransler, L. K. Berkman, and T. W. Quinn. 2007. A rangewide population genetic study of trumpeter swans. *Conservation Genetics* 8:1339–1353.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Shenk, T. M., G. White, and K. Burnham. 1998. Sampling-variance effects on detecting density-dependence from temporal trends in natural populations. *Ecological Monographs* 68:445–463.
- Smith, D. W. 2005. Ten years of Yellowstone wolves. *Yellowstone Science* 13:7–33.
- Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour* 64:283–290.
- Taper, M. L., and P. Gogan. 2002. The northern Yellowstone elk: density dependence and climatic conditions. *Journal of Wildlife Management* 66:106–122.
- U.S. Fish and Wildlife Service [USFWS]. 1998. *Pacific flyway management plan for the Rocky Mountain population of trumpeter swans*. Subcommittee on Rocky Mountain trumpeter swans, Pacific flyway study committee, Portland, Oregon, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2002. *An assessment of information pertaining to the status of trumpeter swans (Cygnus buccinator)*. Division of Migratory Birds and State Programs, Denver, Colorado, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2003. *Trumpeter swan survey of the Rocky Mountain population, winter 2003*. Division of Migratory Birds and State Programs, Denver, Colorado, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2006. *The 2005 North American trumpeter swan survey*. Division of Migratory Birds and State Programs, Denver, Colorado, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2007. *Trumpeter swan survey of the Rocky Mountain population, winter 2007*. Division of Migratory Birds and State Programs, Denver, Colorado, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2008. *Trumpeter swan survey of the Rocky Mountain population, fall 2007*. Division of Migratory Birds and State Programs, Denver, Colorado, USA.
- White, P. J., and R. A. Garrott. 2005. *Yellowstone's ungulates after wolves—expectations, realizations, and predictions*. *Biological Conservation* 125:141–152.
- Whitman, C. L., and C. D. Mitchell. 2004. *Winter trumpeter swan mortality in southwestern Montana, eastern Idaho and northwestern Wyoming, November 2000 through January 2003*. *North American Swans, Bulletin of the Trumpeter Swan Society* 32(1):96–100.

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