Retrospective analysis of Trumpeter Swan *Cygnus buccinator* decline in Yellowstone National Park, USA

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Abstract

The Trumpeter Swans *Cygnus buccinator* that nest and winter in Yellowstone National Park (YNP) played an important role in the survival of the species when unregulated shooting and habitat loss threatened them with extirpation. While conservation measures saved the Trumpeter Swan, and their numbers have increased greatly across North America, the abundance and productivity of YNP's resident Trumpeter Swans declined from about 1960 until 2010, when captive-bred releases began to supplement their numbers. Many hypotheses for the initial decline in YNP Trumpeter Swans exist, including human disturbance at nesting areas, changes in habitat quality, predation and lower Trumpeter Swan abundance in the broader geographic region reducing the immigration of swans into YNP. This study used long-term historical Trumpeter Swan monitoring data and existing covariate data to explore competing hypotheses about possible factors associated with temporal and spatial variation in swan abundance and reproductive success in YNP during 1931–2011. Bayesian reversible jump Markov chain Monte Carlo (RJMCMC) methods were used to evaluate whether covariates representing swan decline hypotheses explained variation in annual, wetland-level patterns of where swans were absent (Absent), present but without fledged young (Present), and bred successfully with fledged young (Successful) each year. Model covariates that explained variation in wetland status supported several of the hypotheses for Trumpeter Swan decline. Wetlands within YNP were more likely to have Trumpeter Swans Present as opposed to Absent during 1931–1959 in years when the total abundance of Trumpeter Swans in the broader geographic area around YNP was greater. During 1960–2011, wetlands within YNP were more likely to have Trumpeter Swans Present as opposed to Absent when estimated Grizzly Bear *Ursus arctos* abundance was lower and when YNP recorded fewer annual visitors, although these covariates correlated strongly with time, making it difficult to distinguish between the underlying causes of temporal trends and preventing stronger inferences from being made. The lakes, rivers and wetlands identified quantitatively in this study as being the most likely to have swans Present and/or Successful can be a useful tool to help YNP staff manage important swan habitat or justify future management actions.

Key words: Bayesian, conservation management, Markov chain Monte Carlo, non-migratory swans, reversible jump.

By 1933, the number of Trumpeter Swans *Cygnus buccinator* in the continental United States was reduced to *c.* 70 individuals, nesting and wintering in Yellowstone National Park (YNP or Park) and the surrounding Greater Yellowstone area (Banko 1960). Conservation efforts to protect the dwindling Trumpeter Swan (hereafter Trumpeter Swan or swan) population proved successful and their numbers increased across North America in subsequent decades. Despite current restoration to much of their former range, the slowing or declining growth rates of groups of Trumpeter Swans in some regions continues to give cause for concern due to the long-lived species' delayed maturity and inconsistent production of young (Mitchell & Eichholz 2020). Non-migratory Trumpeter Swans nesting and wintering within YNP and the surrounding Greater Yellowstone area represent one such group. After increases during the 1940s and 1950s, YNP Trumpeter Swan numbers declined from a maximum of 87 total swans in 1954 to only two in 2010 (based on autumn survey data; see Fig. 1). There was serious concern that if the low swan numbers could not be increased, YNP Trumpeter Swans, which had helped to perpetuate the species when it was threatened with extirpation in the early 20th century, could disappear.

Three populations have been defined in North America to facilitate monitoring and management of the species: the Pacific Coast Population (PCP), the Rocky Mountain Population (RMP) and the Interior Population (IP) (Pacific Flyway Council 2017). Situated within the U.S. breeding segment of the RMP, which summers in YNP and portions of Idaho, Montana and Wyoming (tri-state area) within the Greater Yellowstone area, YNP Trumpeter Swans are generally non-migratory but are believed to move short distances outside the Park to access food resources or more moderate winter conditions. During winter, the U.S. breeding segment is joined by swans from the migratory Canadian breeding segment of the RMP in the Greater Yellowstone area, where the two population segments can intermingle. While the RMP has grown consistently since regular monitoring began in 1968, much of that growth is attributed to the Canadian breeding segment; the tri-state area had a slightly negative growth rate from 1968–2015 (Groves 2017; Olson 2024). Core areas of the RMP that were once productive strongholds for Trumpeter Swans, such as YNP, Red Rock Lakes National Wildlife Refuge (RRLNWR) and Grand Teton National Park (GTNP), have experienced declining swan abundance in recent decades.

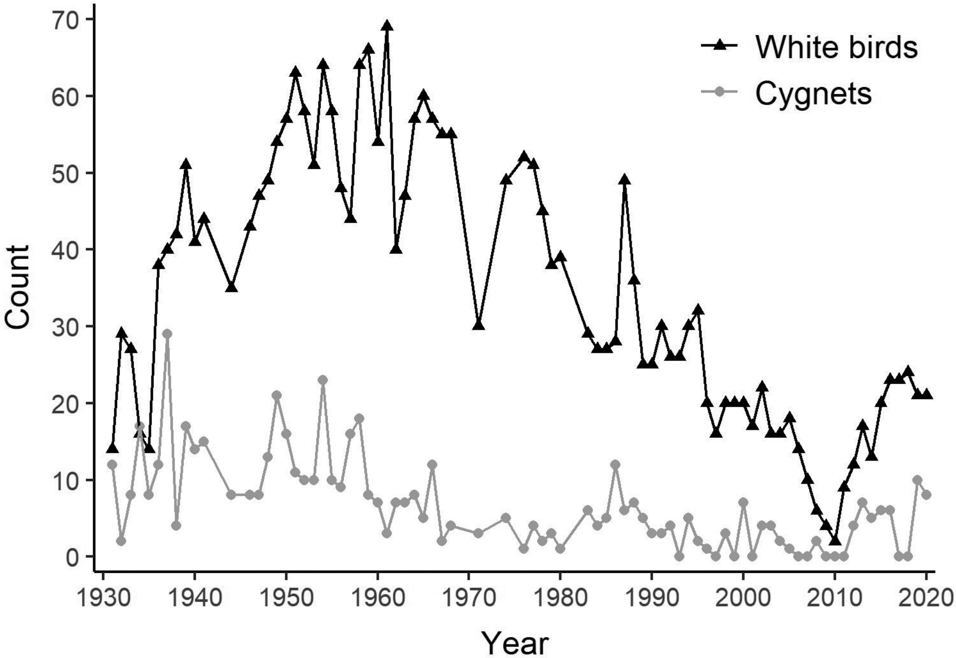

Figure 1. Count data of white birds (adult and yearling swans) and cygnets recorded during autumn Trumpeter Swan surveys in Yellowstone National Park, USA from 1931–2020.

Recognising the precarious state of Trumpeter Swans in YNP, a workshop in 2011 gathered swan and wetland experts to assess possible explanations for the decline in swan abundance and to recommend management strategies to halt and/or reverse the decline (Smith & Chambers 2011). Although the experts did not reach agreement on the best methods for achieving either of these two objectives, several potential reasons for the swan decline were identified: 1) human disturbance at nesting areas; 2) predation; 3) habitat change of historic nesting areas, possibly due to climate change; and 4) changes in YNP Trumpeter Swan immigration and/or emigration, possibly due to changes in swan abundance in the broader geographic region surrounding the Park (Smith & Chambers 2011). These four hypotheses were chosen as the focus of the analyses presented here.

Human disturbance has long been recognised for its potentially detrimental impacts on Trumpeter Swans. In a preliminary report from 1941 on YNP Trumpeter Swans, four of seven management recommendations related to minimising the impacts of human disturbance (Condon 1941). Since that time, human activity has been shown to have a negative effect on Trumpeter Swans and other bird species by reducing their productivity in various ways, including nest abandonment, egg mortality due to exposure, increased predation of eggs and hatchlings, depressed feeding rates of adults and avoidance of otherwise suitable habitat (Page 1976; Cooper 1979; Shea 1979; Henson & Grant 1991). The number of annual visitors to YNP has increased markedly from 221,000 in 1931 (when regular monitoring of swans began) to over four million in recent years (NPS 2019). Furthermore, the peak of Trumpeter Swan breeding activity occurs in June, July and August, when swans incubate eggs, hatch young and raise broods (Banko 1960; Shea 1979; Shea *et al.* 2013). This time period coincides with a surge in Park visitation, accounting for roughly 64% of annual visits (2014–2018 data in NPS 2019). These seasonal and long-term trends in Park visitation may have increased the potential for human disturbance impacts on nesting and brood-rearing Trumpeter Swans.

Predation and the reproductive failure of Trumpeter Swans due to predators is another possible reason for the decline in YNP Trumpeter Swans. Many of the predators found in YNP today have been reported as causing reproductive failure or mortality of Trumpeter Swans, including Bald Eagles *Haliaeetus leucocephalus*, Golden Eagles *Aquila chrysaetos*, Common Ravens *Corvus corax*, Coyotes *Canis latrans*, Grey Wolves *Canis lupus*, Grizzly Bears *Ursus arctos* and Black Bears *Ursus americanus* (Banko 1960; Hansen *et al.* 1971; McEneaney 2006; Koel *et al.* 2019). Since the cessation of predator control in YNP in 1935, there have been natural and human-influenced increases in the overall abundance of several predator species (Stahler *et al.* 2002; White *et al.* 2017; Smith *et al.* 2020). Although observations from early decades of the study period were made sporadically, evaluation of those records and of recent Park data suggests that predation of Trumpeter Swans may occur more frequently than previously thought. One recent study of YNP Trumpeter Swan productivity and fledging success, based on data from 1987–2007, found that 41% of egg failure (n = 35) and 100% of pre-fledging cygnet mortality (n = 18) were attributed to predation (Proffitt *et al.* 2010).

The habitat quality of Trumpeter Swan breeding and foraging areas in YNP has been considered marginal by some researchers despite the diversity of water resources present within the Park. Compared to other areas, even within the Greater Yellowstone area, nesting lakes in YNP are relatively small and have timbered shorelines with low complexity, feeding and nesting habitat are often discontinuous, and foraging areas are typically limited to the shallow periphery of deeper wetlands and lakes (Shea *et al.* 2013). Furthermore, many water bodies in the Park are thought to be unsuitable for nesting because of their high elevation, fluctuating water levels, oligotrophic conditions or unusual water chemistry due to geothermal activity (Shea 1979). YNP did however support over 60 total Trumpeter Swans and produce 10 cygnets annually on average during the 1940s and 1950s before numbers began to decline during the 1960s. Many historically productive lakes and wetlands that were regularly occupied by Trumpeter Swans for years or decades have ceased to be recorded with cygnets or even be visited by swans in recent years. These temporal and spatial patterns in Trumpeter Swan habitat use and productivity suggest that something about their habitat may have changed over time. Furthermore, it is generally believed that Trumpeter Swan habitat and reproductive success is negatively affected by cool, wet springs and hot, dry summers; long term trends in annual temperature and precipitation, possibly linked to climate change, therefore may be making these unfavourable environmental conditions more common in YNP (Smith & Chambers 2011).

The abundance of Trumpeter Swans in the broader geographic area around YNP may influence the movement of swans in (immigration) and out (emigration) of the Park. Management practices in some areas surrounding YNP, which changed during the course of this study, could have reduced the ability of these areas to act as sources of Trumpeter Swans. RRLNWR, located *c.* 50 km west of YNP, was created in 1935 to halt illegal Trumpeter Swan shooting and to protect vital nesting habitat. Data from banding and marking programmes at RRLNWR provide evidence that local movements of Trumpeter Swans within the Greater Yellowstone area are common and that some swans emigrated from the refuge to establish nesting territories in YNP, but the limited nature of the available data prevented stronger inferences from being made (McEneaney 1986; McEneaney & Sjostrom 1986; Mitchell & Shandruk 1992; Olson *et al.* 2013). As Trumpeter Swan numbers increased in response to initial conservation measures, managers began translocating swans from RRLNWR to other areas as early as 1938. Translocation efforts were redoubled in subsequent decades and would eventually relocate more than 1,500 swans from RRLNWR and Harriman State Park (*c.* 30 km west of YNP) outside of the Greater Yellowstone area (Drewien *et al.* 2002; Shea *et al.* 2002). Other management actions included supplemental feeding at RRLNWR from 1936–1992, hazing of swans at high-risk wintering sites, and the draining of ponds to reduce concentrations of wintering swans (Proffitt *et al.* 2009). While helping to expand the overall geographic range of Trumpeter Swans, these management actions may have impacted swan numbers in the Greater Yellowstone area and prevented areas like RRLNWR or the tri-state region from acting as sources of immigrants into YNP.

Despite a lack of consensus regarding the factors contributing to the decline in YNP swan abundance following the expert workshop in 2011, the decision was made to install artificial nest platforms at two important swan nesting locations and to augment Trumpeter Swan numbers while swans were still occurring within the Park. From 2012–2021, in partnership with the Wyoming Wetlands Society, a total of 51 captive-reared Trumpeter Swans were released in the Park. While restoration efforts may be acting to combat the multi-decadal decline, the initial cause(s) and current drivers of Trumpeter Swan abundance and productivity in YNP are not well understood. Given the current number of swans in YNP, especially those that breed and successfully fledge cygnets, opportunities to make direct observations of Trumpeter Swans breeding in the Park are limited. Further, as intensive management actions have taken place for over a decade now and are ongoing, observations can no longer be made on the system that first experienced declining swan abundance and productivity in the 1960s. Consequently, this retrospective analysis was undertaken to take advantage of the long-term monitoring of Trumpeter Swans in YNP by exploring the potential of existing data sets to investigate the various hypotheses regarding the decline in their abundance and productivity. Analysis details and results of this study expand on Smith *et al.* (2023) to try to obtain a better understanding of the drivers of swan abundance and productivity trends, and the efficacy of ongoing restoration efforts in YNP.

Methods

Study area

YNP encompasses approximately 9,000 km^2 of northwestern Wyoming and small portions of neighbouring Idaho and Montana. The Park's elevation ranges from 1,600 m in the northwest (where the Gardner River drains into the Yellowstone River) to nearly 3,500 m in the southeast at the summit of Eagle Peak, with much of the Park being situated on a forested plateau at 2,128–2,432 m (Shea 1979). Varying greatly in their size, depth and seasonal fluctuations, YNP's water resources make up *c.* 10% of the Park's area (Elliot & Hektner 2000). Characterised by its varied topography, weather conditions in YNP can vary greatly between different geographic areas of the Park and between years, but it generally experiences short, cool summers and long, cold winters (Shea 1979; Despain 1990).

Data collection

Autumn Trumpeter Swan surveys were conducted annually in YNP from 1931 to 2020, except in 1942–1943, 1945, 1969–1970, 1972–1973, 1975, 1981 and 1982 when there was insufficient funding. The survey generally took place during the second or third week of September, so that adults and subadults could be distinguished from cygnets produced during the current breeding season. Surveys were generally conducted from a fixed-wing aircraft with one pilot and one observer counting birds at *c.* 60 m above ground level along established transects. High continuity among pilots and observers combined with high visibility of Trumpeter Swans likely resulted in very high detection probability and consistency across years (Bart *et al.* 2007). Consequently, counts of white birds (*i.e.* adults and yearlings) and cygnets were not adjusted for detection probability. The 194 unique locations, or wetlands, where Trumpeter Swans were observed in at least one year during autumn surveys from 1931–2020, were grouped into 50 wetland complexes based on their geographic location. Here, the term "wetland" is used generically to include both wetlands and deepwater habitats, including lakes, rivers and other bodies of water where Trumpeter Swans were observed during autumn surveys. Some individual wetlands remained that did not fit within a larger geographic grouping, but individual wetlands and grouped wetland complexes are simply referred to as wetlands hereafter. The 194 unique wetland locations that comprise the 50 wetland complexes are delineated in Shields (2021).

The autumn survey is designed to capture productivity as well as total abundance and distribution, and is conducted at a time when swans are generally situated on breeding territories and cygnets are close to fledging (Groves 2017; Olson 2024). Thus, observations during the autumn surveys of cygnets at wetlands other than those where they were produced are thought to be rare; it therefore was assumed that the wetland where cygnets were observed was the same wetland where they were produced. It should also be acknowledged that, given the timing of the autumn survey, it is possible that failed nesting attempts could have been overlooked, or that non-breeding swans may have been observed at a wetland different from the one where a failed nest attempt was made. Additional survey flights in the early breeding period were not conducted regularly, however, so it was not possible to investigate these cases in further detail. Despite these difficulties, the autumn surveys remain the longest-term, most consistent effort to monitor the Park's Trumpeter Swans, and these data are used here because they provide the best data available for describing spatio-temporal variation in swan use of the Park over the extensive time period considered in this study.

Wetland-specific counts of white birds and cygnets from YNP autumn Trumpeter Swan surveys were used to develop the two response variables used in the analysis. First, the status of each wetland where Trumpeter Swans were observed was classified for each year of the study as having Trumpeter Swans: (1) "Absent" (*i.e.* no white bird or cygnet was observed at that location during the autumn survey), (2) "Present" (if one or more white birds but no cygnets were observed) or (3) "Successful" (if one or more Trumpeter Swan cygnets were observed, regardless of the presence of white birds, indicating that a pair had bred successfully; see Fig. 2 for time series of annual Park-wide counts of swan wetlands by status). Hereafter, Absent, Present and Successful (capitalised) refer to their respective wetland status level. The levels of wetland status were chosen for their biological significance and to prevent overlap of the response data. Next, the three wetland status levels described above were used to create two binary response variables to differentiate between wetlands where swans were: (1) Present *versus* Absent (Present/Absent), where wetlands were coded annually as Absent = 0 and Present = 1, and (2) Successful *versus* Present (Successful/Present), where wetlands were coded annually as Present = 0 and Successful = 1. The two binary wetland status response variables were used separately; *i.e.* each model included either the Present/Absent or the Successful/ Present response variable, which allowed for the exploration of covariates that were associated with the probability of a wetland being classified as Present *versus* Absent, and also as being classified as Successful *versus* Present.

As covariate data sets relating to the potential mechanisms behind YNP Trumpeter Swan decline had not previously been fully assessed, we also described and collated the covariate data potentially available through a literature review, meetings with YNP staff from various disciplines, and records in the YNP archives. In total, 14 covariate data sets were developed to test the four hypotheses for Trumpeter Swan decline in YNP (Table 1).

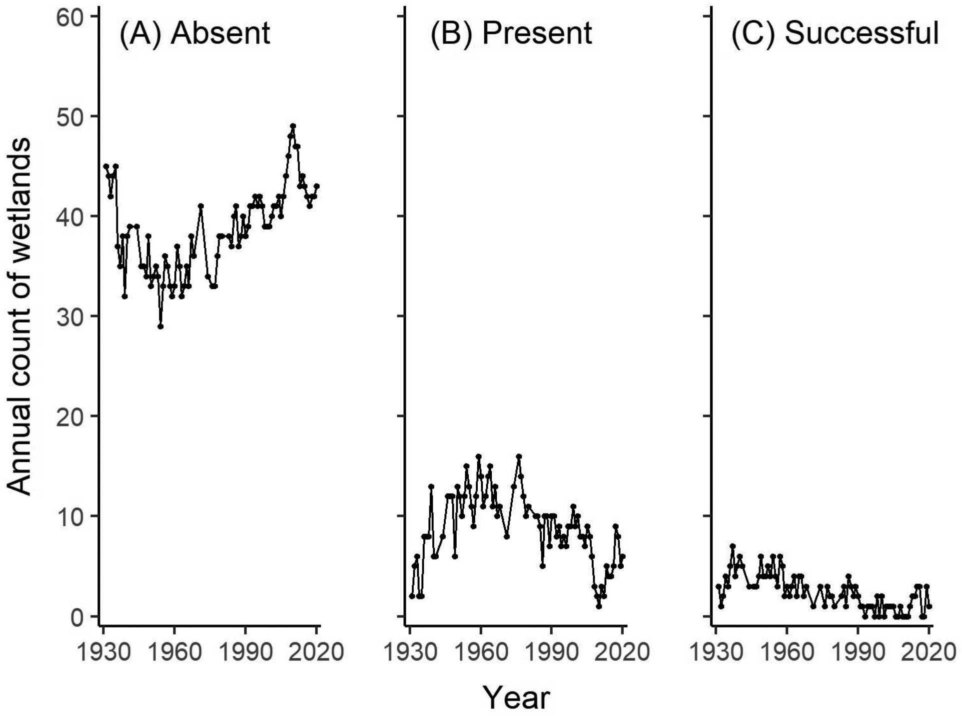

Figure 2. Annual Park-wide counts of Trumpeter Swan wetlands, by wetland status, in Yellowstone National Park, USA from 1931–2020. (A) Absent = no Trumpeter Swans observed at that location during the autumn survey; (B) Present = one or more white birds but no cygnets observed, and (C) Successful = one or more Trumpeter Swan cygnets observed, indicating that a pair had bred successfully.

Only the number of annual YNP visitors (*Visitor*) could be used to quantify the human disturbance hypothesis; attempts to develop other human disturbance data sets were unsuccessful as more detailed YNP visitor-use statistics are not available until 1979. Annual abundance estimates for Greater Yellowstone area Grizzly Bears (*Grizzly*) and YNP Grey Wolves (*Wolf*) were used to quantify the potential for predators to have a negative impact on Trumpeter Swan survival and productivity. Additional data sets of predator abundance were sought, but there is only sporadic information for Coyotes and Ravens, and regular Bald Eagle monitoring did not take place for most of the time period covered by this study, preventing the investigation of these predator species within the models. Total (both white birds and cygnets) annual Trumpeter Swan abundance estimates for RRLNWR (*RRLtrus*) and the tri-state area (*TRItrus*) were used to investigate whether swan trends in the broader region around YNP affected the presence or fledging success of swans within YNP.

Table 1. Description of RJMCMC model covariates used to quantify the four hypotheses for Trumpeter Swan decline in Yellowstone National Park, USA evaluated in this study.

Covariate abbreviation	Covariate description	Hypothesis addressed
Grizzly	Annual Greater Yellowstone area Grizzly Bear abundance	Predation
Iceoff	Annual ordinal date that Yellowstone Lake became ice-free	Habitat quality
PHDI	Annual Palmer Hydrological Drought Index	Habitat quality
RRLtrus	Total annual RRLNWR Trumpeter Swan abundance	Swan movement/ management
SpPCP	Cumulative spring precipitation (cm)	Habitat quality
SpTAVG	Average monthly spring temperature (°C)	Habitat quality
SuPCP	Cumulative summer precipitation (cm)	Habitat quality
SuTAVG	Average monthly summer temperature (°C)	Habitat quality
TRItrus	Total annual tri-state area Trumpeter Swan abundance	Swan movement/ management
Visitor	Annual number of YNP recreation visitors	Human disturbance
Wolf	Annual YNP Grey Wolf abundance	Predation
Year	Linear trend through time	N/A
YRmax	Max. annual discharge of Yellowstone River (m^3/s)	Habitat quality
YRodate	Ordinal date of max. annual discharge of Yellowstone River	Habitat quality

In the absence of repeated, direct measurements of YNP wetlands, many covariate data sets describing environmental conditions likely to influence the extent or quality of swan habitat were used to quantify the habitat quality hypothesis, including the annual Palmer Hydrological Drought Index (*PHDI*), cumulative spring (March through June) and summer (June through September) precipitation (*SpPCP* and *SuPCP*, respectively), and average monthly spring and summer temperature (*SpTAVG* and *SuTAVG*, respectively). Combined with low temperatures, heavy spring precipitation may present challenging conditions for swan eggs and young cygnets, and increase the risk of nest flooding (Shea *et al.* 2013). Hot, dry conditions during the summer could affect wetland drying and reduce the amount of time seasonal wetlands are inundated with water, diminish foraging opportunities, and impede the ability of swans to take refuge from predators (Proffitt *et al.* 2010). The ordinal date (*YRodate*) and cubic meters per second (*YRmax*) of the Yellowstone River's maximum annual discharge was used as a proxy for peak snowmelt, a time when swan habitat (*i.e.* nest sites) may be most vulnerable to flooding. The ordinal date that Yellowstone Lake became completely free of ice (*Iceoff*) was used as a proxy to quantify the variability in spring melt and the timing when swan nesting habitat would become available to breeding Trumpeter Swans. Lastly, although not tied directly to a hypothesis for declining YNP swan abundance, a linear year term (*Year*) was also included as a covariate to assess whether declining Trumpeter Swan abundance in YNP could be attributed to a linear trend through time. Despite being highly correlated with covariate data that also trended strongly through time (*Grizzly*, *RRLtrus*, *TRItrus*, *Visitor* and *Wolf*), inclusion of the *Year* term allowed the effect of a trend through time to be addressed within the models. A more detailed description of covariate data sets used in this analysis, including summary statistics and time series plots, can be found in Shields (2021).

Statistical analysis

All statistical procedures were conducted in the R statistical computing environment (R Core Team 2023) and a Bayesian modelling framework was used to evaluate multiple hypotheses while accommodating the hierarchical nature of the data. Analyses of the annual, wetland-level binary response values were performed using hierarchical, generalized logistic regression models to evaluate which covariates were useful for distinguishing between wetlands where swans were: (1) Present *versus* Absent, and (2) Successful *versus* Present. Separate analyses for each pair of response outcome levels (Present/Absent and Successful/Present) were conducted because covariates could have had different impacts depending on the wetland status levels being investigated. The swan count data (Fig. 1) as well as the prevalence of predator species within YNP suggested that a different set of drivers could have been affecting swan trends during the early (1931–1959) and later (1960–2011) time periods of the study. Moreover, autumn survey data collected after 2011 were not included in the analysis because intensive management actions (*e.g.* the use of artificial nest platforms and release of captive-reared Trumpeter Swans) commenced in 2012 and artificially increased swan numbers. Accordingly, analyses of temporal and spatial patterns of wetland status were conducted separately for 1931–1959 (increasing decadal growth rates) and for 1960–2011 (decreasing decadal growth rates). This resulted in four separate model suites: (1) Present/Absent from 1931–1959, (2) Present/Absent from 1960–2011, (3) Successful/Present from 1931–1959 and (4) Successful/Present from 1960–2011. Originally planned to be just four models, pairwise covariate correlation prevented some strongly correlated covariates from being evaluated in the same model. As a result, multiple different versions of the models were run with slightly different covariate combinations, yielding 31 separate models that were run across the four time-period by response-value pair combinations described above. This allowed each of the covariate data sets, individually developed to address a specific hypothesis for Trumpeter Swan decline in YNP, to be evaluated in at least one model while avoiding strong pairwise correlations with other covariate data sets.

Reversible jump Markov chain Monte Carlo (RJMCMC) methods (Green 1995) were used to perform regression modelling and evaluate which covariates the data supported including in models explaining variation in the Present/Absent and in the Successful/Present binary responses for both early and later time series. At each iteration of the RJMCMC work, any covariate being considered could be included or not in the model, and the model structure was allowed to change at each new iteration of the Markov chain. To achieve this, a sampler algorithm was used to select one value for the coefficient associated with a given covariate, then the model's predictive ability was evaluated. This process was repeated for all potential covariates across many thousands of model iterations, with values being chosen based on the performance of covariate coefficient values from previous Markov chains, or MCMC samples. By summarising the posterior, it was possible to evaluate how often each covariate was chosen for inclusion in the models and to summarise the coefficient for any given covariate across all models fit. Covariates that were useful were included in the model structure of a larger fraction of MCMC samples than covariates that were not. The number of times a given covariate was included in the structure of MCMC samples relative to the total number of samples was a measure of that covariate's predictive ability and importance of its relationship to the response. Covariates could come in or out of the model as the model iterations progressed, hence "reversible", and allowed the model structure to accommodate a different number and combination of covariates. Thus, Bayesian RJMCMC methods used in this study allowed both variable and model selection to be performed simultaneously.

The modelling approach always included an intercept term and random effects for both wetlands and for years. The autumn YNP Trumpeter Swan surveys made repeat observations of the same wetlands across years; random effects for both wetlands and years therefore were included in all RJMCMC models to account for the potential lack of independence between these observations. All continuous covariate values were centred using the mean and scaled by one standard deviation (s.d.) to increase the speed of model simulations and allow for more direct comparison of coefficient estimates. Pairwise correlations between covariates were assessed using the ggcorr function from the GGally R package (Schloerke *et al.* 2021). Standard pairwise Pearson correlation coefficients were examined after filtering the input data to include only the two focal levels of wetland status and desired time period for a given model. Covariates with an absolute correlation coefficient value of ≥ 0.70 were not included within the same RJMCMC model.

RJMCMC models were fitted using the nimble R package (de Valpine *et al.* 2017).

Three chains were run in parallel for each RJMCMC model with each chain creating 100,000 MCMC samples and discarding 10,000 burn-in samples. To reduce the output file size and streamline posterior calculations, MCMC samples were thinned so that one in every ten samples was stored, resulting in a posterior distribution with 27,000 total MCMC samples for each model fit. Model convergence was assessed using the standard Geweke diagnostic (which compares whether the beginning and end of each MCMC sample were equal), Gelman-Rubin diagnostic values, and visual inspection of trace plots using output and functions from the MCMCvis R package (Gelman & Rubin 1992; Youngflesh 2018). Random effects for wetlands and years were assumed to be normally distributed around a mean of zero with variance $\sigma_{wetland}$ and σ_{year}, respectively. Standard uninformed priors were used for fixed and random effects in the models.

RJMCMC model output and coefficient estimates were centred and scaled. In analyses of Present/Absent wetlands, models estimated the log-odds of a wetland being in the Present category, given the effect of all measured covariates also included in the models. In analyses of Successful/Present wetlands, models estimated the log-odds of a wetland being in the Successful category, again given the impact of all covariates included in the models. The log-odds, or the natural logarithm of the odds, are symmetric around zero and are therefore useful for analysis. For reference, log-odds values ranging from –5 to 5 correspond to probabilities that range from just above zero to very close to one, while log-odds values ranging from –1 to 1 correspond to probabilities that range from about 0.25 to 0.75. Coefficient estimates were model-averaged and represent the average of all MCMC samples regardless of whether a given covariate was included in the model structure, thus incorporating the uncertainty of the variable-selection process. As a result, a covariate that was included in the model structure for only a small number of MCMC samples, for example, would have its coefficient estimate pulled towards zero by the large number of samples for which the covariate was not included in the model, and thus had a coefficient value of zero.

Results

Autumn aerial Trumpeter Swan surveys were conducted annually in the YNP for 80 years of the 90-year period from 1931–2020. During that time, 2,749 white birds (annual mean ± s.d. = 34.36 ± 17.27 individuals) and 533 cygnets (6.66 ± 5.90) were observed at 194 unique wetlands within the Park (Fig. 1). Total swan abundance tended to increase from 1931 through the 1950s, decline steadily from about the 1960s through 2011, and increase in recent years at about the time that management actions to restore Trumpeter Swans began in 2012. In RJMCMC models investigating the impact of covariates in determining whether wetlands had swans Present as opposed to Absent for the early (1931–1959) period, four of 12 possible covariates were found to be important to include in the structure of the models. Both total RRLNWR and tri-state area Trumpeter Swan abundance (*RRLtrus* and *TRItrus*, respectively) were selected for inclusion in nearly all RJMCMC model iterations, or MCMC samples, measured by the proportion of iterations where the covariate was included in the model structure (ppn. sel. = 0.99). The total number of annual YNP visitors (*Visitor*) was also highly selected in RJMCMC models (ppn. sel. = 0.94), as was the linear year term, *Year* (ppn. sel. = 0.99), although pairwise correlation prevented the *TRItrus*, *RRLtrus*, *Visitor* and *Year* covariates from being evaluated within the same RJMCMC model. When evaluated separately, each covariate was selected in nearly 100% of MCMC samples; all other covariates were selected for inclusion in < 5% of MCMC samples (see Table 2).

Model-averaged results show the scaled impact of both *RRLtrus* and *TRItrus* were positive (mean = 0.76 ± 0.15 and 0.74 ± 0.17, respectively), such that when Trumpeter Swans were more abundant at RRLNWR or in the tri-state area, wetlands within YNP were more likely to have swans Present as opposed to Absent. The coefficient estimate of *Visitor* was also positive (mean = 0.69 ± 0.23), opposite the negative direction predicted by the hypothesis that human disturbance in YNP has detrimental impacts on the Park's Trumpeter Swan population. However, it is important to note that *Visitor* and *Year* were very strongly correlated (correlation coefficient = 0.95), which resulted in multiple interpretations of this result: a negative effect of annual visitor numbers on the likelihood of swans being Present as opposed to Absent, or a negative trend through time for other, un-measured reasons. Similarly, total RRLNWR swan abundance and total tri-state area swan abundance were strongly correlated with each other, and with a temporal trend, making it impossible to attribute their similar impact on wetland status to one or the other.

Random effects of wetlands ($\hat{\sigma}_{RE_{wetland}}$; mean = 2.99 ± 0.48) were much larger than the values for random effects of year ($\hat{\sigma}_{RE_{year}}$; mean = 0.49 ± 0.20), a pattern that was observed across all four model suites (see Table 2). Estimates of wetland-specific intercept adjustments could take on a wide range of negative or positive log-odds values, translating to adjustments to the probability of swans being Present as opposed to Absent at a given wetland (during an average year) between approximately 0.04 and 0.99. On the other hand, estimates of year-specific intercept adjustments fell within a much narrower range, translating to adjustments to the probability of swans being Present as opposed to Absent during a given year (at an average wetland) between approximately 0.39 and 0.65 (see Figs. 3 & 4 for example wetland and year random effect plots). Random effects of wetland, adjustments to the log-odds of a given water body having Trumpeter Swans Present, were found to correspond well with observations from autumn swan surveys. Intercept adjustments for the Fern-Tern-White Complex, Riddle Lake Complex, Trumpeter Lake Complex, Swan Lake Complex and Geode Lake Complex had the largest positive values for 1931–1959 (Supporting Materials Fig. S1).

In RJMCMC models investigating the impact of covariates in determining whether wetlands had Trumpeter Swans Present as opposed to Absent more recently, for 1960–2011, three of 14 possible covariates were found to be important to include in the

Table 2. Model-averaged RJMCMC results, indicating covariates associated with whether swans were Present *versus* Absent on wetlands in Yellowstone National Park, USA each year during 1931–1959. "Ppn. selected" represents the proportion of MCMC samples that a given covariate was selected for inclusion in the model structure; *i.e.* the number of times the covariate was included in the structure of the models (No. included) divided by the number of times that covariate could have possibly been included (No. possible). Coefficient estimates, with corresponding standard deviations (s.d.) and 90% credible intervals (90% CrI), represent the log-odds of being classed as Present, given the impact of all measured covariates also included in the models.

Model parameter	No. included	No. possible	Ppn. selected	Estimate (s.d.)	90% CrI
Intercept	–	–	–	–2.63 (0.51)	(–3.49, –1.85)
$\hat{\sigma}_{RE_{wetland}}$	–	–	–	2.99 (0.48)	(2.30, 3.85)
$\hat{\sigma}_{RE_{year}}$	–	–	–	0.49 (0.20)	(0.17, 0.82)
RRLtrus[a]	53,683	54,000	0.99	0.76 (0.15)	(0.53, 1.01)
RRLtrus[b]	53,225	54,000	0.99	0.74 (0.17)	(0.50, 1.00)
Year[c]	53,405	54,000	0.99	0.76 (0.17)	(0.52, 1.02)
Visitor[d]	50,899	54,000	0.94	0.69 (0.23)	(0.00, 0.99)
PHDI[e]	4,041	216,000	0.02	0.00 (0.04)	(0.00, 0.00)
SuPCP[f]	3,612	216,000	0.02	0.00 (0.04)	(0.00, 0.00)
YRmax[g]	1,177	216,000	0.01	0.00 (0.02)	(0.00, 0.00)
YRodate[h]	3,029	216,000	0.01	0.00 (0.03)	(0.00, 0.00)
SpTAVG[i]	846	108,000	0.01	0.00 (0.02)	(0.00, 0.00)
SuTAVG[j]	1,016	108,000	0.01	0.00 (0.03)	(0.00, 0.00)
Iceoff[k]	1,061	216,000	0.00	0.00 (0.01)	(0.00, 0.00)
SpPCP[l]	1,076	216,000	0.00	0.00 (0.01)	(0.00, 0.00)

[a]RRLtrus: RRLNWR total annual swan abundance.
[b]TRItrus: tri-state area total annual swan abundance.
[c]Year: linear trend through time.
[d]Visitor: total annual YNP visitor abundance.
[e]PHDI: annual Palmer Hydrologic Drought Index.
[f]SuPCP: cumulative summer precipitation.
[g]YRmax: maximum annual flow of Yellowstone River at Corwin Springs.
[h]YRodate: ordinal date of maximum annual flow of Yellowstone River at Corwin Springs.
[i]SpTAVG: average monthly spring temperature.
[j]SuTAVG: average monthly summer temperature.
[k]Iceoff: annual ordinal date Yellowstone Lake became ice-free.
[l]SpPCP: cumulative spring precipitation.

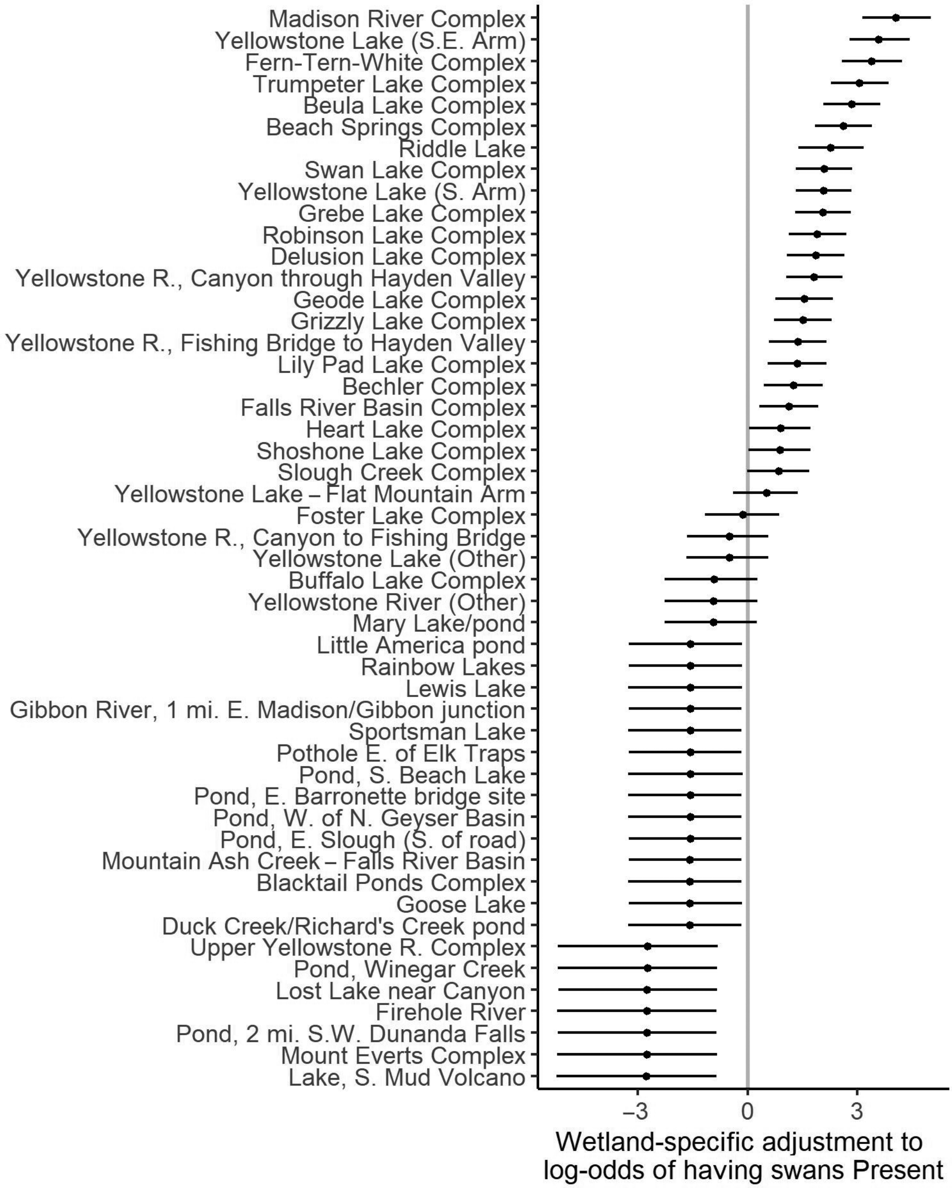

Figure 3. Caterpillar plot of wetland random effects for a model investigating whether Trumpeter Swans were Present *versus* Absent on wetlands in Yellowstone National Park, USA during 1960–2011. Wetlands are listed along the y-axis. The x-axis represents wetland-specific intercept adjustments to the log-odds of wetlands having swans Present during an average year under average covariate conditions, and whiskers represent 90% credible intervals. The grey vertical line represents an average wetland, or an intercept adjustment of zero.

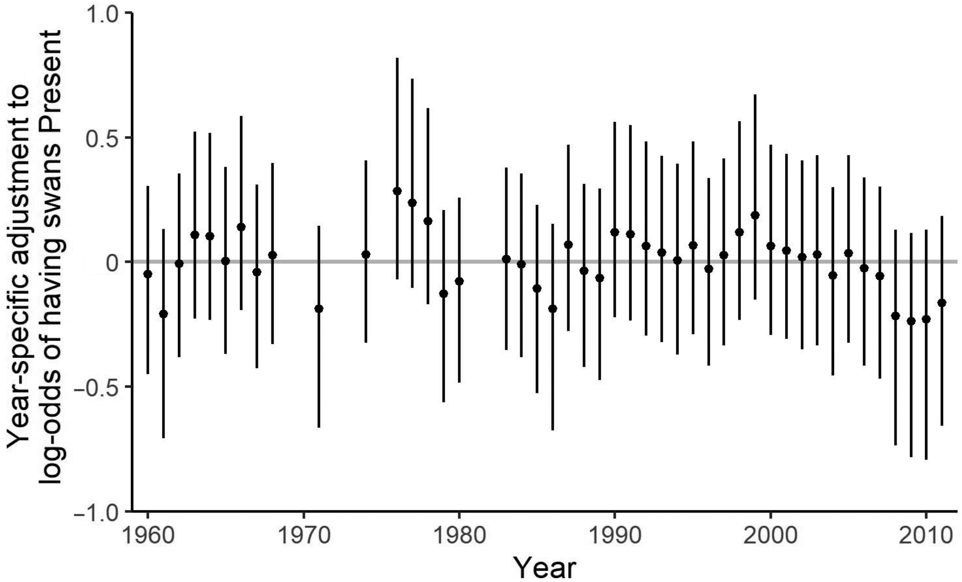

Figure 4. Plot of year random effects for a model investigating whether Trumpeter Swans were Present *versus* Absent on wetlands in Yellowstone National Park, USA during 1960–2011. The y-axis represents year-specific intercept adjustments to the log-odds of an average wetland having swans Present under average covariate conditions, and whiskers represent 90% credible intervals. The grey horizontal line represents an average year, or an intercept adjustment of zero.

models' structure (see Table 3). Greater Yellowstone area Grizzly Bear abundance (*Grizzly*) was selected in a large proportion of RJMCMC model iterations (ppn. sel. = 0.82). In addition, *Visitor* was selected in a large proportion of models (ppn. sel. = 0.74) and the temporal trend term *Year* was also selected in every RJMCMC model where it was available for inclusion in the models' structure (ppn. sel. = 1.00). Again, pairwise covariate correlations prevented the three highly selected covariates (*Grizzly*, *Visitor* and *Year*) from being evaluated within the same RJMCMC model and created alternative interpretations of the results. Grizzly and visitor abundance may have had a negative impact on wetlands having swans Present as opposed to Absent, or the association could have been due to some other time-trending reason. The annual ordinal date that Yellowstone Lake was free of ice was included in a small proportion of model iterations (ppn. sel. = 0.05). All other covariates were selected for inclusion in only 0–1% of model iterations (Table 3).

Model-averaged results show the scaled impact of *Grizzly* was negative (mean = –0.42 ± 0.23 s.d.), as was predicted given that swan mortality and egg failure in YNP have been attributed to Grizzly Bears. In contrast to the previous model suite investigating Present/Absent wetlands for 1931–1959, the coefficient estimate of *Visitor* was negative (mean = –0.37 ± 0.16

Table 3. Model-averaged RJMCMC results, indicating covariates associated with whether swans were Present *versus* Absent on wetlands in Yellowstone National Park, USA each year during 1960–2011. "Ppn. selected" represents the proportion of MCMC samples that a given covariate was selected for inclusion in the model structure; *i.e.* the number of times the covariate was included in the structure of the models (No. included) divided by the number of times that covariate could have possibly been included (No. possible). Coefficient estimates, with corresponding standard deviations (s.d.) and 90% credible intervals (90% CrI), represent the log-odds of being classed as Present, given the impact of all measured covariates also included in the models.

Model parameter	No. included	No. possible	Ppn. selected	Estimate (s.d.)	90% CrI
Intercept	–	–	–	–2.41 (0.35)	(–2.99, –1.86)
$\hat{\sigma}_{RE_{wetland}}$	–	–	–	1.79 (0.25)	(1.42, 2.24)
$\hat{\sigma}_{RE_{year}}$	–	–	–	0.19 (0.11)	(0.03, 0.35)
Year	54,000	54,000	1.00	–0.60 (0.08)	(–0.73, –0.47)
Grizzly[a]	88,678	108,000	0.82	–0.42 (0.23)	(–0.71, 0.00)
Visitor	160,635	216,000	0.74	–0.37 (0.16)	(–0.64, –0.21)
Iceoff	13,560	270,000	0.05	–0.01 (0.04)	(–0.06, 0.00)
YRmax	1,964	270,000	0.01	0.00 (0.01)	(0.00, 0.00)
SpTAVG	976	135,000	0.01	0.00 (0.02)	(0.00, 0.00)
RRLtrus	1,474	108,000	0.01	0.00 (0.03)	(0.00, 0.00)
TRItrus	2,052	162,000	0.01	0.00 (0.02)	(0.00, 0.00)
Wolf[b]	611	54,000	0.01	0.00 (0.01)	(0.00, 0.00)
PHDI	819	270,000	0.00	0.00 (0.01)	(0.00, 0.00)
SpPCP	1,196	270,000	0.00	0.00 (0.01)	(0.00, 0.00)
SuPCP	667	270,000	0.00	0.00 (0.01)	(0.00, 0.00)
YRodate	644	270,000	0.00	0.00 (0.00)	(0.00, 0.00)
SuTAVG	478	135,000	0.00	0.00 (0.01)	(0.00, 0.00)

[a]Grizzly: annual abundance estimate of Greater Yellowstone area Grizzly Bears.
[b]Wolf: annual abundance estimate of YNP Grey Wolves.
See Table 1 and the footnote to Table 2 for details of the other model parameters.

s.d.) for 1960–2011, in accordance with the hypothesis that human disturbance can have detrimental impacts on nesting and brood-rearing Trumpeter Swans. It is again important to note that *Grizzly*, *Visitor* and *Year* were highly correlated and could not be evaluated within the same RJMCMC models. As was the case with the model suite investigating 1931–1959, models evaluating Present/Absent wetlands for the time period of 1960–2011 showed random effects of wetlands (mean = 1.79 ± 0.25 s.d.) to be much larger than random effects of years (mean = 0.19 ± 0.11 s.d.). The specific wetlands with the largest intercept adjustments changed for 1960–2011 to reflect decreased use of previously productive areas and new areas of increased swan use. Intercept adjustments for the Madison River Complex, Yellowstone Lake (Southeast Arm), Fern-Tern-White Complex, Trumpeter Lake Complex and Beula Lake Complex had the largest positive values for 1960–2011 (Fig. 3).

On investigating the importance of covariates in determining whether wetlands had Trumpeter Swans that were Successful as opposed to Present, no covariates were selected for inclusion in a large proportion of RJMCMC models for either the 1931–1959 or the 1960–2011 time periods. Covariates highly selected for inclusion in the model structure for Present/Absent, such as *RRLtrus*, *Grizzly*, *Visitor* and the temporal trend *Year*, were not found to be important covariates when modelling variation in Successful/Present wetland status levels. Model-averaged RJMCMC model results showed that all covariates were selected for inclusion in < 10% of model iterations (Supporting Materials Tables S1 & S2); however, the same random effect pattern was observed for analyses of Successful/Present wetlands where random effects for wetlands were much larger than those for years (see Fig. S2). Rankings of the best wetlands, this time representing an adjustment to the log-odds of a wetland being classed as Successful as opposed to Present, were re-ordered to reflect those wetlands that most successfully fledged swan cygnets during the two time periods (see Figs. S3 & S4).

Discussion

In total, 14 covariate data sets were developed to investigate the four main hypotheses for Trumpeter Swan decline in YNP. Although it was difficult to find data sets with the geographic coverage and repeated measures necessary to be included in a long-term, retrospective study of this kind, a number of new covariate data sets were ultimately developed and utilised. Results of the RJMCMC models of binary annual wetland status indicated that: (1) random effects of wetlands were larger than random effects of years, (2) just a few covariates were typically important to consider, (3) the covariates important to consider changed depending on which model suite was being considered (Present/Absent or Successful/Present and 1931–1959 or 1960–2011) and (4) it was important to consider a trend through time. RJMCMC model results provided some support for the human disturbance, predation, and swan movement/management hypotheses for swan decline, but strong temporal trends in the covariates used to quantify these hypotheses created multiple interpretations of the results and prevented stronger inferences from being made. Model random effects were used to identify quantitatively the wetlands in YNP most likely to have Trumpeter Swans Present and most likely to have swans Successful, providing information that Park staff can use to help manage important swan habitat or justify future management actions.

Inclusion of the *RRLtrus* and *TRItrus* covariates in the structure of a large proportion of RJMCMC models investigating Present/Absent wetlands from 1931–1959 supported the hypothesis that immigration of swans from other portions of the RMP may play a role in the persistence of the Park's resident Trumpeter Swans. Given their high correlation and similar performance in RJMCMC models when evaluated separately, it's not clear whether there is a stronger connection between the Park and the tri-state area (*TRItrus*) or RRLNWR (*RRLtrus*), but it is the case that wetlands in YNP had a greater probability of having Trumpeter Swans being Present rather than Absent when there were more total Trumpeter Swans in either the tri-state area or RRLNWR specifically. Management actions outside of YNP implemented during the earlier time period (1931–1959), including protection from illegal shooting, winter feeding, predator control and reduction of human disturbance at nesting areas, likely contributed to conditions favourable for increased swan abundance and potential for immigration into YNP (Shea *et al.* 2002). In contrast, neither *RRLtrus* nor *TRItrus* were important covariates in Present *versus* Absent models during the later time period (1960–2011), when the goal of local swan management had shifted to reducing concentrations and expanding the wintering distribution of Greater Yellowstone area Trumpeter Swans (Drewien *et al.* 2002).

RJMCMC model results also provided some support for the predation hypothesis for YNP Trumpeter Swan decline on investigating Present/Absent wetlands during the later time period (1960–2011), when swan numbers drastically declined. Although Grizzly Bear and Grey Wolf abundance data were included as model covariates, information for a variety of other YNP predator species was notably absent. Both Coyotes and Ravens were identified as great threats in the "trumpeter's struggle for existence" in preliminary YNP Trumpeter Swan reports from the 1930s and 1940s, but neither species has been regularly monitored in the Park (Barrows 1936; Condon 1941). Recent observations of Bald Eagles in YNP suggest that their diet may be switching to include newly hatched Trumpeter Swans and Great Northern Divers *Gavia immer* as their preferred food source, Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, have declined precipitously since non-native Lake Trout *Salvelinus namaycush* were introduced to the system in the mid-1990s (Smith *et al.* 2016; Koel *et al.* 2019). However, regular monitoring of Bald Eagles did not begin until the 1980s, preventing information on their abundance or behaviour from being included in the models. Only covariate data for Grizzly Bears and Grey Wolves could be included in the analysis, but only for the later time period (1960–2011). No covariates related to predators were included for the earlier time period (1931–1959) because these types of records are absent or incomplete for YNP. Nonetheless, overall predator abundance in the Park was lower during the earlier time period of the study and increased during the decades that Trumpeter Swans declined, an increase that may be reflected in the increasing trends of the Grizzly Bear and Grey Wolf covariates (*Grizzly* and *Wolf*, respectively).

The human disturbance hypothesis for YNP Trumpeter Swan decline also received some support from RJMCMC model results investigating Present/Absent wetlands from 1960–2011 with the annual number of YNP visitors (*Visitor*) being selected for inclusion in a large proportion of model iterations. Attempts were made to develop more detailed covariate data sets that would focus on specific components of visitor use, such as backcountry campsite use near important swan habitat or filtering park-wide visitors to include only those that visited during the swan breeding season, but these attempts to capture YNP visitor use in greater detail were unsuccessful because of limitations in the data available. The coarser-scale, Park-wide, annual visitation data therefore were used to quantify the human disturbance hypothesis. It is again important to note that, although some support was found for the human disturbance, predation and swan movement/management hypotheses, the covariate data sets used to quantify these hypotheses (*RRLtrus*, *TRItrus*, *Grizzly*, *Wolf* and *Visitor*) were strongly correlated with a trend through time (*Year*), resulting in multiple interpretations. The covariate data sets included in the RJMCMC modelling were chosen because of their biological merit and ability to quantify potential aspects of the four main hypotheses for YNP swan decline. While there was no *a priori* reason to expect year to affect swan presence or fledging success, it is possible that there were unmeasured time-trending covariates that were not included in the analysis.

Both model suites investigating Successful/Present wetlands, 1931–1959 and 1960–2011, were unable to identify any covariates that were important to include in the structure of RJMCMC models. Model covariates that were highly selected in other model suites, including *Year* and other time-trending covariates like *Visitor*, *Grizzly* and *RRLtrus*, were no longer important to include when investigating Successful/Present wetlands, likely as a result of the relative paucity of observations of Successful wetlands during autumn surveys. This is particularly true of the later time period when the annual count of Successful wetlands was regularly zero (Fig. 2). Nonetheless, the same pattern was observed in model random effects for Successful/Present wetlands across both the earlier and later time periods, where wetland-specific random effects were much larger than year-specific random effects (see Supporting Materials Tables S1 & S2). This result further highlights the importance of specific water bodies that are far more likely to have Trumpeter Swans Present and Successful.

Although YNP swan researchers have recognised many of the locations that are most frequently visited or used successfully by breeding Trumpeter Swans, the analyses presented here identified quantitatively the wetlands that are most likely to have swans Present and those that are most likely to have Trumpeter Swans Successful. The ranking of these wetlands (Fig. 3) can be a useful management tool to help focus targeted management actions, such as the installation of artificial nest platforms or release of captive-raised swans outside of the areas already frequently used. This information could also be used to suggest areas where additional survey flights or ground observations may be most useful to further investigate the potential impacts of human disturbance, predation, or nest flooding (*e.g.* to compare wetlands that were most likely to be Successful with wetlands that were least likely to be Successful). Lastly, the wetlands that were identified as being the most likely to be Successful could be used to suggest specific locations where temporary closures, such as those around important nesting lakes and/or hiking trails, may help to reduce the potential for negative human disturbance impacts during the Trumpeter Swan breeding season.

Wetland-specific RJMCMC model random effects also serve to reinforce something observed by YNP swan researchers for some time: a few swan territories function as "hot spots", or "productivity engines" which tend to produce most swan cygnets, with < 20% of YNP wetlands contributing > 60% of all fledged cygnets during 1987–2007 (Proffitt *et al.* 2009). Wetland-specific random effects were larger than any of the effect sizes of covariates that were highly selected for inclusion in RJMCMC model structures (*e.g. RRLtrus*, *Grizzly* and *Visitor*), suggesting that unknown sources of spatial variation were more important to consider than the model covariates used to explore the habitat quality hypothesis (*e.g. SpPCP*, *SuTAVG*, *YRmax* and *Iceoff*). While this finding serves to reinforce the importance of habitat quality, what makes some specific wetlands consistently better swan habitat than others in YNP remains unknown. Stable water levels, nesting substrate, number of potential nest sites, aquatic plant diversity and availability, and shoreline complexity have all been shown in other studies to be important to the nesting success of Trumpeter Swans (Hansen *et al.* 1971; Page 1976; Kiviat 1978; Shea 1979; Maj 1983; Lockman *et al.* 1987; Squires & Anderson 1995; Proffitt *et al.* 2010). We lack a consistent record of these types of habitat quality metrics in YNP, making it difficult to explore changes in habitat quality. In their absence, weather and climate data were instead used in this study to describe conditions that were likely to impact swan habitat. Climate data from the last century suggests that climate change is responsible for wetland loss across YNP and GTNP (Schook & Cooper 2014; Ray *et al.* 2016). At the time of their study, McMenamin *et al.* (2008) found that drought was more frequent and more severe from 2000–2007 than at any time during the last century. Field surveys from 1992–1993 and 2006–2008 also found that the number of permanently dry ponds in northern YNP increased four-fold from 1992–2008 (McMenamin *et al.* 2008). Furthermore, nearly 50% of annual YNP precipitation is contained in the snowpack on 1 April, making snowpack size and melt phenology over the following months critical to soil and surface water conditions (Despain 1990).

Environmental and climate covariates therefore seemed to be important proxies for quantifying habitat quality in the models. Despite a strong basis for including these types of data as model covariates, no environmental or climate covariates were highly selected for inclusion in the structure of any RJMCMC models. Weather and climate proxies may not be able to substitute for a more direct observation or measurement, and some information is likely lost when some form of proxy is instead used. Further direct field observations of Trumpeter Swans may help to understand the underlying reasons why swans were present and successful on some wetlands but absent or unsuccessful at others, such as causes of mortality, anthropogenic or natural disturbance of swans, and factors associated with nest flooding. As most swans in YNP are currently not marked, additional insight into swan behaviour and patterns of habitat use, especially for the captive-reared swans that are released annually as part of restoration efforts, may be improved through the use of field-readable bands. Recent advancements in analytical methods suggest that there may be another viable option. One particular approach uses Landsat satellite imagery to accurately estimate surface water extent from 1984 to the present to reconstruct hydrological information and to describe the resiliency of various wetland types to predicted impacts of climate change (Halabisky *et al.* 2016). Such approaches have documented surface water decline in snowmelt-driven watersheds in the western U.S. (Donnelly *et al.* 2020) and the misalignment of seasonal wetland flooding with migrating waterbirds in semi-arid landscapes (Donnelly *et al.* 2019). Applied to the water resources of YNP, these methods could support the investigation of changes in habitat quality on Trumpeter Swan population trends, and consider how the Park's swan habitat may be changed due to the projected impacts of long-term climate change.

Overall, RJMCMC methods for logistic regression were useful to explore a variety of covariates representing four hypotheses for swan decline in YNP, perform both variable and model selection, and accommodate the hierarchical nature of the Trumpeter Swan survey data. Use of model random effects facilitated the development of a management tool identifying the lakes, rivers and wetlands in YNP where Trumpeter Swans are most likely to be present and most likely to successfully fledge young. Further development of covariate data sets, especially those with wetland-specific values and those that describe visitor use within YNP in greater detail, will likely improve the utility of this modelling approach and allow a more robust data set to be explored. Intensive field observations of nesting Trumpeter Swans and additional survey flights may allow more detailed covariate data sets to be developed and some highly correlated covariate information to be disentangled.

Patterns in the temporal trends of Absent, Present, and Successful wetlands suggest that current restoration activities in the Park are helping; trends in the number of Absent, Present and Successful wetlands shift around the time intensive restoration efforts began in 2012 (Fig. 2). A sharp decrease can be seen in the number of wetlands with swans Absent in the five years after captive-raised swan releases began in the Park. In addition, the annual number of wetlands with Trumpeter Swans Present has remained higher after the implementation of restoration efforts than during the five years preceding them. Additional monitoring of cygnets observed in the Park, field-readable bands on all released restoration swans, or telemetry work may help to attribute observations of new swan individuals within the Park to swan releases or to immigrants from outside the Park and further evaluate the efficacy of ongoing restoration efforts in YNP. Analytical methods that utilise Landsat satellite imagery to reconstruct wetland hydrology may help to further investigate the habitat quality hypothesis for swan decline. Evidence found in this study, that swan trends in the broader geographic area have an effect on the persistence of swans in the Park, suggests that a collaborative, regional management strategy may further contribute to the efforts being made within YNP to increase Trumpeter Swan abundance and productivity.

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Photograph: Trumpeter Swan in flight, by Scott Heppel.

