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Whooping crane demographic responses to winter drought focus conservation strategies

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ABSTRACT

Focusing conservation strategies requires identifying the demographic parameters and environmental conditions affecting the growth of animal populations most. Therefore, we examined relationships between population demographics and winter drought (1950–2011) for endangered whooping cranes (*Grus americana*) wintering in Texas, USA. We modeled winter loss and its contribution to annual mortality as functions of winter drought, determined recruitment needed to maintain population growth after drought, and identified which demographic parameters underpin this population's growth. Previous research assumed winter loss (i.e., birds missed in subsequent surveys) represented mortality. We show that loss includes temporary emigration to upland habitats, early migration, and incomplete detection. Despite this, we maintained this assumption to evaluate the relevance of winter mortality to population growth. We found that winter loss ($\widehat{\beta} = -0.308$, SE = 0.042) and its contribution to annual mortality ($\widehat{\beta} = -0.318$, SE = 0.047) increased with drought severity (Palmer hydrological drought index; PHDI). Given average recruitment (0.145, SD = 0.090), this population increases 1.2% (95% CI = −2.9% to 4.2%) after extreme drought (PHDI = −4). No recruitment must occur for 3 years with moderate to severe drought (PHDI < −2.5) to delay species' recovery ≈7 years. This scenario has not occurred since population monitoring began in 1938. Of the demographic parameters we examined, winter loss explained population growth least (14.4%; 95% CI = 3.6–35.8%), and it was partially compensatory. Breeding–migratory mortality explained 42.2% (95% CI = 19.1–61.5%) of population growth and recruitment 49.9% (95% CI = 20.6–75.2%). Our results focus conservation on breeding and migratory periods, and deemphasize winter mortality and drought. On the wintering grounds, conservation of whooping cranes should emphasize maintaining coastal, upland, and interior habitats for this population.

1. Introduction

Understanding animal population demographics and their ecological drivers helps focus conservation and management strategies on the relevant life-history traits or environmental conditions that impact population growth most (e.g., Caughley, 1994; Mills, 2007; Grande et al., 2009; Schaub et al., 2012). When such information is lacking, or inadequate, then biologists risk ineffective conservation actions in inappropriate places and periods. For the Aransas–Wood Buffalo whooping crane (*Grus americana*) population, long-term monitoring on its wintering grounds has provided a rich data source for modeling relationships between demographic parameters and the environment (Lewis et al., 1992; Link et al., 2003; Stehn and Taylor, 2008; Butler et al., 2013; Stehn and Haralson-Strobel, 2014). Our objective was to use this information for steering conservation strategies for this endangered bird.

A current paradigm holds that winter mortality is an important component of whooping crane population dynamics. Further, it contends that whooping cranes wintering along the Texas coast of the Gulf of Mexico are highly territorial, so during adverse drought conditions, they run out of resources in their territories and perish (Stehn and Johnson, 1987; Stehn, 2009; Pugesek et al., 2013; Stehn and Haralson-Strobel, 2014). Alternatively, whooping cranes may vacate coastal saltmarshes and seek resources in other habitats such as upland areas, interior regions, or elsewhere along the gulf coast, instead of dying from insufficient food and water in their territories during drought.

This distinction is important. If drought conditions directly increase mortality of whooping cranes on their winter territories, then it supports management actions (e.g., supplemental feeding) that may mitigate winter mortality (U.S. Fish and Wildlife Service

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[USFWS], unpublished), although unintended consequences may ensue (e.g. increased disease, poisoning, and predation; Baskin, 1993; Oberheu and Dabbert, 2001; Miller et al., 2003). However, if the assumed mortalities represent birds vacating their territories in search of resources elsewhere, then an appropriate management response would be to identify the alternative habitats in which whooping cranes select and conserve or restore those areas. Clearly, biologists must untangle how this population responds to winter drought to identify appropriate conservation and management strategies.

We address this issue by analyzing 61 years of demographic data for the Aransas–Wood Buffalo whooping crane population. This population overwinters on and around Aransas National Wildlife Refuge (NWR), Texas, USA, and breeds on and around Wood Buffalo National Park, Alberta and Northwest Territories, Canada (CWS and USWFS, 2007). Since 1950, the USFWS has conducted annual whooping crane surveys from fixed-wing aircraft in Texas (Stehn and Taylor, 2008). Some consider that these aerial surveys provided a technique for documenting mortality during the winter period (Lewis et al., 1992; Pugesek et al., 2008, 2013; Stehn and Taylor, 2008; Stehn and Haralson-Strobel, 2014). The technique relied on repeated, though unequal, survey effort during each winter, assumptions of whooping crane territorial fidelity, identification of individual birds with many lacking unique marks, and the interpretation of changes in the composition of whooping crane family groups (Pugesek et al., 2013; Stehn and Haralson-Strobel, 2014). Therefore, when observers failed to record the presence of individual birds in their territories on two consecutive surveys, they counted those missing birds as mortalities (Stehn and Haralson-Strobel, 2014). Reliance on such clues to count mortalities allows for many other possible explanations, such as temporary emigration from winter territories to upland or interior habitats, early departure to the breeding grounds, or incomplete detection of birds within a family group (Stehn, 1992; Strobel and Butler, 2014). The difficulty in making clear inference from these survey data is indicative of a poor technique, suggesting that the mortality data may represent a combination of mortality, early migration, temporary emigration, and incomplete detection. Thus, estimates previously interpreted as winter mortality are best described as "loss" from the coast during winter, instead of mortality alone.

By examining the extent that reported losses (Stehn and Haralson-Strobel, 2014) varied with survey effort and the use of upland habitats by whooping cranes, we illustrate that there are explanations other than mortality for the missing birds. An inverse relationship between winter loss and survey effort would suggest the technique produced results dependent upon methodological differences between years instead of generating a consistent index of winter mortality. Additionally, if the use of upland habitats by whooping cranes increased during years of higher loss, then some losses reported were likely due to temporary emigration, not death. Despite these potential sources of bias, we considered winter loss to consist entirely of deaths to evaluate the relevance of winter mortality on the dynamics of this population.

We modeled the effects of 7 climatic indices on whooping crane winter loss, the contribution of winter loss to annual mortality, and use of upland habitat. The climatic variables served as surrogates for habitat conditions (i.e., food availability, hyper-salinity, and drought) during the winter period. Identifying which climatic indices were most associated with winter loss enabled us to gauge and predict the amount of winter loss that could occur under a variety of drought scenarios. The relationship between climate and the contribution of winter loss to annual mortality revealed the influence of winter mortality on annual mortality during the worst drought conditions. Relating climatic factors to upland use demonstrated behavioral responses of this population to drought.

After establishing these relationships, we examined the impact of winter drought on whooping crane population growth. First, we identified the drought conditions, if any, that could result in population decline. Second, we determined the combination of drought on the wintering grounds (that indicated potential winter mortality) and the reduction in recruitment necessary to delay this species' recovery (by tying into modeling scenarios outlined in Butler et al. (2013)). We show that reductions in population growth and delays in population recovery are contingent upon extreme drought conditions on the wintering grounds and poor recruitment the following year, not simply drought alone. Third, we quantified the importance of recruitment, plus mortality during the breeding and migratory periods, winter mortality, and annual mortality to population growth. Their effects on population growth are unlikely to be equal (Mills, 2007). Determining which demographic parameter(s) this population's growth hinges upon focuses when and where management intervention might be most effective and warranted.

For over 6 decades, the whooping crane monitoring technique was trusted to produce information that it could not credibly provide (e.g., winter mortality). Unfortunately, this represents a common story in which poorly designed monitoring programs become institutionally ingrained and relied upon to inform conservation strategies (Anderson, 2001; Legg and Nagy, 2006; Nichols and Williams, 2006; Lindenmayer and Likens, 2009, 2010). Dependence on inadequately designed monitoring programs often results in poor inference and misplaced conservation actions. By evaluating and addressing the situation for whooping cranes, our results focus research and management of this population on the life-history traits, locations, and periods that matter most.

2. Methods

2.1. Study area and aerial surveys

Whooping cranes arrive on their wintering grounds on and around Aransas NWR beginning in October and depart by late April (Johnsgard, 1983). On the wintering grounds, the birds are distributed in coastal saltmarshes, tidal flats, and shallow bay edges with occasional use of upland areas (CWS and USWFS, 2007). Though the population has been surveyed since 1938, consistent aerial survey efforts did not begin until 1950 (Stehn and Taylor, 2008; Butler et al., 2013, 2014; Strobel and Butler, 2014). Since then, repeated aerial surveys of whooping cranes have been conducted each year during the winter period resulting in indices of abundance, winter mortality (i.e., loss), and the number of hatch-year (HY) birds (Lewis et al., 1992; Link et al., 2003; Stehn and Taylor, 2008; Stehn and Haralson-Strobel, 2014).

The survey has been primarily conducted from a fixed-wing aircraft with transects spaced approximately 250–800 m apart and flown parallel to the coast (Stehn and Taylor, 2008; Butler et al., 2014). Transect spacing was varied according to flight conditions by the observer in an attempt to detect all whooping cranes (Stehn and Taylor, 2008; Butler et al., 2014; Strobel and Butler, 2014). Prior to revision of the survey technique in winter 2011–2012, the surveyed area was not recorded for each year and likely fluctuated from year to year (Butler et al., 2014). Though the survey did not result in a true census of the population, many have treated these data as a census (Boyce and Miller, 1985; Boyce, 1986; Dinsmore and Johnson, 2005; CWS and USWFS, 2007; Stehn and Taylor, 2008).

Estimates of winter abundance and the number of HY birds were compiled from multiple sources (Table 1; Boyce, 1986; Link et al., 2003; CWS and USWFS, 2007; Butler et al., 2013). Estimates of the number of whooping cranes lost during the winter period