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Integrated population modeling to assess demographic variation and contributions to population growth for endangered whooping cranes

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ABSTRACT

Management efforts for endangered species are enhanced by knowledge of the causes and extent of demographic variation, but this information is often lacking even when abundance is well known. We developed an integrated population model to study the dynamics of the only remnant population of endangered whooping cranes (*Grus americana*) in North America, 1977–2013. Despite much conservation attention for this species, there has been little study on temporal variability in demography and how that variation contributes to population dynamics. Demographic rates were most variable for fledge rate and survival of the youngest age classes while adult survival was less variable. Population growth was influenced mainly by variation in fledge rate, breeding propensity and survival of hatch year and second year cranes while survival of older age classes had less influence. Fledge rates were correlated to the boreal snowshoe hare (*Lepus americanus*)–Canada lynx (*Lynx canadensis*) cycle and were lowest 2 years after increases in lynx population growth. In terms of management, mean annual fledge rates were similar between years with and without egg collection for captive rearing (0.523 vs 0.518), suggesting no influence of this practice on population-level productivity. Our findings add to the growing body of results showing that while population growth may be most sensitive to changes in adult survival in long-lived vertebrates, variation in breeding parameters often drives annual fluctuations in abundance. Maintaining adult whooping crane survival at currently high rates and increasing breeding output where possible may be effective management strategies for achieving conservation goals.

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1. Introduction

Attempts to evaluate the success of conservation efforts for endangered species are greatly enhanced by a knowledge of the mean and variability in demographic rates and an understanding of the environmental and population factors that influence them (Sibly and Hone, 2002; Mills, 2013). Abundance is often well known for endangered species, but due to small sample sizes, it can be difficult to obtain data on the demographic rates leading to poor precision and an insufficient time series to measure temporal variation, both of which could result in flawed inference when used in subsequent population analyses (Doak et al., 2005). Recently developed integrated population models (IPM) combine information on abundance with data for the estimation of demographic rates under a common analytical framework (Brooks et al., 2004; Schaub et al., 2007). This combination provides greater precision and an ability to estimate parameters where data are unavailable. These models have recently been used to assess population dynamics and management options for several threatened or rare species (Rhodes et al., 2011; Tenan et al., 2012; Schaub et al., 2013). Here, we develop and apply an IPM to 37 years of abundance and demographic data (1977–2013) for the only remnant population of the whooping crane (*Grus americana*) in North America.

Whooping cranes are among the rarest North American birds. The remnant population breeds in and around Wood Buffalo National Park (WBNP) in Alberta and the Northwest Territories, Canada, and overwinters along the Texas Gulf Coast, USA, primarily at Aransas National Wildlife Refuge (Urbanek and Lewis, 2015). Prior to the 1850s, the whooping crane breeding range extended in a narrow band from central Alberta in the west, through the southern Canadian prairies and northern Great Plains states to central Illinois in the east (Allen, 1952). Preferred breeding habitats were extensive marshes in mixed and tallgrass prairie but the widespread conversion of this habitat to agriculture combined with hunting led to a dramatic reduction in the population by the early 1900s (Urbanek and Lewis, 2015). As of 1942, only 16 individuals in the Aransas-Wood Buffalo population (AWBP)

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remained (CWS and USFWS, 2007). Since then, the species has received much conservation attention including protection of individual birds and their habitat as well as captive rearing programs. Several re-introduction attempts have been made across North America whose goal is to establish other self-sustaining populations and so lower the risk from having only a single population (Ellis and Gee, 2001; CWS and USFWS, 2007). Re-introductions have met with limited success (Ellis et al., 1992; Moore et al., 2012; Urbanek et al., 2014), but with protection the AWBP population has grown at an average of about 3.8% per year and reached 283 individuals in 2011 (Butler et al., 2013).

We first develop an IPM to estimate temporal variability in all demographic rates (breeding propensity, fledge rate and survival of multiple age classes) and determine the extent to which these rates influence population dynamics. Then, we use a version of this model to test the effects of egg collection and breeding ground predator abundance on annual fledge rates. Egg collection was conducted from 1967 to 1996 to establish the current captive populations (CWS and USFWS, 2007). This practice ceased in 1997 in part due to concerns that it might negatively affect the population, although research has shown that it does not appear to affect recruitment for manipulated pairs (Boyce et al., 2005) or winter abundance (Butler et al., 2013). Egg collecting has been an important tool for the North American Whooping Crane recovery program and the resumption of this practice may enhance research and management options. To better understand how egg collecting affected the population, we compare population-level fledge rates during 21 years with egg collection and 17 years post-egg collection.

The AWBP population has exhibited periods of strong growth interrupted by periods of weak or even slightly negative growth (Boyce and Miller, 1985; Butler et al., 2013). Studies have suggested that this pattern is related to the effects of predators (Boyce et al., 2005) linked to the boreal snowshoe hare (*Lepus americanus*)–Canada lynx (*Lynx canadensis*) cycle (Krebs et al., 2001, 2013). Snowshoe hare densities vary approximately 10-fold over the 8 to 11 year cycle with regional predator numbers increasing with hare abundance due to higher productivity and immigration (Krebs et al., 2013). Predator–prey cycles can influence the broader community as predators switch to less abundant alternate prey following the collapse of the primary prey (Marcström et al., 1988; Boutin et al., 1995). In this case, declines in alternate prey abundance may be lagged to the peak abundance of primary prey and predators. We use a time series of fur returns for lynx to assess the influence of predator abundance on whooping crane fledge rates from 1977 to 2013 and test current and delayed effects of predator population growth.

2. Materials and methods

2.1. Data collection

The US Fish and Wildlife Service conducted aerial counts of the population on its wintering grounds in and around Aransas National Wildlife Refuge (hereafter 'Aransas') with repeated surveys between November and April (Stehn and Taylor, 2008). These surveys were carried out between 1950 and 2010 and attempted to 1) census the entire population of hatch year ($C_{hy,t}$) and after hatch year individuals ($C_{ahy,t}$), 2) record the identity of banded birds (see below) and 3) count the number of territories held by breeding-age pairs through the full winter period (Wt_t). While the winter surveys were assumed to represent a census until 2011, the methodology did not allow for an unbiased estimate of population size (Butler et al., 2014). True abundance may have been underestimated if some individuals were missed or overestimated if individuals were counted more than once since there were no years when all birds were marked. Beginning in 2011, the USFWS switched to line transects and abundance estimation methods (Butler et al., 2014). From these annual surveys we used the winter abundance counts for hatch years, after hatch years (both from 1977 to 2010) and total individuals (1977–2012). The sex of whooping cranes cannot be determined visually and we assumed an even sex ratio in the winter counts such that 50% of all individuals observed at Aransas were female ($C_{f.hy,t}$, $C_{f.ahy,t}$ and $C_{f.tot,t}$, respectively).

Reproductive data were obtained by the Canadian Wildlife Service during annual aerial surveys covering ~925 km^2 of Wood Buffalo National Park between 1977 and 2013. Surveys were conducted in May, June and August and recorded the number of active nests (J_t) and fledged chicks (F_t) from nesting pairs, which were used to estimate the annual fledging rate (f_t). The collection of single eggs from 2-egg nests for captive rearing occurred in the first 20 years of this time series (1977–1996, see Ellis and Gee, 2001 for additional details on egg collecting). From 1977 to 1988, 132 whooping cranes were banded on the breeding grounds at 60–65 days of age (Kuyt, 1979). Of these individuals, 46 were female, 47 were male and 39 were unknown sex. Systematic searches for banded individuals occurred at Aransas each winter with some additional sightings from stopover locations during migration or on the breeding grounds. Information on banded birds was compiled to the winter of 2006–07 (Gil-Weir, 2006; Gil-Weir et al., 2012).

2.2. Integrated population model

The IPM was comprised of separate likelihoods using the three data sources: 1) annual female winter counts of hatch year ($C_{f.hy,t}$), after hatch year ($C_{f.ahy,t}$) and total individuals ($C_{f.tot,t}$) at Aransas assuming a 50:50 sex ratio, 2) reproductive data collected at WBNP to estimate annual fledging rate (f_t) and breeding propensity (proportion of breeding age females that nest each year, bp_t), and 3) the re-sighting of color-banded individuals to estimate age-specific annual survival (ϕ_t). The estimated population size in winter is constructed as a state-space model (Brooks et al., 2004), with a state process model describing the abundance of the AWBP population and an observation model linking the winter counts at Aransas to the estimated abundance. We used a female-based population projection model and six age classes after fledging (Fig. 1). Reproductive data and initial marking of individuals occurred on the breeding grounds while the population count and re-sighting of marked individuals was from the early winter period (assumed to be December 1). Therefore, individuals occupy the initial age class for a 6-month period from June 1 to December 1. Individuals occupy the next four age classes for a 12-month period from December 1 in year t − 1 to December 1 in year t and we defined these age classes as sub-adult1 (sad1, 6–18 months), sub-adult 2 (sad2, 18–30 months), sub-adult 3 (sad3, 30–42 months) and adult 1 (ad1, 42–54 months). Females are assumed to breed for the first time at age 4 (Urbanek and Lewis, 2015) as they transition from the sad3 to the ad1 age class. When individuals reach 54 months (4.5 years) they enter the final adult2 age class (ad2).

For each age class, we specify "N" as the estimated abundance from the model with the number of female hatch-year individuals reaching the wintering grounds at Aransas ($N_{f.hy,t}$) as:

$$\left[\left(N_{f.sad3,t-1}\cdot\left(\phi_{ad1.month,t-1}{}^{5}\right)\right)+\left(\left(N_{f.ad1,t-1}+N_{f.ad2,t-1}\right)\cdot\left(\phi_{ad2.month,t-1}{}^{5}\right)\right)\right]\cdot bp_{t-1}\cdot f_{t-1}\cdot 0.5\cdot\phi_{hy,t-1}$$

where $N_{f.sad3,t-1}$, $N_{f.ad1,\,t-1}$ and $N_{f.ad2,\,t-1}$ are the number of sad3, ad1 and ad2 females, respectively, in winter of the previous time step, bp_{t-1} and f_{t-1} are the breeding propensity and fledging rate in the previous summer, and $\phi_{hy,t-1}$ is the 4-month survival rate from August 1 through November 30. We assumed that 50% of fledglings were female. To allow for the possibility of mortality during the five month period from December 1 to the start of the following breeding season (assumed to be May 1) we multiplied $N_{f.sad3,t-1}$, $N_{f.ad1,\,t-1}$ and $N_{f.ad2,\,t-1}$ by a five-

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