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# Considering transient population dynamics in the conservation of slow life-history species: An application to the sandhill crane



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### article info abstract

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The importance of transient dynamics of structured populations is increasingly recognized in ecology, yet these implications are not largely considered in conservation practices. We investigate transient and long-term population dynamics to demonstrate the process and utility of incorporating transient dynamics into conservation research and to better understand the population management of slow life-history species; these species can be theoretically highly sensitive to short- and long-term transient effects.We are specifically interested in the effects of anthropogenic removal of individuals from populations, such as caused by harvest, poaching, translocation, or incidental take. We use the sandhill crane (Grus canadensis) as an exemplar species; it is long-lived, has low reproduction, late maturity, and multiple populations are subject to sport harvest. We found sandhill cranes to have extremely high potential, but low likelihood for transient dynamics, even when the population is being harvested. The typically low population growth rate of slow life-history species appears to buffer against many perturbations causing large transient effects. Transient dynamics will dominate population trajectories of these species when stage structures are highly biased towards the younger and non-reproducing individuals, a situation that may be rare in established populations of long-lived animals. However, short-term transient population growth can be highly sensitive to vital rates that are relatively insensitive under equilibrium, suggesting that stage structure should be known if perturbation analysis is used to identify effective conservation strategies. For populations of slow life-history species that are not prone to large perturbations to their most productive individuals, population growth may be approximated by equilibrium dynamics.

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### 1. Introduction

Understanding the driving influences (endogenous and exogenous) on wild animal populations is of primary concern in ecology and conservation. Ecologists are often interested in the relationships among demographic rates, life-history variation, and natural selection processes, which often involve the study of population change due to vital rate variation over time and/or space ([Caughley, 1977](#page--1-0)). In concert, this information is also essential in science-directed wildlife conservation and management to better understand how to protect small populations from going extinct, control pest populations, and manage populations for sustainable consumptive (e.g., hunting and fishing) and nonconsumptive purposes (e.g., wildlife viewing). For both ecological and conservation focused studies, prospective analyses using population projection matrices (PPMs) have been especially integral for

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understanding dynamics of structured populations (i.e., variation in vital rates by sub-groups of the whole population; [Crouse et al., 1987,](#page--1-0) [Caswell, 2001\)](#page--1-0). The intuitive structure, analytical tractability (in contrast to high dimensional stochastic models), and considerable literature on application and interpretation of PPMs, solidifies their importance in ecological inference. In addition, conservation practitioners often use PPMs to identify effective strategies that manipulate populations through actions directed at specific vital rates [\(Mills and](#page--1-0) [Lindberg, 2002\)](#page--1-0).

Until recently, most prospective PPM analyses have focused on longterm (i.e., asymptotic) dynamics, including asymptotic-population growth ( $\lambda_{\infty}$  = dominant eigenvalue of PPM) and its sensitivity and elasticity to vital rate perturbations [\(Caswell, 2001](#page--1-0), pages 210 & 226, unscaled and scaled derivative of  $\lambda_{\infty}$  with respect to each element of PPM, respectively). However, focusing only on long-term dynamics may be misleading in studies of many wild animal populations and precipitate poor conservation recommendations because a population is unlikely to remain stable for long-term dynamics to shape trajectories [\(Koons et al., 2005; Koons et al., 2006a](#page--1-0)). Instead, focusing on short-

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term dynamics may lead to developing more accurate predictive models [\(Stott et al., 2010\)](#page--1-0) and a better understanding of perturbation effects on vital rates, such as management actions, because these often occur on relatively short time scales ([Koons et al., 2007; Stott et al.,](#page--1-0) [2012a\)](#page--1-0). For structured populations, investigating transient dynamics may be critical to understanding short-term population change and long-term population abundance [\(Ezard et al., 2010\)](#page--1-0).

Wild animal populations are exposed repeatedly to environmental and anthropogenic perturbations of varying types and magnitudes. These may differentially affect a structured population, moving it from equilibrium (i.e., stable stage distribution  $(SSD) =$  dominant right eigenvector of PPM) and producing short-term dynamics that are different than long-term population trajectories [\(Stott et al., 2011](#page--1-0)). Transient dynamics consist of population change arising from current or historical stage structures that are not the SSD. Unlike equilibrium dynamics, in which a population grows or declines exponentially at a fixed geometric rate ( $\lambda_{\infty}$ ), transient dynamics can be highly unstable and even oscillate widely between growth and decline until stabilizing at the SSD [\(Koons et al., 2007\)](#page--1-0). Modeling of structured populations that assume SSD should be based on empirical evidence of the appropriateness of this assumption, or otherwise evaluating non-equilibrium dynamics is critical ([Koons et al., 2005](#page--1-0)).

Populations with a comparatively high potential for some form of transient dynamics include those species with a relatively slow lifehistory (sensu [Sæther and Øyvind, 2000;](#page--1-0) long-lived and slow reproduc-ing) and that are exposed to frequent disturbance [\(Koons et al., 2005;](#page--1-0) [Koons et al., 2006a; Gamelon et al., 2014](#page--1-0)). Investigating transient dynamics is often encouraged when a population is being harvested [\(Koons et al., 2006a; Ezard et al., 2010; Stott et al., 2011\)](#page--1-0). More generally, this could be a concern whenever there is anthropogenic removal of individuals from a population, including both intentional removal by hunting or fishing, poaching, translocation, and incidental take (e.g., bycatch, collisions with man-made structures). These removals are direct perturbations to system dynamics that can affect vital rates and stage structure, which could dominate short-term population change. In addition, transient dynamics can also have long-term effects on a population's size through population inertia ([Hodgson and Townley,](#page--1-0) [2004\)](#page--1-0). Population inertia is the relative difference in long-term abundance between populations, where one has stayed at the SSD and the other has a non-equilibrium structure in its history ([Koons et al.,](#page--1-0) [2007\)](#page--1-0). The population with a non-equilibrium structure will achieve an abundance at a fixed ratio either above or below that of the population at equilibrium. Population inertia could move a population past defined objectives or influence the time it takes for a population to reach a population objective ([Koons et al., 2006a](#page--1-0)).

Despite the recent advancements and recommendations for evaluating transient dynamics in wild animal populations, their application in conservation and management remains largely in plant ecology [\(Stott](#page--1-0) [et al., 2010; Ellis, 2013](#page--1-0), but see [Buhnerkempe et al., 2011\)](#page--1-0). We are interested in exploring both short- and long-term population change to demonstrate the process and utility of combining transient and asymptotic analyses to gain a deeper understanding of stage-structured dynamics and relevant conservation implications, as well as to better understand implications of removing individuals from populations of slow life-history species. We do so while considering a range of common uncertainties in population modeling, including population structure and parameterization (i.e., age specific reproduction, population stage distribution). We use the sandhill crane (Grus canadensis) as a model species, as it has a relatively slow life-history with several populations that are exposed to sport harvest and thus known direct perturbations (see [Gerber et al., 2014](#page--1-0)). In addition, crane researchers and managers have identified the importance of better understanding transient dynamics for future conservation and management of cranes [\(Case and Sanders, 2009\)](#page--1-0); such knowledge is equally important for the conservation of any long-lived and slow reproducing species [\(Koons et al., 2005\)](#page--1-0).

We constructed and parameterized stage-structured population models under different hypotheses for the sandhill crane to, 1) evaluate characteristics of maximum potential transient dynamics of slow lifehistory species, 2) examine how stage structure affects population growth and the time it takes for population recovery, 3) examine the robustness of asymptotic sensitivity to vital rate perturbations informing conservation strategies by investigating transient vital rate perturbations, and 4) evaluate the potential for observed sandhill crane harvest to affect the stage structure and cause population inertia. Our findings provide 1) a coherent and direct application of integrating transient investigations into conservation research and practices, 2) insights into short- and long-term dynamics of species that are long-lived, slow-reproducing, and with delayed reproduction, which may be subjected to anthropogenic removal of individuals (e.g., harvest, poaching, translocation, incidental take), and 3) guidance on using vital rate perturbation analysis to inform the effectiveness of conservation actions in population management. We provide specific recommendations informing sandhill crane population management and outline the general context of when conservation practitioners should be most concerned with transient effects.

### 2. Materials and methods

### 2.1. Study species and population

The sandhill crane is one of fifteen species belonging to the family Gruidae and only one of two cranes that are native to North America (Sandhill and Whooping Crane, Grus americana). Sandhill cranes are large birds that primarily nest in shallow freshwater wetlands (see [Gerber et al., 2014](#page--1-0)). Age at first breeding appears to vary by population and subspecies, but generally cranes attempt breeding at 2–3 years of age and are first successful by 5 years of age with most of the production coming from birds ≥8 years of age (see [Gerber et al., 2014\)](#page--1-0). Typically, a pair of sandhill cranes produce a single clutch of two eggs per nesting season. They maintain long-term pair bonds ([Tacha, 1988\)](#page--1-0), except when pairs fail to produce young, in which case they will then remate the following year ([Nesbitt and Tacha, 1997\)](#page--1-0). Sandhill cranes have been known to live up to 30 to 40 years of age.

We focus on the Rocky Mountain Population (RMP) of sandhill cranes, as there is detailed information on vital rates and the removal of individuals via harvest is known. The RMP is migratory, nesting in low densities throughout the central Rocky Mountains of North America, stopping over during spring and fall migration in the San Luis Valley (SLV) of Colorado, and wintering primarily in the Rio Grande Valley of New Mexico [\(Drewien and Bizeau, 1974\)](#page--1-0). Historical abundances have been estimated to be as low as 400–600 in the mid-1940s [\(Walkinshaw, 1949](#page--1-0)) and 10,000–15,000 in 1971–1972 ([Drewien and](#page--1-0) [Bizeau, 1974](#page--1-0)). More recently, the population has been estimated to average 19,560 between 2000 and 2013 (SD = 1268.10, range = 17.468– 21,614; [Kruse et al., 2014](#page--1-0)). There is no information on the full current or past age structure of the RMP.

The RMP has been subject to annual harvest since 1981, following 63 years since the passing of the Migratory Bird Treaty Act of 1918, which closed legal hunting. Between 2000 and 2013, the estimated harvest has averaged 902.50 cranes per year (SD = 279.76, range =  $528-$ 1392; [Kruse et al., 2014](#page--1-0)) with approximately 20% being juveniles (i.e., young of the year, unpublished data). The RMP management plan outlines the population objective is to maintain a 3-year average fall count of 17,000 to 21,000 ([The Subcommittee on Rocky Mountain](#page--1-0) [Greater Sandhill Cranes, 2007](#page--1-0)); no harvest is allowed if the 3-year average is below 15,000. The population objective is intended to provide recreational opportunities for bird watchers and hunters, while minimizing crop damage, and disease and overcrowding in the wintering grounds ([The Subcommittee on Rocky Mountain Greater Sandhill](#page--1-0) [Cranes, 2007](#page--1-0)).

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