



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



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ABSTRACT

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). 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 non-consumptive purposes (e.g., wildlife viewing). For both ecological and conservation focused studies, prospective analyses using population projection matrices (PPMs) have been especially integral for

understanding dynamics of structured populations (i.e., variation in vital rates by sub-groups of the whole population; Crouse et al., 1987, Caswell, 2001). 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 Lindberg, 2002).

Until recently, most prospective PPM analyses have focused on long-term (i.e., asymptotic) dynamics, including asymptotic-population growth (λ_∞ = dominant eigenvalue of PPM) and its sensitivity and elasticity to vital rate perturbations (Caswell, 2001, pages 210 & 226, unscaled and scaled derivative of λ_∞ 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). Instead, focusing on short-

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term dynamics may lead to developing more accurate predictive models (Stott et al., 2010) 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., 2012a). For structured populations, investigating transient dynamics may be critical to understanding short-term population change and long-term population abundance (Ezard et al., 2010).

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). 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 (λ_∞), transient dynamics can be highly unstable and even oscillate widely between growth and decline until stabilizing at the SSD (Koons et al., 2007). 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).

Populations with a comparatively high potential for some form of transient dynamics include those species with a relatively slow life-history (sensu Sæther and Øyvind, 2000; long-lived and slow reproducing) and that are exposed to frequent disturbance (Koons et al., 2005; Koons et al., 2006a; Gamelon et al., 2014). Investigating transient dynamics is often encouraged when a population is being harvested (Koons et al., 2006a; Ezard et al., 2010; Stott et al., 2011). 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, 2004). 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., 2007). 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).

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 et al., 2010; Ellis, 2013, but see Buhnerkempe et al., 2011). 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). 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); such knowledge is equally important for the conservation of any long-lived and slow reproducing species (Koons et al., 2005).

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 life-history 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). 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). Typically, a pair of sandhill cranes produce a single clutch of two eggs per nesting season. They maintain long-term pair bonds (Tacha, 1988), except when pairs fail to produce young, in which case they will then re-mate the following year (Nesbitt and Tacha, 1997). 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). Historical abundances have been estimated to be as low as 400–600 in the mid-1940s (Walkinshaw, 1949) and 10,000–15,000 in 1971–1972 (Drewien and Bizeau, 1974). 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). 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) 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 Greater Sandhill Cranes, 2007); 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 Cranes, 2007).

2.2. Population models

We hypothesized four population models that integrate available empirical population-level vital rates and capture uncertainties about age-specific reproduction. Survival parameters are based on results from a long-term mark-resight study (1972–1992, R.C. Drewien, unpublished data) that captured and tagged individuals across their breeding area and resighted individuals throughout the year. A multi-state mark-recapture model was used to integrate resightings and dead recoveries to simultaneously correct for resighting probability and tag loss. Results indicated differential survival without harvest by young of the year, 1-year olds, and ≥2 year olds (survival estimates below). We consider four PPMs: 1) 5 stages with non-zero fecundity only occurring for the oldest stage (see below, PPM1), 2) 9 stages with non-zero fecundity only occurring for the oldest stage (PPM2, see Supplementary data), 3) 9 stages with non-zero fecundity starting at 5 years of age based on the proportion of parents by age group from the mid-continent population (Tacha et al., 1989, PPM3, see Supplementary data), and 4) 9 stages with non-zero fecundity increasing starting at stage 3 (PPM4, see Supplementary data).

We parameterized all PPMs using a birth-pulse, post-breeding stage-structured model,

$$PPM1 = \begin{pmatrix} 0 & 0 & 0 & 0 & F \\ S_1 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & S_4 & S_5 \end{pmatrix}$$

where S_i for stages 1–4 is the survival between ages i and $i + 1$, S_5 is the survival for all ages greater than four, and F is the per capita fecundity in the SLV. For all PPMs, S_1 and S_2 are unique values, while survival remains constant after 2 years of age ($S_1 = 0.848$, SE = 0.06; $S_2 = 0.947$, SE = 0.02; $S_{2-3} = 0.955$, SE = 0.03). We derived F based on the average number of young per pair observed in the SLV on fall migration over a 40 year period (*brood*, mean = 1.23, range = 1.13–1.39; Drewien, 2011) and the proportion of breeders, which is believed to be ≈20% (*PropBreeders*; Drewien, R.C., pers. comm.; Case and Sanders, 2009). To make fecundity apply to those individuals in the terminal class that reach the breeding area, we scaled fecundity by partial year terminal survival. The fecundity per individual was thus derived as, $F = S_5^{8/12} \times PropBreeders \times brood$. We currently lack empirical evidence for vital rate senescence. There is currently no indication that brood size decreases substantially with age, for those birds that do breed (Drewien, 2011), and no indication that survival declines with age (R.C. Drewien, unpublished data). Therefore, we do not evaluate PPMs that include

reproductive or actuarial senescence. Analyses were performed in the R language (Core Team, 2015) using the package ‘popdemo’ (Stott et al., 2012b); for measures of time to convergence, we used an error tolerance of 1%.

2.3. Transient potential of an unharvested population

The most extreme effects of the stage structure occur when a population consists of individuals only in the first and terminal stages. This maximum transient potential has been termed the transient bounds and represents a best- and worst-case scenario when the stage structure is unknown (Stott et al., 2011), which is common and is also the case for the RMP. Relevant metrics include reactivity, first-time step attenuation, maximum amplification and attenuation, and amplified and attenuated inertia (see Table 1 for definitions); all metrics are standardized to remove effects of initial population size and asymptotic growth (Stott et al., 2011). In addition, we explore intermediate transient dynamics where the population is initialized with only individuals of a single stage and then projected through time, relative to a population at the SSD, as it has been recommended when the stage structure is unknown (Stott et al., 2011).

2.4. Transient population change and projected recovery

We consider transient population growth ($GR = \frac{\sum_i n_{i,t}}{\sum_i n_{i,t-1}}$, where $n_{i,t}$ is the i th element of the population stage vector in year t) by projecting PPM1–4 using initial stage distributions from the complete set of permutations of each stage at increments of 0.05. We initialize each population projection at 14,000 cranes to consider the scenario where the population is below the current harvestable level and the lower-bound of the population objective for the RMP. We investigate the proportion of populations for each year that are growing ($GR > 1$), that are growing faster than asymptotic growth ($GR > \lambda_\infty$), that are harvestable ($\sum_i n_{i,t} \geq 15,000$), and that are above the lower RMP objective ($\sum_i n_{i,t} \geq 17,000$). We also more closely examine four initial stage structures: 1) only individuals of the terminal stage (*Adult*), 2) the SSD (*SSD*), 3) the only published estimate of sandhill crane stage structure (9 stages = [0.11 0.10 0.09 0.08 0.07 0.06 0.06 0.05 0.38]; Tacha; Tacha et al., 1989), and 4) an even distribution of individuals across all stages (*Even*). We consider these stage structures to better understand the impact of over-harvest of juveniles in sequential years, capture long-term baseline dynamics, to provide an empirical basis of a realistic crane stage structure, and to capture an extremely skewed stage structure from the SSD, respectively.

Table 1
Biological interpretations of transient indices and their values for four hypothesized sandhill crane population models for the Rocky Mountain Population.

Index	Interpretation	PPM1 ^a	PPM2 ^b	PPM3 ^c	PPM4 ^d
Asymptotic growth (λ_∞)	Population growth of a structured population at the stable stage distribution	1.03	1.02	1.09	1.02
Reactivity (\bar{P}_1)	Maximum population size of a structured population not at equilibrium in a single time step, relative to a population at equilibrium.	1.04	1.06	1.22	1.05
First time step attenuation (\underline{P}_1)	Minimum population size of a structured population not at equilibrium in a single time step, relative to a population at equilibrium.	0.82	0.83	0.78	0.83
Max. amplification ($\bar{P}_{.max}$)	The maximum population size achievable for all time steps for a population initialized not at equilibrium, relative to a population initialized at the same population size and at equilibrium.	1.07	1.14	1.34	1.12
Max. attenuation ($\underline{P}_{.min}$)	The minimum population size achievable for all time steps for a population initialized not at equilibrium, relative to a population initialized at the same population and at equilibrium.	0.65	0.52	0.45	0.59
Amplified inertia (\bar{P}_∞)	The maximum asymptotic (long-term) population of a population initialized not at equilibrium, relative to a population of the same size and initialized at equilibrium.	1.06	1.12	1.29	1.11
Attenuated inertia (\underline{P}_∞)	The minimum asymptotic (long-term) population of a population initialized not at equilibrium, relative to a population of the same size and initialized at equilibrium.	0.69	0.59	0.53	0.62

^a PPM1: 5 stages, oldest stage class only reproduce.
^b PPM2: 9 stages, oldest stage class only reproduce.
^c PPM3: 9 stages, empirical proportion of stage-based reproduction.
^d PPM4: 9 stages, stages 4 to 9 have a non-zero probability to reproduce.

2.5. Perturbation analyses of an unharvested population

Considering the relative effects each vital rate has on population change is both important for understanding life-history strategies and of critical importance in managing a population (Crouse et al., 1987; Mills and Lindberg, 2002). However, the commonly used asymptotic sensitivity analysis (Caswell, 2001) can be misleading because of its linear approximation between a vital rate and characteristics of population change, as this relationship can be highly non-linear (Stott et al., 2012a; Hodgson and Townley, 2004). We explore vital rate perturbations using traditional asymptotic sensitivity, as well as using a transfer function analysis, to consider the non-linear relationship between a perturbation to vital rates of our population models and the resulting effect on λ_∞ and population inertia (Stott et al., 2012a; Hodgson and Townley, 2004). We are also interested in understanding the maximum impact harvest could have on each vital rate without causing the RMP to decline; thus, we derive the level of perturbation on each vital rate (singularly) that will create a stable population ($\lambda_\infty = 1$).

To understand the influence of stage structure on vital rate sensitivity, we also examine the temporal sensitivity of transient growth by considering all permutations of stage structures (increments of 0.05). Transient sensitivities are expected to converge to traditional asymptotic sensitivities, but may vary under non-equilibrium. We use the methods developed by Caswell (2007) for transient sensitivity of time-invariant models based on fundamental matrix calculus (consistent differentiation of scalar-, vector- and matrix-valued functions of scalar, vector or matrix arguments) and apply them to PPM1.

2.6. Transient dynamics under simulated harvest

We investigate harvest effects on crane stage structure by projecting 10,000 populations, initialized at 17,000 cranes, with an initial population structure at the unharvested SSD or using *Even*. Populations that exceed 15,000 are subject to stochastic harvest with equal probability between the lower and upper bound of the estimated harvest from the RMP since 2000 (Min = 528, Max = 1392; Kruse et al., 2014). Harvest proportionally affected stage structures stochastically using a Dirichlet distribution with mean parameters of μ_i for each *i*th stage. We considered two scenarios, 1) where harvest of juveniles averages 20% and the rest of the harvest is equally distributed, on average, among the remaining stages (e.g., PPM1, $\mu_i = 1$ and the expected probability = 1/5 for the *i*th stage) and 2) mean harvest is proportional to the distribution of individuals of each stage in each year. We measured the proportional difference between projected populations for each year and the unharvested SSD using Keyfitz's $\Delta = \frac{1}{2} \sum_i |n_{i,t} - w_i|$, where w_i is the proportion of individuals at the SSD (Keyfitz, 1968). Keyfitz's Δ ranges from zero to one with zero indicating the same proportion of individuals among stages between two population vectors; a higher Keyfitz's Δ can indicate stronger transient dynamics. Under our scenario, the non-zero harvest rate per year on the entire population is minimally 3.5% and maximally 9.3%.

Under stochastic harvest, the population will eventually stabilize to a constant mean distribution of harvested stage structures. We examine whether harvest has a large effect on how the stage structure varies by measuring the average Keyfitz's Δ of the harvested stochastic stage structures as the proportional difference between the expected harvested stage distribution and all stage distributions that vary from it. We also measure the maximum possible difference in stage structure between the unharvested SSD and any harvested stage distribution and the time it would take to converge to asymptotic dynamics if harvest was ceased. In addition, we measure the maximum inertia that could occur in a population that was under harvest, which then was halted, to allow the population to recover.

Lastly, because RMP stage structure is unknown, we use PPM1 to investigate a full range of proportional harvest across stages (all

permutations of proportional harvest on each stage at increments of 0.05). We project populations, as described above, except here we vary the harvest effect on each stage (across simulation, not years) and derive Keyfitz's Δ and population inertia for the most extreme and mean stage structures. We also consider a few specific cases by estimating inertia using only the minimum and maximum estimated RMP harvest between 2000 and 2013 and define the proportional harvest on each stage as, 1) only juveniles are harvested, 2) only individuals of the terminal stage are harvested, 3) harvest is proportional to the stage distribution, or 4) harvest is evenly distributed across all stages.

3. Results

3.1. Transient potential of unharvested populations

Population models indicate the RMP would be growing slowly without harvest (Table 1); λ_∞ was comparable for all models except PPM3, which indicated more than twice the annual growth of the other models. Overall, PPM1 was least sensitive to extreme transient dynamics, while PPM3 was the most sensitive. Relative to a population at the SSD and over the same time frame, we found an overall greater potential to achieve lower abundances than higher abundances (Table 1). Thus, there is a high potential for non-SSD to reduce population growth. The RMP could grow to an absolute maximum of 7 to 34% greater than a population growing at the SSD (max. amplification) and an absolute minimum (maximum attenuation) of between 45 and 65% less (Table 1). A structured population biased towards the older stages generally leads to increased population sizes relative to those at the SSD, while the opposite is true for structures biased to younger non-productive stages (Fig. 1). In addition, an increasing number of stages that do not contribute to producing young, increase the number of bias initialized states that will produce attenuated inertia (Fig. 1). Lastly, an increase in delayed reproduction (PPM1 vs. PPM2) has a minor effect on reactivity and first-time step attenuation, but has a relatively large effect on long-term outcomes of population size (Table 1).

3.2. Transient population change and projected recovery

Population structure has considerable influence on short-term projected population size, time until the population converges to asymptotic dynamics, time until the population is harvestable, and above the lower population objective of the RMP (Figs. 2, A1–A3). Convergence to asymptotic dynamics can take longer for populations with more stages (7 years for PPM1 and 15 years for PPM2–4) and higher reproduction can lead to increased positive growth above λ_∞ (i.e., PPM3), but otherwise overall patterns are consistent across models. Oscillating dynamics between population growth and decay were not observed, except for an initial short population decline due to biased structures to younger stages that would eventually grow. Most initial stage structures lead to immediate growth below λ_∞ , but also to eventual growth above, which then stabilized to λ_∞ . For PPM1, as long as the majority of the population has a non-zero probability of producing young, the population will almost always be growing (Fig. 2). Immediate population growth ($GR > 1$) in the first year was low across all initial stage structures (6–19%) for PPM1–2 and 4; it takes 3 to 7 years before $\geq 95\%$ were positively growing (Fig. A4). Very few initial stage structures produced immediate short-term growth that exceeded λ_∞ ; the proportion of populations that exceeded λ_∞ peaked for PPM1–2 in the year where populations initialized with only the youngest stage first became reproductive. The vast majority of populations reached a harvestable level ($\geq 95\%$) in 4–12 years and the lower RMP objective in 5–18 years (Table 2).

A population initialized with *Even* produced a short-term decline in abundance (all models except PPM3), which began growing in less than four years. Transient dynamics persisted for 3 to 13 years, depending on the model and initial stage structure (Fig. 3). The *Tacha* stage structure

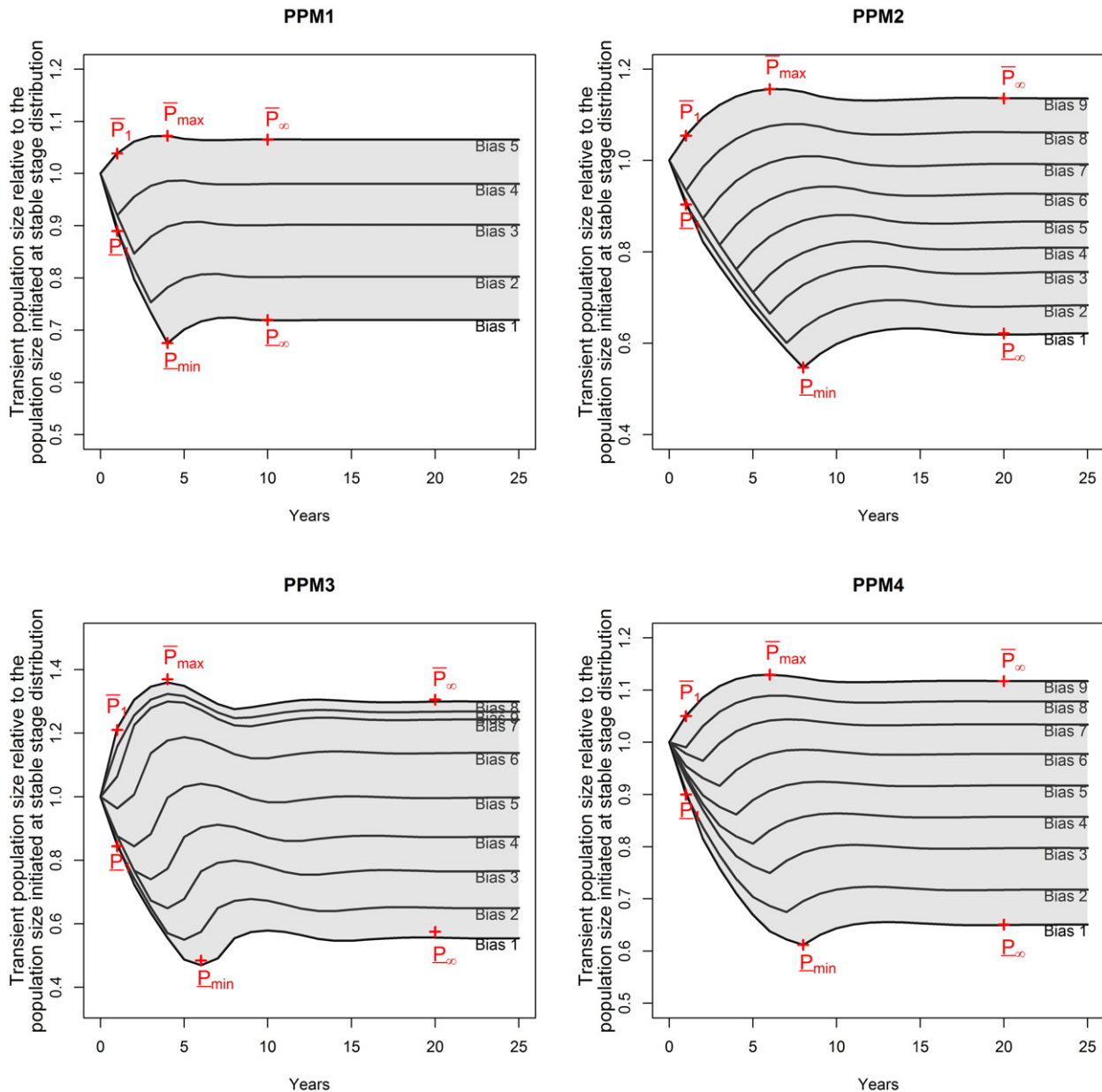


Fig. 1. Stage-biased transient potential for sandhill cranes of the Rocky Mountain Population. Each line is a population initialized with individuals only belonging to a single stage, relative to a population initialized at the stable stage distribution. \bar{P}_1 = reactivity. \underline{P}_1 = first time step attenuation. \bar{P}_{max} = maximum amplification. \underline{P}_{min} = maximum attenuation. \bar{P}_{∞} = amplified inertia. \underline{P}_{∞} = attenuated inertia.

was similar to SSD dynamics for all population models. The time it took the population to reach harvestable levels was highly variable by population and initial stage structure (Table 2). At the SSD, it could take up to 4 years, while *Tacha* could take 7 years; reaching the minimum RMP objective would take even longer at 9 or 12 years at the SSD and *Tacha*, respectively. The least amount of time to attain a harvestable population would be 1 year, if the entire population was only made up of individuals contributing to breeding production and up to 4 years to reach the minimum RMP objective.

3.3. Perturbation analyses of an unharvested population

Traditional sensitivity analyses produced biased effects of large vital rate perturbations on λ_{∞} (Figs. A5–A8; e.g., PPM1 perturbation on survival >0.2); large perturbations to terminal-stage fecundity and non-terminal-stage survival were underestimated, while terminal stage survival was overestimated. A large drop in survival of the oldest

individuals would lead to a declining population in the long-run, but not decline as quickly as we would expect from the traditional sensitivity analysis. Survival parameters that are not of the terminal stage are robust to perturbations; a decrease in survival by 0.4 would not cause λ_{∞} to decline below one (Figs. A5–A8). Across all models, we found λ_{∞} most sensitive to survival and fecundity of the terminal stage. There are no feasible singular perturbations to non-terminal stage fecundities that could decrease λ_{∞} to 1 (Table A.1). However, an absolute decrease in terminal stage fecundity by 0.06 or 0.05 would cease growth for PPM1–2, and 4. This could occur either due to a decrease in the number of pairs that attempt breeding or a decrease in the number of eggs that are successful in hatching, fledging, and migrating to the SLV. Similarly, survival of the terminal stage could incur a decrease of 0.03 or 0.04 before population growth ceased.

Perturbation results on population inertia are complex and strongly dependent on the initial population structure and magnitude of the perturbation (Figs. A9–A12). The *most sensitive vital rates to population*

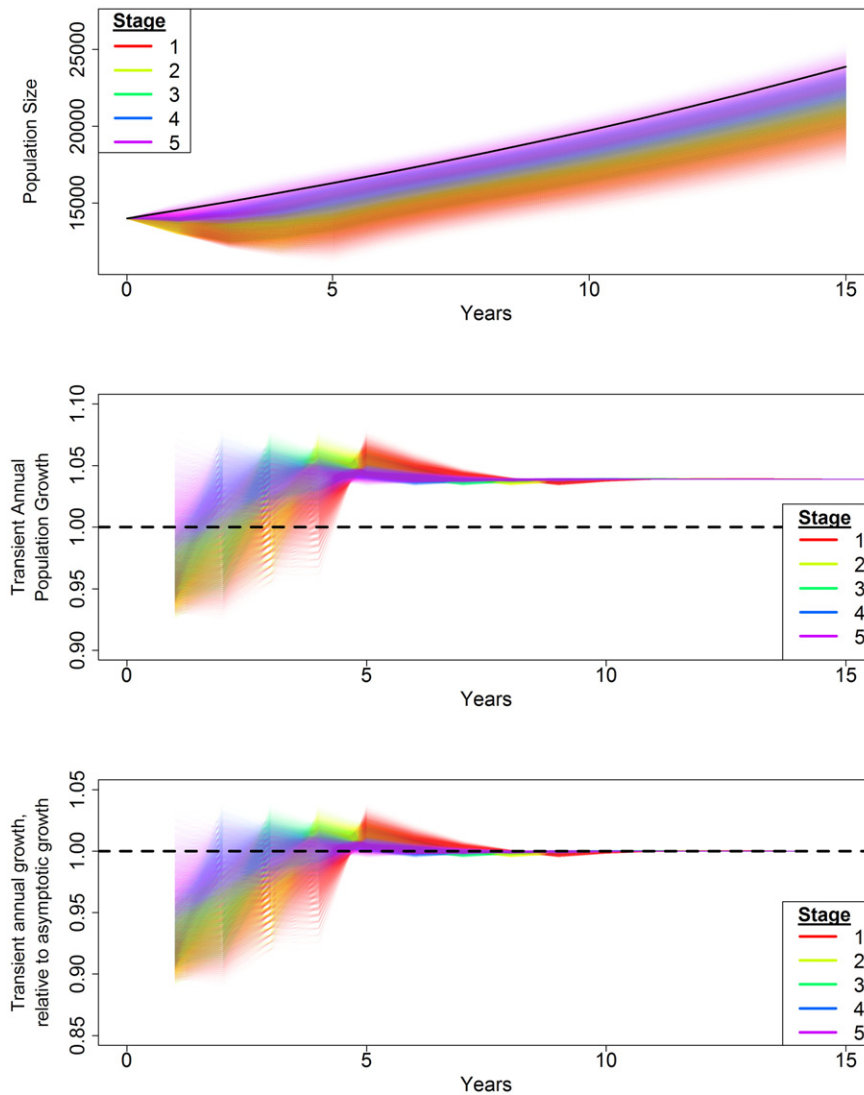


Fig. 2. Projected population size over time (top), transient population growth (middle), and transient population growth relative to λ_∞ (bottom) across all permutations of initial population structures for PPM1. The legend indicates the initial stage (1 = juvenile, 5 = oldest stage) with the majority of individuals ($\geq 50\%$). The solid black line in the top figure is population growth according to the stable stage distribution.

inertia are terminal survival and fecundity. Regardless of initial population structure, a decrease in terminal survival by ≈ 0.1 would stabilize population inertia for PPM1–2, and PPM4. For population models with single-stage productivity (PPM1–2), perturbing the single and terminal-fecundity to near zero largely removes any population inertia, regardless of the initial population structure. Stages with positive

fecundity that are not the terminal stage are highly resistant to perturbations inducing population inertia different than that caused by their initial population structure (Figs. A9–A12). Across models, a population initialized at the SSD is resistant to departures for relatively large negative perturbations to non-terminal survival (up to -0.45), as well as negative perturbations to terminal-survival (up to -0.1). Perturbations on terminal-survival when initialized at *Even* had a strong and highly non-linear effect on population inertia for PPM1–2, but not as much for PPM3–4. *Adult* induces positive population inertia across all models, which remains as such under all vital rate perturbations, except for a decrease in terminal-survival, which can halt or even reverse the positive inertia. The *Tacha* stage structure and effects of perturbations are mostly similar to the SSD for all models.

Table 2

The predicted number of years for a population starting at 14,000 cranes to reach a harvestable level (15,000) and reach the lower population objective (17,000), following the management plan for the Rocky Mountain Population.

Model	Years to population > 15,000				Years to population > 17,000			
	Adult ^a	Stable ^b	Tacha ^c	Even ^d	Adult	Stable	Tacha	Even
PPM1 ^e	1	2	3	5	4	6	6	9
PPM2	1	4	7	10	4	9	12	15
PPM3	1	1	1	2	1	3	2	3
PPM4	1	3	5	7	4	8	10	11

^a Initial population of only the terminal stage.

^b Initial population following the stable stage distribution.

^c Initial population at the stage distribution according to Tacha et al. (1989).

^d Initial population evenly distributed among all stages.

^e Population projection matrix (PPM).

Transient sensitivity of population growth to vital rates of PPM1 were highly variable depending on the stage structure (Fig. 4). There was strong temporal variation until sensitivities converged to asymptotic results, which occurred in 10 to 15 years. The sensitivity of survival rates of non-productive stages could exceed the sensitivity of the terminal productive survival stage when the majority of population was not in this stage, but this effect was short-lived. For example, population growth was immediately very sensitive to survival of individuals aged three when the majority of the population started in this stage.

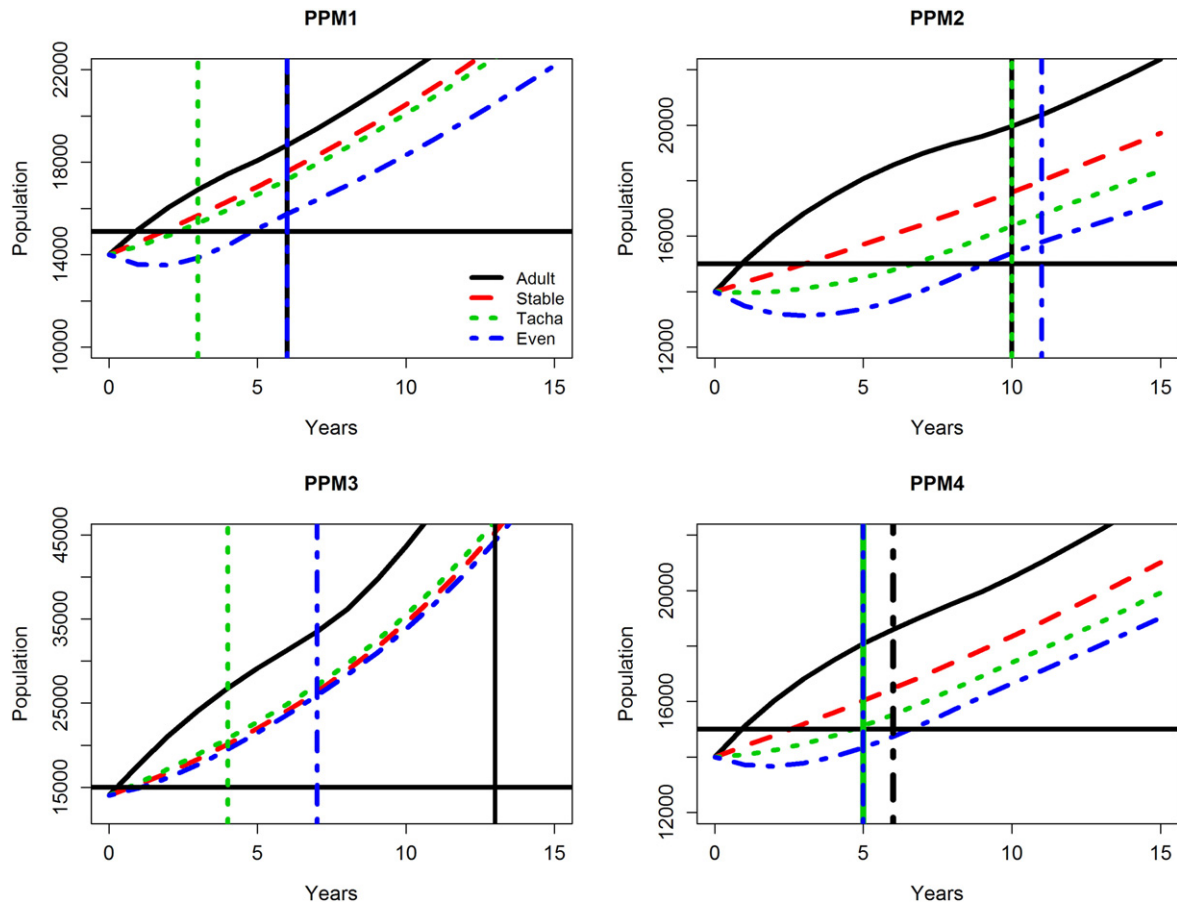


Fig. 3. Projected populations under four population projection matrices (PPM) for sandhill cranes of the Rocky Mountain Population (RMP). Each is initialized at 14,000 birds with four alternative initial stage distributions. The vertical lines indicate convergence to asymptotic dynamics and the horizontal line indicates when RMP cranes can begin to be harvested. Notice the y-axes are not equivalent.

However, it was equally sensitive 2–3 years after a population that was initially mostly aged 2, and 3–4 years after a population that was initially mostly juveniles (Fig. 4). In addition, while asymptotically population growth is more sensitive to terminal-stage survival than fecundity (Figs. A5–A8), under non-equilibrium dynamics with even the majority of the population in the terminal stage, transient growth is fairly equally sensitive to both vital rates (Fig. 4; i.e., high overlap in transient sensitivity between 0 and 5 years).

3.4. Transient dynamics under simulated harvest

The proportional difference between population sizes of the unharvested SSD and harvested stage distributions varied through time and depended strongly on the initial population structure, but not largely on the PPM or how harvest was distributed among the stage structure (Figs. 5, A13). The expected harvested stage distribution stabilized after 15 years for all models, regardless of initial stage distribution or the type of proportional harvest on the stage structure. The Keyfitz's Δ between the long-run harvest stage distribution and the unharvested SSD was similar and relatively small across population models and effects of harvest at between 0.02 and 0.04. Once stable, the average Keyfitz's Δ for all population models and effects of harvest was small at ≤ 0.05 . The maximum possible difference between the unharvested SSD and the harvested stage structures was fairly large at between 0.10 and 0.22, depending on the population model and how harvest affected the different stages. However, these stage structures did not induce considerable inertia (0.98–1.03, across models); convergence to non-harvested asymptotic dynamics occurred in one or two years.

Considering all permutations of proportional harvest on PPM1 resulted in an expected stage structure that varied temporally until stabilizing at six years. After six years, the difference between the harvested stage distributions and the unharvested SSD were minimally 0.04, maximally 0.17, and averaged 0.1. These stage distributions would produce inertia in an unharvested population of 1.01, 1.03, and 1.02, respectively. The maximum time it would take for asymptotic dynamics to dominate would occur in three years. Lastly, in the case-specific scenarios, the minimum and maximum inertia from only harvesting juveniles (1.010, 1.024), only harvesting the terminal stage class (0.998, 0.994), harvesting in proportion to the stage structure (1.000, 1.000), and an even distribution (1.000, 1.001) were not considerable.

4. Discussion

4.1. Transient dynamics and life-history

For a slow life-history species, such as the sandhill crane, there can be relatively high potential for transient dynamics to limit short-term population growth and thus reduce long-term abundance compared to what would be expected under equilibrium. Considering all possible stage structures, it is likely that λ_{∞} would often over-predict population growth of these species. The primary reason is delayed reproduction, which is common for long-lived vertebrates (Wittenberger, 1979). Delayed reproduction is thought to have high adaptive value when successful breeding is lower for younger individuals and carries high mortality risk (physiologically or behaviorally). Each year a species delays reproduction adds an age class that does not contribute to reproduction; thus, a population structure biased towards these individuals will have a

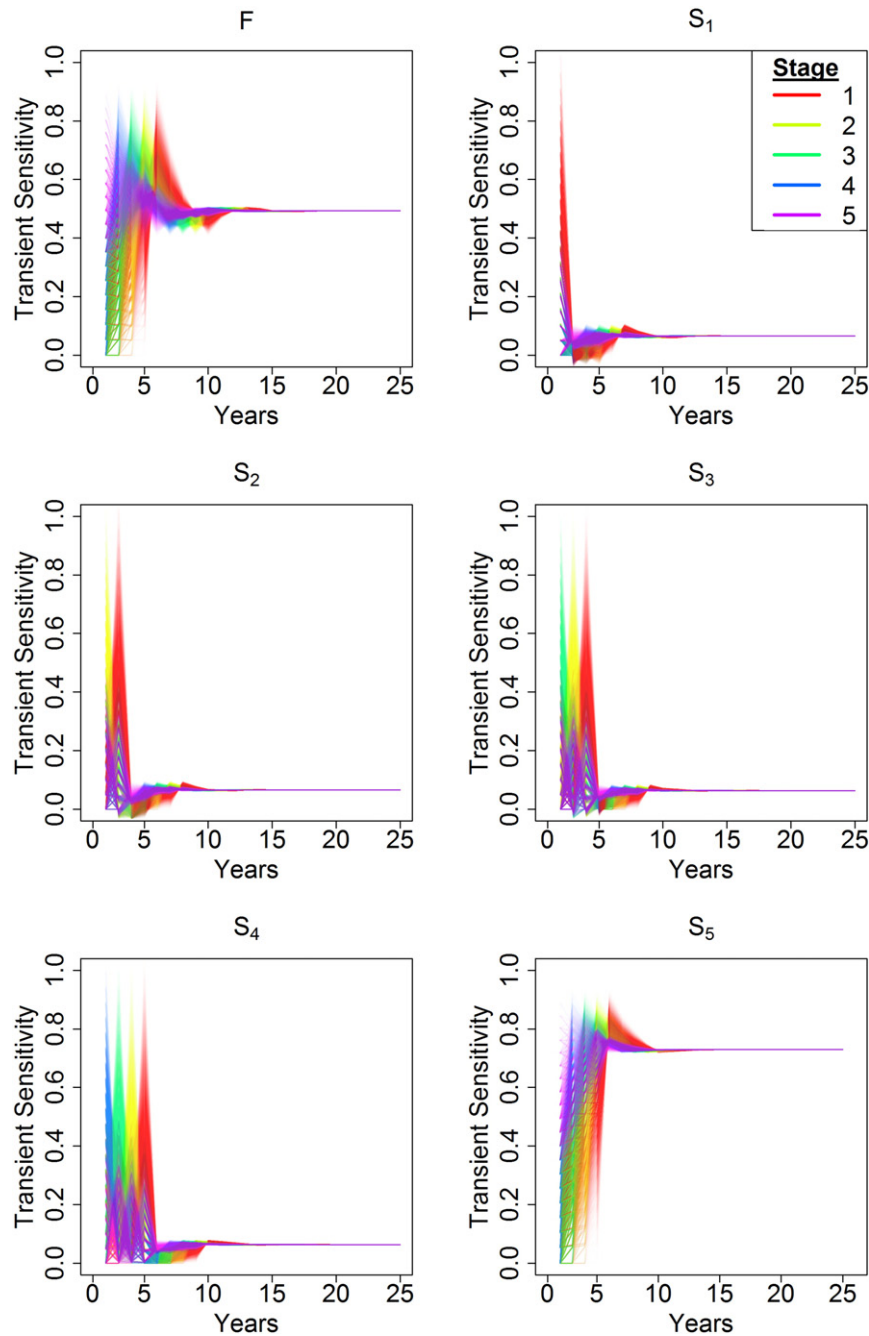


Fig. 4. Transient population growth sensitivity of PPM1 vital rates through time under the complete set of permutations of the initial stage structure. The legend indicates the initial stage (1 = juvenile, 5 = oldest stage) with the majority of individuals ($\geq 50\%$).

lower short-term population growth compared to a population at the SSD. The time it takes to reach a population objective will be much longer than predicted when assuming a SSD, which is common in many studies (Stott et al., 2011).

However, should we expect slow life-history species to have stage distributions skewed towards younger individuals? We might observe this in 1) newly established populations (e.g., translocated or founder populations), 2) a population that has recently succumbed to a die-off of the older/productive individuals, or 3) small populations which are likely influenced by demographic stochasticity. Generally, the first scenario will likely be rare in systems that are not highly managed or not dynamic meta-populations. The second scenario may also be generally uncommon unless facing high anthropogenic pressure (Wittemyer et al., 2014); long-lived species are just that because they maintain

high annual adult survival with low variation. Empirical evidence has shown that for long-lived species, there is often higher variability in the less sensitive vital rates (e.g., fecundity), suggesting that these species have evolved mechanisms (e.g., bet-hedging) to reduce high variability in population growth due to reduced variation in their most sensitive vital rates (i.e., adult survival; Sæther and Øyvind, 2000; Gaillard and Yoccoz, 2003). A population with high adult survival with low variability will eventually accrue high proportions of individuals into the terminal-stage (but see Crouse et al., 1987) and thus a stage structure that is skewed towards the SSD. The third scenario may be becoming more common, as habitats are globally fragmented (Haddad et al., 2015) and many vertebrate species are exhibiting population declines, with slow life-history species particularly vulnerable (Collen et al., 2009). Small populations are perhaps becoming common, which

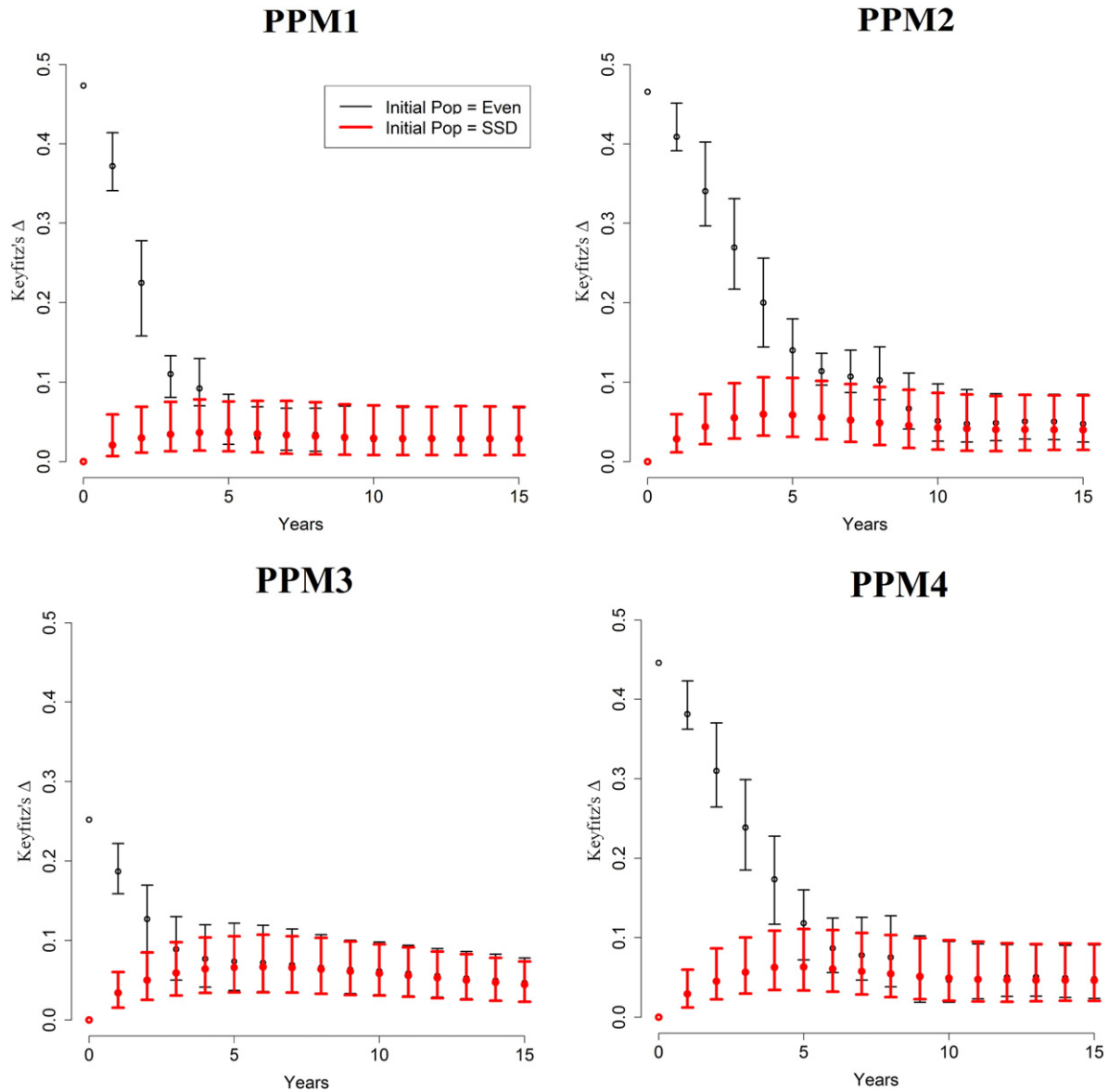


Fig. 5. The Keyfitz's Δ between the stable stage distribution (SSD) of non-harvested and stochastically harvested populations, initialized at either the SSD of the non-harvested population or an even stage distribution; zero indicates no difference between two population stage structures. Harvest affected the stage structure on average in proportion to the number of individuals in each stage.

suggests transient dynamics will be increasingly important. To our knowledge no study has yet explored how much observed population process variance in vertebrate populations can be explained by transient effects; in a long-term demographic study of plant populations, the potential for large transient responses did not reflect the observed dynamics (Ellis, 2013), while another study showed that many plant populations were often near the SSD (Williams et al., 2011).

Slow life-history species may be robust to transient dynamics due to their low growth rate. We observed no significant oscillating dynamics in our population projections between growth and decay, with one exception. When the population is highly skewed away from the productive stages there is a short population decline until enough individuals become productive for the population to start growing. More dramatic oscillations appear to be symptomatic of species with high growth rates (Gamelon et al., 2014). We also found that amplified inertia and transient growth above λ_∞ is limited by the slow reproductive potential. In contrast, attenuated inertia and transient growth is unlikely because of evolutionary strategies that have minimized natural variability of adult survival (Sæther and Øyvind, 2000; Gaillard and Yoccoz, 2003),

which could perturb the stage structure to have an overabundance of younger, non-productive individuals, relative to the SSD. We also found that our population models at the SSD were resistant to relatively large perturbations to survival ($S_i \pm 0.2$), variation in age-specific fecundity (across population models), or relatively high harvest (max harvest rate of 9%), such that very minor population inertia would be expected ($\leq 3\%$). Lastly, as long as the majority of the population was in the terminal-stage, transient population growth was at most $\pm 5\%$ from λ_∞ . Our findings are in accordance with life-history studies that found a positive association between population growth and the magnitude of transient dynamics, demonstrating that slow life-history species are buffered against disturbance because their populations are slow to change (Stott et al., 2010; Gamelon et al., 2014). But conversely, this makes for a slow population recovery.

Vital rate sensitivity has important implications in how conservation practitioners choose to affect population dynamics. We found that vital rate sensitivity can vary substantially due to the stage structure, where transient population growth becomes more sensitive to a vital rate depending on the proportion of individuals of the population in the

specific stage. In cases where the population structure is known, it is important to consider how short-term management actions could be most effectively directed at vital rates by examining sensitivity with specified stage structures. When stage structure is unknown, like with the RMP, we can still benefit from a more general understanding of vital rate sensitivity.

The effect of anthropogenic removal of individuals on population stage structure and its consequences on transient dynamics, will depend both on the magnitude and variation of the removal and how it differentially affects each stage. Perturbations that are directed at the most productive individuals of a slow life-history species can cause short-term population declines for several years, even after survival returns to pre-perturbation levels. For harvested populations, detailed studies have documented how selective harvesting can affect population demography (Fenberg and Roy, 2008), but the extent to which this pressure affects population growth and especially short-term dynamics through skewed stage distributions is still poorly understood (Milner et al., 2007). Many harvested avian species, including sandhill cranes, cannot be sexed or aged (beyond a short immature stage), thus harvest programs are neither sex- nor age-specific by design; it is much more common for targeted selective harvest by sex and/or age (via size) to occur in mammals and fish than it is for birds (Fenberg and Roy, 2008). Incidental selective harvesting does of course occur, depending on differential vulnerability to harvest.

The most common targeted stage-specific pressure on avian species may be egg/chick collecting for subsistence consumption or the illegal pet trade (e.g., parrots). For fledged individuals, it may be common for harvest to be spread across age classes and even likely to be in proportion to the population of each age class, assuming each age class has similar behaviors that make them equally vulnerable to harvest. We know this not to be true for some populations where fledged-juvenile birds are more vulnerable to harvest than older birds, such as the sandhill cranes of the RMP (Drewien, R.C., unpublished data) and bobwhite quail (*Colinus virginianus*, Roseberry and Klimstra, 1992). However, this additional impact on juveniles may have little effect on short- or long-term dynamics, because population growth and inertia are highly robust to perturbations in juvenile survival.

The cases where we should expect transient dynamics to dominate population dynamics are when the most productive individuals are being selectively removed, such as the removal of wild adult birds-of-paradise (*Paradisaeidae*) for the pet trade (Pangau-Adam and Noske, 2010) or harvest of adult sea turtles, sharks, and marine mammals. Alternatively, incidental take due to bycatch of sea turtles, seabirds, sharks and marine mammals by fishing activities can also have dramatic impacts on adult populations (Lewison et al., 2004). When population decline of slow life-history species is caused by increased harvest, poaching, or incidental take of the most productive individuals of the population, wildlife practitioners should be concerned about transient dynamics. Asymptotic growth will likely overestimate the short-term population growth because of a disproportionate number of non- or poor-breeders and thus be overly confident in the time it takes to reach a population objective.

However, density-dependent compensation may buffer against transient dynamics. Delayed reproduction of slow life-history species may be in part due to behavioral and physiological constraints, but could also be because of competition with older individuals for high-quality breeding areas. A decrease in older/productive individuals may not necessarily cause transient dynamics if younger individuals are able to claim vacant breeding territories and become successful reproducers at similar rates as older individuals. For large losses of highly productive individuals, complete replacement may not be possible, but the effect of habitat-limitation due to density dependence may buffer against transient effects. In addition, a perturbation that causes a loss of older individuals does not necessarily have to decrease annual survival probability, thus affecting the stage structure. As long as these deaths are compensated for by a decrease in deaths due to other causes, annual

survival may be unchanged. For RMP sandhill cranes, there is evidence that harvest mortality of cranes ≥ 1.5 were being compensated for between 1981 and 1992 (Drewien, R.C., unpublished data), such that transient effects predicted in our perturbation analyses to these age classes are at least somewhat exaggerated. Of course, for long-lived animals with low natural mortality, the window for compensation is small. Generally, long-lived species may be less adept at compensation than short-lived species and that transient buffering by harvest compensation should not be expected, even perhaps for all sandhill crane populations (Péron, 2013).

The effect of removal of individuals on social dynamics should not be overlooked. Selective removal of certain 'keystone' individuals from the population can have an overwhelming disproportional effect on social and population dynamics (Milner et al., 2007). This is certainly true for removal of older individuals, which may be socially dominant and a reservoir of important ecological knowledge (e.g., elephants, *Loxodonta africana*; McComb et al., 2001). For the Wandering Albatross (*Diomedea exulans*), bonding with a new mate after a loss is not immediate and is perhaps conditional on the availability of similar aged birds or other widowers being available (Jouventin et al., 1999). Thus, after the loss of a mate there is a delay in becoming productive once again, which will ultimately exacerbate transient dynamics. The behavioral impacts of harvest is still poorly known for sandhill cranes. Selective removal of certain sexes, which can skew the sex ratio, may also lead to non-equilibrium dynamics (Dobson and Poole, 1998).

4.2. RMP transient dynamics

Based on the increasing conservation of wetland habitats in the 20th century, a long duration during which the RMP was not exposed to sport harvest, substantial population growth between the 1940s and the beginning of harvest in 1981, and low variability in adult survival (Drewien, R.C., unpublished data), it is reasonable to suspect that the RMP is near the SSD, or at least positively skewed to the older stages, which is congruent with the SSD. If the RMP did eventually stabilize near the SSD prior to legal hunting, our findings suggest that harvest would not have moved the population far from equilibrium. While slow life-history species may have a larger potential for population inertia than species that are shorter-lived and reproduce quickly (Koons et al., 2006b), effects may have to be relatively large and skewed towards the productive stages to actually cause considerable population inertia (this study; Koons et al., 2006a). If an extreme event did occur to the RMP and biased the stage structure towards the younger and non-reproducing cranes, we could expect convergence to equilibrium dynamics to take as long as 20 years; however, considering that die-offs of all non-juveniles are highly unlikely, we would expect transient growth rates for <10 years.

Under most stage structures with the majority of the population in the terminal-stage, we can expect the RMP to grow. However, it would be prudent to assume that population growth would not be as high as under asymptotic dynamics, as most stage structures that are skewed to the older stages do not grow as fast. RMP stage structures skewed towards the older stages are most sensitive to terminal-fecundity and survival, while relatively insensitive to perturbations on non-terminal survival. Based on observed vital rate variation, the RMP stage structure is likely most affected by variation in juvenile productivity, which is thought to vary according to the availability of quality breeding areas mediated through climatic variation (Gerber et al., 2015). However, our results do not indicate significant long-term transient effects, but short-term population change is likely to vary.

Assuming the RMP is both declining and near the SSD, the most effective reversal of population declines would be to decrease adult mortality, increase juvenile production, or increase reproduction of younger age classes; depending on the exact stage structure either one of these will be most effective. Positive population inertia that would overshoot the RMP management objective should not be a significant concern. The

current RMP harvest decision rule reactively reduces harvest based on lower annual observed juvenile production, but there is a lag in its effect. Based on our results, we can expect that if the RMP declines to 14,000, it will likely take between 2 and 4 years before the population will be harvestable and 6–9 years (without harvest) before the population exceeds the lower population objective. If the population is already close to or less than the minimum population objective and long-term drought in the Rocky Mountains is expected, it would be prudent to proactively reduce harvest and/or encourage local managers of breeding areas to sustain water levels that would benefit crane production. However, this does not take into account that the RMP is monitored with an index of abundance (i.e., pre-migratory fall count) that is subject to considerable annual variation in the availability or detection of the population (Gerber, 2015), thus obscuring true abundance and the time it would take to detect a population decline and adjust harvest.

Our findings mitigate concerns about making harvest decisions about Rocky Mountain Population sandhill cranes without annual information on stage structure. Cranes are likely near the SSD, especially given evidence of compensation for adult mortality in survival rates. The rate of harvest could in the near future reach and eventually exceed the level of natural mortality, at which point compensation would no longer apply. However, the harvest rate increase is slow, and based on our results, we anticipate that even if this impact causes the population to dip below the objective, remedial action to reduce harvest would be effective at returning the population to the objective relatively quickly, without concern of inertia.

4.3. Modeling limitations

The lack of reliable annual population estimates (Gerber, 2015) inhibits our ability to validate whether our hypothesized population models are accurate representations of sandhill crane dynamics. Three of our models (PPM1–2, 4) had similar λ_{∞} and were close to expectation for a long-lived and slowly reproducing animal. These growth rates were also comparable to a population of whooping cranes, which was estimated to average near 4% growth (Butler et al., 2013). Golden eagles, which also have a similar life-history to cranes (delayed reproduction to 5 years of age and a typical clutch of two eggs per nest) are estimated to have a similar growth rate ($\approx 2\%$ annual growth; Tack, 2016). We suggest that despite the empirical basis for the age-specific breeding propensity for PPM3, it is much too optimistic in its asymptotic growth of 9% annually, which predicts a tripling in abundance in a 15-year time span. Although highly variable, population counts prior to 2000, when harvest was relatively low (1981–1999, mean = 347), do not indicate a potential for tripling the population (Kruse et al., 2014). While not a primary validation of PPM1, 2, and 4, it is interesting to note that the SSD of these models indicated a proportion of juveniles in the SLV (0.08, 0.07, 0.07, respectively) very similar to the 42-year average that has been observed (0.08; Drewien, 2011).

Our approach to understanding transient dynamics was focused on mathematical modeling of the PPM. We thus did not consider population-level process variances in our vital rates (i.e., stochasticity). We should expect our results to reflect mean-level responses and perhaps under-represent the expected variability. Methodologies on transient dynamics from stochastic models are an active area of research that we expect to see greater use of in the future (see, Caswell, 2007).

4.4. Conclusion

Recently developed tools to investigate transient dynamics enable ecologists and conservation practitioners to better understand animal population dynamics. Transient tools are a pathway for investigating how likely population perturbations affect stage structures, and thus moving beyond either the simplistic assumption that a population is either at or cannot be at the SSD. Maximum transient potential may be informative for some populations, such as those exposed to extreme

disturbances, but generally may lead to extreme conclusions (Ellis, 2013) and confound the real issue, which is the likely effect of disturbances on short-term dynamics. For populations potentially exposed to anthropogenic removals, it is important to consider the variability in the pressure of removals on different stages, particularly the extremes, which would cause the largest potential differences between stage structures.

Conservation practitioners may be interested in management actions on different time scales. If goals are very short, transient sensitivities to population growth and reactivity could be used in guiding short-term management decisions. However, we found that transient population growth was highly variable in its sensitivity depending on the stage structure, which suggests that some knowledge of the stage structure is important in determining effective strategies to impact immediate population growth. For longer-term goals, understanding the effects of vital rates on population inertia could be used to either reduce or increase long-term abundances, relative to current stage structure. However, for slow life-history species that are at or near the SSD, perturbations to single vital rates may have very limited impacts.

Having direct information on the stage or age structure can be beneficial in predicting short-term dynamics that can help guide management decisions (Hauser et al., 2006). However, for many animals this information is not easily obtained. For long-lived species that cannot be aged using natural markings, such as sandhill cranes, a long-term mark-resight study may be necessary. Due to the costs of such a study, it may often be infeasible to obtain population numbers by ages or even stages.

For long-lived species, it may be reasonable to assume that the population is near the SSD. However, pertinent information to make this assumption include knowledge of population size and declines, natural and anthropogenic perturbations, and whether these differentially affect individuals by age. This information could be then used to investigate whether realistic effects could move a population far from the SSD. If a population is shown to have declined due to adult mortality, understanding the potential for transient effects will be highly important to help the species recover quickly. This is also true for small populations, for which determining the stage structure may be more logistically feasible and will certainly produce beneficial knowledge for understanding realistic population growth.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.06.014>.

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