DISSERTATION

SANDHILL CRANE POPULATION MONITORING, MODELING, AND HARVEST DECISION MAKING

Submitted by

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Abstract

Sandhill crane population monitoring, modeling, and harvest decision making

Managing wild animal populations can be challenging. There are often uncertainties about population dynamics, the short- and long-term effects of management actions, and challenges to logistically and financially monitoring key population parameters, which can lead to uncertainty about the meaning of parameters that are monitored and result in many parameters not being monitored and thus unknown. This dissertation research was motivated by information needs outlined by sandhill crane (*Grus canadensis*) researchers and managers. Questions and concerns arose about the current management strategy for the Rocky Mountain and Mid-Continent Populations (RMP, MCP, respectively), including whether there is potential for transient dynamics to dominant population change, what the limitations of the current population monitoring programs mean for making harvest decisions, and whether the current harvest decision process is appropriate to meeting long-term population objectives. Addressing these questions is pertinent to other crane populations as well, because as sandhill crane populations expand and increase, there is increasing interest in crane harvest of other populations, such as the Eastern Population. The dissertation research presented here is partially aimed at addressing some of the concerns of sandhill crane population management.

My focus was on synthesizing available population level-data to develop models that could be used to investigate population dynamics and the potential limitations of current sandhill crane monitoring and harvest frameworks. In addition, I outline an adaptive management

framework that could be useful for making future harvest management decisions. More generally, findings presented in this dissertation have implications for those interested in predictive modeling, the influence of stage-structure on population dynamics, monitoring populations using an index, and making recurrent management decisions in the face of multiple uncertainties.

In Chapter 1, the objective was to organize the current scientific and management literature of sandhill cranes, as no such effort had been done since the mid-1990's. This work was motivated by a number of reasons. First, it was to ensure I was well acquainted with the current body of research on sandhill cranes, as well as the focus of management agencies through the years, from early conservation efforts when sandhill crane populations were relatively small to more harvest management approaches when populations began expanding. Second, it was to better understand population-level differences in behavior and vital rates. Since this dissertation is directly aimed at understanding RMP sandhill cranes, it was important to be able to frame research findings in the broader context of sandhill crane conservation and management. One significant finding is that, despite a considerable effort from researchers and management agencies dedicated to the conservation of sandhill cranes, there are surprisingly few studies that estimate population-level parameters. This made it challenging to construct realistic population models. The reasons are probably many, but a primary reason is likely because studies of migratory crane populations are logistically and financially challenging. Regardless, the management of sandhill cranes over the past many decades, since the passing of the Migratory Bird Treaty Act in 1918, can be hailed as a conservation success story. Once isolated in the 1950's, crane populations are now expanding back into previously occupied areas and likely new areas as well, and beginning to overlap not only in wintering and migratory areas, but also breeding areas. A small group of dedicated researchers (Rod C. Drewien, Gary L. Ivey, Gary L. Krapu, Carroll D. Littlefield, Stephen A. Nesbitt, Thomas C. Tacha, Paul A. Vohs, and Lawrence H. Walkinshaw) has contributed substantially to our current understanding of this amazing species, thus greatly aiding its recovery and success across North America. Looking forward, perhaps the most important avenue for future research on sandhill cranes is the continued application of modern genetic tools to investigate questions regarding relationships between populations and subspecies. If there is continued interest in developing empirically based population models, there is a significant gap of understanding in regard to age-specific breeding probabilities, as well as information about the activities of non-breeders.

In Chapter 2, I investigate the relationship between the annual proportion of juveniles in the RMP of sandhill cranes and hypotheses related to variability in climate factors. Specifically, I was interested in simultaneously evaluating hypotheses about how short- and long-term drought, as well as weather patterns, affect the production of juvenile sandhill cranes while also developing a predictive model. Since climate variables are often collinear, I chose to evaluate a continuous set of models using statistical regularization that can handle multicollinear predictor variables. I discuss predictive modeling and discuss how generalizable predictive models (trained by out-of-sample fit and based on ecological hypotheses) can be useful and perhaps needed by conservation and management decision makers. A major finding was that both short- and long-term drought, but mostly long-term drought, may severely limit the ability of sandhill cranes to produce young because of breeding habitat limitations. In addition, I found the number of freezing days and snowpack during the summer months can also negatively affect juvenile recruitment, while spring snow-pack has a positive effect.

These findings may not be unique to sandhill cranes. Alterations of hydrological patterns and water levels by drought may impact many wetland nesting birds in the Rocky Mountains.

In Chapter 3, I investigate the potential for sandhill crane populations to be governed by non-equilibrium dynamics. More specifically, I investigated transient potential, population growth under non-equilibrium dynamics, transient and asymptotic sensitivity to vital rate perturbations, and whether observed harvest could impact crane stage structure and lead to population inertia. As has been suggested in the literature, sandhill cranes and other long-lived species, have an inherent high potential for transient dynamics. However, the largest transient effects 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. I did not find cause for concern for highly oscillating short-term dynamics, but this could occur due to behavioral variability, which may not have been incorporated into population models due to lack of empirical estimates. In general, I found sandhill cranes to be robust to the effects of population inertia due to vital rate perturbations and that transient population growth can be very sensitive to vital rates that are relatively insensitive under equilibrium; for sandhill cranes, adult fecundity and survival can be equally important to short-term growth when the majority of the population is in the most productive stage. Practitioners often have to manage wild animal populations without current or historical knowledge about the stage structure. For populations of slow life-history species that are not prone to relatively large perturbations to their most productive individuals (e.g., disease die-offs, large-scale over-harvest, major transformation of key habitats), assuming the population is near the stable stage distribution may be reasonable.

In Chapter 4, I focus on assessing the past and current population monitoring data of the RMP. This data are used directly to make annual harvest decisions, but it is unknown whether the variation observed in the fall counts and population index could be indicative of population dynamics. By integrating population-level data, including juvenile recruitment, harvest, and survival estimates into a stochastic stage-based population model, I was able to assess whether annual changes in the observed counts and fall population index were biologically realistic. I found spring migratory (1984-1996) and fall staging area (1997-2014) counts of the RMP to exhibit annual change that was biologically unrealistic with spring counts being more variable that fall counts. In contrast, I found the three-year moving average fall population index to exhibit biologically reasonable annual change. In addition, I investigated the usefulness of smoothing counts using a hierarchical Bayesian time series (HBTS) modeling approach and compare that to the current approach of using a moving three-year average. First, I found differences in the likelihood of meeting the RMP objective depending on assumptions of the observational process for the HBTS model. Second, I found the changes in the predicted mean of the HBTS model to be biologically plausible if observed crane harvest mortality was compensated up to natural mortality. Third, in a simulation exercise, I found that the predicted mean of the HBTS is generally a more reliable estimate of the true population than using the moving three-year average estimator. Lastly, there are some important advantages of the HBTS compared to the moving three-year average, including obtaining measures of uncertainty, incorporating prior information, easily accommodating missing years of data, and being able to forecast the population.

In Chapter 5, I focus directly on the harvest decision process by using a simulation approach to compare the current RMP sandhill crane harvest decision framework and an

adaptive resource management (ARM) framework. I consider nine different scenarios with varying levels of monitoring, modeling, and decision uncertainty. The underlying population dynamics follow a complex stochastic stage-structured, density-dependent population model. The two primary objectives of this study were to evaluate the robustness of the current crane harvest decision framework and to evaluate whether an ARM framework with relatively simplistic population models and uncertainty about the population size could decrease risks associated with the RMP framework. I found that using a model set of relatively simple models in an ARM framework to make annual harvest decisions on average outperformed the current RMP decision process in meeting the population objective across a wide array of scenarios. More specifically, when the population without harvest was stable or declining, I found that the population is harvested to a degree that causes the population to be pushed to and beyond the lower bound of the population objective (17,000), regardless of whether the population is monitored without error. I also found that when harvest decisions are made using the RMP framework, there is only a small improvement in meeting the population objective when resolving monitoring uncertainty, such that the population size was observed without error. In contrast, when using an ARM framework, resolving the uncertainty about the population size meant that the population objective was always maintained, regardless of the model set. I surprisingly found that stage-specific optimal harvest decisions are not always necessary to meet a population objective when population dynamics are stage structured. An optimal population-level harvest decision can lead to meeting population objectives when the stage structure does not vary much. Lastly, when there is considerable uncertainty in estimating annual population size and/or population models are expected to be relatively simple compared to the true population process, learning in an ARM process

may be best viewed as a way to identify reasonable predictive models for the current time period, rather than potential to learn about ecological processes.

Ultimately, the long-term management of sandhill cranes will require integrating harvest management, where decisions occur on a relatively short time-scale, with the long-term decisions associated with habitat management of key breeding, migratory, and wintering areas. Important considerations for future conservation strategies includes ensuring that migratory sandhill crane populations can find suitable breeding wetlands and adequate resources on migration and at wintering grounds. Migratory populations rely on agricultural production to meet energetic requirements, which means that shifting agricultural production may have a significant impact on crane behavior and population dynamics. Sandhill cranes and their ancestors have been in North American for many millennia and with wise and cautious harvest and habitat management they will likely continue to fill summer wetlands with their wild and raucous trumpeting.

PREFACE

A special thanks to my committee and especially to my advisor, Bill Kendall, for his support and patience. The Fish, Wildlife, and Conservation Biology department at Colorado State University has a remarkable graduate student community, which provided endless help and assistance during my tenure. Many people I have interacted with over the last several years from the greater CSU community have been a great source of help and inspiration, including D. Anderson, L. Bailey, K. Burnham, P. Chanchani, L. Cordes, T. Gallo, J. Gallo, B. Noon, J. Northrup, K. Pearson, C. Setash, G. Shannon, V. Steen, L. Stinson, J. Tack, G. White, P. Williams, H. Williams, K. Yeager, and many more. G. Engler and J. Pratt have been remarkable in every way, helping to keep the ship running smoothly. I have also been lucky to interact with a number of conservation researchers and managers beyond CSU that have made significant contribution to my education, including W. Brown, J. Dubovsky, J. Dwyer, Z. Farris, J. Gammonley, J. Ivan, K. Kruse, A. Lyet, D. Olson, B. Parmenter, R. Drewien, and Sunarto. I am also grateful for the funding for this project, which was provided by the U.S. Fish and Wildlife Service's Mountain-Prairie Migratory Bird Office and Webless Migratory Game Bird Program. Lastly, thank you to my family and especially Belita for being wonderful.

This dissertation is organized by chapters, in which each chapter is intended to eventually be published in a research journal. Below are the manuscript titles and intended authorship and target journal/publisher.

Chapter 1: Sandhill crane natural history

An edited and peer-reviewed version of this work has been published online at The Birds of North America website (http://bna.birds.cornell.edu/bna/). This species account is written with a general audience in mind, including bird enthusiasts, ornithologists, researchers, and managers. It is formatted following guidelines for The Birds of North America (BNA) species accounts. This work is reproduced with permission from Dr. Alan Poole, the chief editor at The Birds of North America. Support for the original Sandhill Crane BNA account by T. C. Tacha, S. A. Nesbitt, and P. A. Vohs was provided by the Caesar Kleberg Wildlife Research Institute at Texas A&M University (TCT), the Florida Game and Fresh Water Fish Commission (SAN), and the Iowa Cooperative Fish and Wildlife Research Unit (PAV). Brian D. Gerber was supported by the U.S. Fish and Wildlife Service's Webless Migratory Game Bird Program and their Mountain-Prairie Migratory Bird Office and Colorado State University. James F. Dwyer was supported by R. E. Harness and EDM International, Inc.

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Chapter 2: Optimal population prediction of sandhill crane recruitment based on climate-mediated habitat limitations

This chapter has been published at the Journal of Animal Ecology, which is a journal of the British Ecological Society. The intended audience are ecologists interested in sandhill cranes, predictive modeling, and climate effects on migratory birds. It is reproduced here with permission from the publisher John Wiley and Sons under the license number 3596010280950. This research utilized the Colorado State Universtiy Information Science and Technology Center's Cray High Performance Computing System (ISTeC Cray HPC) Model XE6 supported by NSF Grant CNS-0923386. We are very grateful to L. Cordes, P. Doherty, D. Koons and an anonymous reviewer for providing helpful edits and comments on a prior version of this manuscript.

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Chapter 3: Transient dynamics of a slow life-history species exposed to anthropogenic removal

This chapter is intended to be submitted to Ecology, a journal of the Ecological Society of America. The intended audience are researchers and managers interested in population dynamics. More specifically, it is intended for those interested in short- and long-term population change of staged-structured populations. I am grateful to I. Stott for helping provide guidance of implementing and interpretating measure of transient dynamics. In addition, I am very grateful to P. Doherty, M. Hooten, and J. Tack for providing highly beneficial editorial comments on a previous version of this chapter.

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Chapter 4: Monitoring with an index: investigating variation in the Rocky Mountain Population of sandhill cranes

This chapter is intended to be submitted to either the Journal of Wildlife Management, Ecological Applications, or Condor. The general audience are ecological researchers and managers that are interested in monitoring wildlife populations using indices.

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Chapter 5: 'Adaptive' versus 'reactive' management strategies: implications for sandhill crane and other harvested species

This chapter is intended to be submitted to the Journal of Wildlife Management, Wildlife Monographs, Ecological Applications, or Ecological Modeling. The general audience are ecological researchers and managers interested in sandhill cranes, migratory bird population management, harvest decision making, and adaptive resource management.

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CHAPTER 1

Sandhill crane natural history

1.1. Introduction

Crane species hold an important place in cultures around the globe. Cranes are particularly prominent in traditional Japanese art, which often highlight the generas graceful lines and mesmerizing dances. Cranes, including sandhill cranes (*Grus canadensis*), also feature in contemporary art in North America (Figure 1.1) where their penetrating calls and elaborate dances are both distinctive and spellbinding. Wide interest in sandhill cranes has led to numerous crane festivals during migration (Figure 1.2) when cranes congregate in large flocks (Figure 1.5). A few of these festivals occur in Dayton, Tennessee, Bellevue, Michigan, Kearney, Nebraska, Monte Vista, Colorado, Socorro, New Mexico, Lodi, California, and Fairbanks, Alaska. Such interest has also led to the support of extensive research programs by state and federal agencies, conservation organizations, and research universities. These programs have been directed in particular by Rod C. Drewien, Gary L. Ivey, Gary L. Krapu, Carroll D. Littlefield, Stephen A. Nesbitt, Thomas C. Tacha, Paul A. Vohs, and Lawrence H. Walkinshaw, leading to over 400 reports, book chapters, and peer-reviewed publications cited in this literature review.

Sandhill cranes are heavy bodied, long-necked, long-legged birds inhabiting open grasslands, meadows and shallow freshwater marshes (Figure 1.3). Migrating cranes often are readily observed foraging in cereal fields, particularly the stubble of harvested corn, and roosting along slow moving rivers and other fresh water bodies. Six subspecies of *Grus canadensis* (*G. c. canadensis*, *G. c. nesiotes*, *G. c. pratensis*, *G. c. pulla*, *G. c. rowani*, *G. c. tabida*) organized into nine, sometimes overlapping, populations are currently recognized, including three non-migratory populations (Cuban, Florida, and Mississippi; see Distribution) and six migratory populations (Eastern Flyway, Mid-Continent, Rocky Mountain, Lower Colorado River, Central Valley, and Pacific Flyway) breeding from the northeastern United States, through central Canada to Alaska and eastern Siberia (Walkinshaw 1973, Jones et al. 2005a). The Mid-Continent Population is further divided for management purposes into two subpopulations (Gulf Coast and Western), though recent research suggests additional division into four subpopulations might have biological support (Krapu et al. 2011, see Distribution). The Central Valley Population is divided in northern and southern subpopulations.

Sandhill cranes can live for over 35 years in the wild. First breeding is deferred until 2 to 8 years of age, depending on the subspecies, population, available high quality habitat and individual development, and 0.35 young per year raised to the age of independence (Nesbitt 1992a). Together, delayed age at first breeding and low annual productivity explain the slow population growth inherent in this species. This slow growth has been a key obstacle in the conservation and management of at-risk populations (Tach et al. 1989, Drewien et al. 1995). Pairs and families constitute the primary social units (Figure 1.4), but at times cranes are highly gregarious with extended family members and unrelated birds roosting communally and feeding in large flocks, particularly during migration and on wintering grounds (Drewien 1973, Walkinshaw 1973, Tacha 1988; RCD, Littlefield et al. 1994, Tacha et al. 1994, Ivey et al. 2005, Krapu et al. 2011). Sandhill cranes are socially monogamous, often with long-term pair bonds and extended biparental care of young, though microsatellite DNA markers have recently revealed extra-pair fertilization in some cases (Hayes et al. 2006, 2007, CDL, RCD).

Clutch size is normally 2 eggs, occasionally 1, and rarely 3. Failed nesting often leads to renesting.

The scientific literature on sandhill cranes is organized largely by breeding populations where the term population is used in a broad, flexible sense to describe individuals breeding in generally defined areas (sensu Mills 2007). This approach was adopted during the early days of crane management in North America when habitat loss and overhunting (see Conservation and Management) had lead to distinct breeding populations separated by unoccupied areas. Using this approach, management actions applied to populations have been tailored to meet local and regional recovery goals. Three unintended consequences of this approach can be confusing (see Priorities for Future Research). First, as cranes become more numerous and better understood, some populations have begun to overlap, leading to inconsistencies in terminology. Second, some populations include more than one subspecies. Third, wintering areas often support cranes from more than one breeding population. Together, these sources of variation can make it difficult for readers to identify with certainty an authors intended scope of inference for a given study unless that scope is stated explicitly.

To minimize confusion, Tables 1.1 and 1.2 provide a list of subspecies in each breeding population and summarizes breeding, migratory stopover, and wintering areas by population. We have also consistently organized each chapter, and each section within each chapter, by population from east to west. When information on a specific topic is available from only a subset of populations, we report that information, and leave implied that when other populations are not mentioned, no population-specific information is available. Cardinal directions have been consistently labeled as n, s, e, and w for north, south, east, and west.

1.2. Distinguishing Characteristics

Sandhill cranes are elegant wading birds distinguished by their long legs, necks, and bills, and gray or rust-colored plumage contrasting with a striking red crown present on all but first-year birds (see Appearance, Figure 1.6, 1.7). Height is 1.0-1.2 m, and wing span is 1.8-2.0 m, depending on subspecies and sex, with smaller subspecies breeding farther n and larger subspecies breeding farther s (see Distribution), and males usually larger than females (*G. c. canadensis*: 3.75 ♂, 3.34 kg ♀; *G. c. tabida*; 5.43 ♂, 4.84kg ♀; Lockman et al. 1987). Sexes are similar in plumage (i.e., monochromatic), and indistinguishable even via cloacal examination. Thus, the sex of juveniles and unpaired adults is difficult to determine (Tacha and Lewis 1979, Tacha, 1988) without genetic analyses. Sex can however be distinguished in breeding adults during the Unison Call (Archibald 1975; see Sounds).

Sandhill cranes have 10 primary and 16 secondary feathers. They are diastataxic, i.e., there is no secondary feather corresponding to the fifth feather of the greater coverts, and the innermost secondary coverts and tertials are elongate and ornamental, drooping over the tail, and largely hiding the tail from view when standing. The tail has 12 comparatively short rectrices, leading to a distinct profile in flight with the feet and legs trailing well beyond the end of the tail.

The foot is anisodactyl (3 toes point forward and one toe, the hallux, points back), which is the most common arrangement of avian toes. But unlike most anisodactyl feet, the hallux is elevated, contacting the ground only when a bird sinks into soft mud or sand. This leads to a unique 3-toed footprint in solid soils, and explains why members of the subfamily Gruinae, including sandhill cranes, do not typically use elevated perches like tree limbs. This is however, not true of all cranes; cranes of the subfamily Balearicinae have a non-elevated hallux that allows them to perch in trees. The bill of sandhill cranes is elongated and stout, used to probe for plant materials, cultivated grains, small vertebrates, and invertebrates on or below the soil surface (see Food Habits). From the base of the bill above the eyes to the back of the head, bare, mostly unfeathered skin, sparsely covered with black hairlike bristles, encompasses the forehead, lores, and crown. White cheeks contrast with a gray neck. Young are nidifugous, i.e., they leave the nest shortly after hatching, and are covered with orange-brown down. By early winter young cranes appear adult-like with some brown juvenile feathers remaining in hind neck and primary coverts (see Appearance).

The only other crane species native to the Americas is the whooping crane (*Grus americana*). Body proportions are similar, but sandhill cranes are 15-28 cm shorter, are primarily grey in plumage rather than white, and have primaries tipped in black rather than entirely, boldly black. The common crane (*Grus grus*), an old world species accidental in North America (American Ornithologists Union 1983), is similarly gray but with a black forehead, lores, and neck, and a more elongated white cheek.

1.3. Distribution

Sandhill cranes have traditionally been delineated as populations distinguished by breeding areas. For clarity, non-migratory populations are described first, followed by breeding and then wintering areas of migratory populations. Populations and descriptions therein are organized from east to west regardless of subspecies because subspecies can overlap in distribution on breeding areas, stopover sites, wintering areas, or all three. Six subspecies are recognized (see Systematics): Cuban (*G. c. nesiotes*), Florida (*G. c. pratensis*), Mississippi (*G. c. pulla*), Greater (*G. c. tabida*), Lesser (*G. c. canadensis*), and Canadian (*G. c.*

rowani). To minimize confusion in discussing populations and subspecies, latin nomenclature is used for subspecies names throughout.

It is reasonable, although speculative, to hypothesize that breeding ranges of both migratory and non-migratory sandhill cranes were once mostly contiguous (Johnson et al. 2005). Presumably, continent-wide reductions in numbers and distribution of cranes over the last two centuries caused populations to become fragmented into mostly discrete ranges. With numbers increasing, cranes are now expanding into previously used areas and where breeding was previously unrecorded, thus blurring separation among long-standing populations. Recent technological advances in satellite telemetry also indicate that at least a few individuals move between adjacent populations (Krapu et al. 2011; see Priorities for Future Research).

1.3.1. BREEDING RANGES OF NON-MIGRATORY POPULATIONS. The three population thats are non-migratory are separate and contain only a single subspecies each: Cuban Population, Florida Population, and Mississippi Population (Jones et al. 2005a, 2005b).

1.3.1.1. *Cuban Population.* The Cuban Population consists of the subspecies *G. c. nesiotes*, the only crane species that occurs in the Caribbean; no cranes occupy Central or South America. This non-migratory population is isolated on mainland Cuba and nearby islands. Occupied areas appear locally isolated in six provinces, Isle de Juventud, Camagey, Ciego de Avila, Sanci Spiritus, Matanzas, and Pinar del Rio (Aguilera 2002, Aguilera and Chavez-Ramirez 2010).

1.3.1.2. *Florida Population.* The Florida Population consists of the subspecies *G. c. pratensis.* This non-migratory population ranges from peninsular Florida as far s as Everglades National Park, and as far n as se Georgia (Walkinshaw 1973, Stys 1997). Large concentrations of birds of the Florida Population live on the Kissimmee and Desota Prairies in Florida, and the Okefenokee Swamp in Georgia (Bennett 1989a, Nesbitt and Williams 1990).

1.3.1.3. *Mississippi Population.* The Mississippi Population consists of the endangered subspecies *G. c. pulla* (Endangered Species Act 1973). This non-migratory population only occurs in Jackson County, Mississippi between the Pascagoula River and the Harrison-Jackson county line (Aldrich 1972, Valentine and Noble 1970). Birds of the Mississippi Population primarily live on or near the Mississippi Sandhill Crane National Wildlife Refuge.

1.3.2. Breeding Ranges of Migratory Populations. Migratory sandhill cranes are widely distributed throughout North America, extending from the Great Lakes region to western Alaska, and beyond North America to nw Siberia. The species breeding distribution extends from Baffin Island, south from Mackenzie, British Columbia to s British Columbia, and from Michigan to the Dakotas, west to Colorado, Utah, and ne California. Recent colonization has extended the species range from New Jersey north to Maine. The six migratory populations are defined following breeding area affiliations. These populations are the Eastern Flyway Population, Mid-Continent Population, Rocky Mountain Population, Lower Colorado River Valley Population, Central Valley Population, and Pacific Flyway Population (Jones et al. 2005a, 2005b). Despite the proximity of the Mid-Continent, Central Valley, and Rocky Mountain Populations, there is no evidence of interbreeding or movement among them (Drewien et al. 2000, Krapu et al. 2011).

1.3.2.1. *Eastern Flyway Population.* The Eastern Flyway Population consists of the subspecies *G. c. tabida.* This population has been increasing in numbers and distribution at least since the early 1980's (Kruse et al. 2011) with recent re-occurrence or first nesting reported in Main, Vermont, Massachusetts, New Jersey, New York, Pennsylvania, Ohio, Illinois, Iowa, Nebraska, South Dakota, and North Dakota (Greenberg 1980, Poggensee 1992, Castrale and Bergens 2001, Melvin 2002, Ohio Department of Natural Resources 2006, Melvin 2008, Sauer et al. 2012).

Though referred to as the Eastern Flyway Population, the annual migratory movements of these individuals include periods within the Mississippi and Atlantic North American Flyways. There is also likely overlap in the breeding distribution of the Eastern Flyway Population and the Mid-Continent Population (described below) in Quebec, Ontario, and Minnesota (Krapu et al. 2011), making the delineation of these populations unclear (Ad Hoc Eastern Population Sandhill Crane Committee, 2010). This is particularly true since genetic studies have confirmed occasional gene flow between these two populations (Jones et al. 2005a, 2005b). The most eastern portion of the this population was recently observed flying southward on migration close to the coastline (Halley, 2015). The largest proportion of the population nests in the Great Lakes region of the United States and in se Canada, primarily Ontario, Michigan, Indiana, and Wisconsin (Ad Hoc Eastern Population Sandhill Crane Committee 2010). Though nesting records in sc Ontario were few in the 1980's (Tebbel 1981, Tebbel and Ankney 1982), more recent surveys suggest a growing population throughout available habitat (Bird Studies Canada 2006). The Eastern Flyway Population in Wisconsin is largely located in the sc part of the state (Su et al. 2004). Eastern Flyway Population birds also breed in n Illinois, n Iowa, and se Minnesota (Meine and Archibald 1996a). Minnesotas breeding sandhill cranes were clearly delineated in the 1970's (Henderson 1978), but are now loosely split between the Eastern Flyway Population in ec Minnesota and the Mid-Continent Population in nw Minnesota (Tacha and Tacha 1985, Drewien and Lewis 1987). In 1992, when the last Birds of North America species account for sandhill crane was published, 1,200 nesting pairs of cranes were observed in these two areas. Today, the Minnesota Department of Natural Resources (2012) reports up to 5000 birds of the Eastern Flyway Population and a minimum of 7000 birds of the Mid-Continent Population.

1.3.2.2. *Mid-Continent Population.* The Mid-Continent Population consists of all three migratory subspecies (*G. c. tabida*, *G. c. canadensis*, *G. c. rowani*). This population includes birds breeding in northern temperate, subarctic, and arctic regions of North America, and despite the population name, birds breeding in eastern Asia. Thus, breeding occurs in Canada, the United States, and Russia (Johnson and Stewart 1973; Krapu et al. 2011). Within North America, the population breeds from n Minnesota, across c Canada (from Hudson Bay to Canadian Rockies and n to Nunavut and Northwest Territories), to Alaska, and e Siberia (Jones et al. 2005a). This population's annual cycle spans the Mississippi, Central, and Pacific North American Flyways. Within the Mid-Continent Population, the Yukon Delta in Alaska has the highest nesting density of breeding pairs with densities up to 0.54 (1975) and 0.78 nests/km2 (Boise 1976, Conant et al. 1985, Melvin et al. 1990, Krapu et al. 2011).

G. c. canadensis, presumably from the Mid-Continent Population have occasionally been identified outside their normal range. At least one case is known of a juvenile, possibly through premature separation from its group or disoriented dispersal, having been observed in Florida. This individual was identified from afar by its body size, bill size, and the color of its primary feathers, but was never measured in hand (Nesbitt 1992b). Additional sandhill cranes thought to be *G. c. canadensis* from the Mid-Continent Population outside of their normal range have occurred in Rhode Island (Brewster 1890), South Carolina (Wayne 1894), and Mississippi (Nestbitt 1992a).

The Mid-Continent Population is managed in two subpopulations, the Gulf Coast subpopulation and the Western subpopulation; the two subpopulations are roughly divided by migration route and wintering area with cranes wintering along the gulf coast identified as the Gulf Coast subpopulation, and cranes wintering inland and west of the Gulf Coast identified as the Western subpopulation (Tacha and Vohs 1984, Tacha et al. 1994). There is known genetic exchange among these two subpopulations (Krapu et al. 2011), and cranes breeding within the breeding range of the Gulf Coast subpopulation spend 28% of fall and 42% of winter, within the fall and wintering ranges of the Western subpopulation. This indicates limited biological support for the designation of the two subpopulations (Krapu et al. 2011). Based on data from 153 satellite-tagged cranes, the Mid-Continent Population may be more meaningfully defined by a total of four subpopulations according to breeding area affiliation, migratory flyway, and wintering grounds (Krapu et al. 2011). Krapu et al. (2011) suggest the following four subpopulations: East-central Canada-Minnesota, West-central Canada-Alaska, Northern Canada-Nunavut, and Western Alaska-Siberia. Space use by the proposed subpopulations indicates mixing on fall staging areas is low, except for the n Canada-Nunavut and w Canada-Alaska subpopulations, though mixing on wintering grounds is likely.

East-central Canada-Minnesota: This subpopulation is proposed to include sandhill cranes breeding in w Quebec, Hudson Bay Lowlands near James Bay, nw Minnesota, n Ontario, and the Interlake region of c Manitoba. The majority of birds breeding in this area are thought to be *G. c. rowani*, with some *G. c. tabida* (Krapu et al. 2011).

West-central Canada-Alaska: This subpopulation is proposed to include sandhill cranes breeding in c Saskatchewan, c and n Alberta, ne British Columbia, the Great Slave Plains in the Northwest Territories, and ec Alaska. The majority of these birds are thought to be *G. c. rowani*, with less of the other two migratory subspecies.

Northern Canada-Nunavut: This subpopulation is proposed to include cranes breeding in Nunavut along the edge of the Arctic Ocean through the Boothia Peninsula, including islands of the Canadian Archipelago (i.e., Richards Island, Banks Island, and Victoria Island), westward from the nw side of the Hudson Bay to the Yukon Territory. The majority of these birds are believed to be *G. c. canadensis*, with some *G. c. rowani* (Krapu et al. 2011).

Western Alaska-Siberia: This subpopulation is proposed to include cranes nesting from interior to coastal Alaska and westward across the Bering Sea into Russia. Cranes of the w Alaska-Siberia subpopulation breed primarily from the Yukon-Kuskokwim Delta northward to the Seward Peninsula, as well as in ne Russia, including the Anadyr basin, and Kamchatka Peninsula, and from Yakutia to Kolyma and Yana (Vladimirtseva et al. 2009). The western boundary of nesting *G. c. canadensis* lies near the Republican Resource Reserve, Kytalyk, in Allaikh ulus of Yakutia along the Indigirka River (Vladimirtseva et al. 2009). Within these boundaries, sandhill cranes nest in ne Siberia (Krapu et al. 2011), the Chyukotski Peninsula, Wrangel Island, and the coast of the Arctic Ocean west to the Yana River drainage (Labutin and Degryavev 1988). Large numbers of cranes nest along one of Chukotkas largest lakes, Lake Krasnoye, which borders the Ust-Tanyurersky Regional Wildlife Refuge. The numbers and distribution of sandhill cranes nesting in ne Siberia have been increasing over the last several decades, and the range of sandhill cranes now overlaps that of the endangered Siberian crane (*G. leucogeranus*; Watanabe 2006). These birds are thought to be primarily *G. c. canadensis*, with only some *G. c. rowani* (Krapu et al. 2011).

1.3.2.3. *Rocky Mountain Population.* The Rocky Mountain Population consists exclusively of the subspecies *G. c. tabida* (though *G. c. tabida* also occur in other populations) breeding throughout c and w Montana, south through c and e Idaho, w and c Wyoming, n and c Utah, and nw Colorado (Drewien and Bizeau 1974, Drewien et al. 2000). There is also evidence of some birds of the Rocky Mountain Population breeding in sw Alberta (Drewien et al. 2000). This population's annual cycle spans the Central and Pacific North American Flyways, though these individuals are not part of the Pacific Flyway Population.

Grays Lake NWR in se Idaho supported the highest concentration of breeding pairs in the Rocky Mountain Population during the 1970s-1980s (Drewien and Bizeau 1974, Drewien 1973). Local abundance increased by 34% from 1970-1971 (549 cranes; Drewien 1973) to 1998-2000 (735 cranes), then more recently declined to a local population of 588 cranes in 2006 (Austin et al. 2007). Though only 200 km separate the Rocky Mountain Population and Central Valley Population at their closest point, there is no known movement or pairing of *G. c. tabida* between these adjacent populations (Drewien et al. 2000). Similarly, movement between the Rocky Mountain Population and Lower Colorado River Valley Population is unknown though the two groups also occur as close as 200 km of one another (Drewien et al. 2000).

1.3.2.4. *Lower Colorado River Valley Population.* This population is comprised of the subspecies *G. c. tabida* breeding primarily in ne Nevada (Elk County), but also in limited locations in Idaho, Oregon, and Utah (Kruse et al. 2012). This is the smallest of all migratory sandhill crane populations, in both numbers and distribution. The highest breeding density occurs in the Ruby Valley, the Independence Valley, and the Upper North Fork Drainage of ne Nevada (Laca et al. 2008).

1.3.2.5. *Central Valley Population.* The Central Valley Population consists of at least the subspecies *G. c. tabida* breeding in Nevada, California, Oregon, Washington, and British Columbia (Littlefield et al. 1994, Pogson and Lindstedt 1991, Pacific Flyway Study Committee 1997). Some members of the subspecies *G. c. rowani* nesting along coasts of British Columbia and southern Alaska (Campbell et al. 1990) may also be part of the Central Valley Population, though they might be better included in the Pacific Flyway Population (Pogson and Lindstedt 1991, Ivey et al. 2005).

Members of Central Valley Population live their entire life-cycle within the Pacific Flyway, but are thought to only overlap with the Pacific Flyway Population on the wintering grounds. The Central Valley Population is divided into two unconnected subpopulations based on breeding affiliation. The northern subpopulation breeding in British Columbia, including the areas of Chilcotin Plateau, Cariboo Basin, Fraser Lowlands, northern Okanogan Valley, East Kootenay Trench, and near Vancouver is likely a mixture of *G. c. tabida* and *G. c. rowani* (Littlefield and Thompson 1979, Cooper 1996, Ivey et al. 2005). The southern subpopulation breeding in sc Washington, e and c Oregon, ne California, and nw Nevada (Littlefield and Thompson 1979, Littlefield et al. 1994, Ivey and Herziger 2000) is likely *G. c. tabida*. The greatest numbers of the Central Valley Population breed in e and c Oregon on the Malheur National Wildlife Refuge, Silvies River floodplain, and Sycan Marsh. Other major nesting concentrations occur in Klamath and Lake Counties of Oregon (Littlefield et al. 1994). In California, large numbers breed in Modoc and Lassen Counties (Littlefield

1989), with fewer birds in Siskiyou, Plumas, Shasta and Sierra Counties (Littlefield et al. 1994, Ivey and Herziger 2000). Non-breeding cranes congregate in common breeding areas in Oregon (Diamond Valley, Klamath Marsh National Wildlife Refuge, Warner Basin, Sycan Marsh, and the Chewaucan marshes) and California (Big Valley, Surprise Valley, and within Modoc County; Stern et al. 1987).

1.3.2.6. *Pacific Flyway Population.* The Pacific Flyway Population is comprised of at least the subspecies *G. c. canadensis*, and possibly *G. c. rowani* nesting in coastal British Columbia and Alaska. Unlike the populations described above, which occur predominantly in one North American flyway, but overlap into others, the Pacific Flyway Population stays entirely within the Pacific North American Flyway. Nevertheless, there may be some genetic exchange between the Pacific Flyway Population and Mid-Continent Population because their breeding areas potentially overlap in Alaska and Canada (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983). *G. c. canadensis* of the Pacific Flyway Population breed in Alaska, within the upper Cook Inlet, from the Kenai Peninsula to the Alaskan Peninsula, and around Bristol Bay (Pogson 1987, Jones et al. 2005b). Cranes breeding in the Yukon-Kuskokwim Delta may be part of this population, or may be part of the Central Valley Population (Conant et al. 1981). *G. c. rowani* breeding along the coastal region of British Columbia, n of Vancouver Island (Cooper 2006), far into the Alexander Archipelago of se Alaska (Willet 1921, Ivey et al. 2005) and reported on Kupreanof, Kuiu, Sergief islands in se Alaska (Gabrielson and Lincoln 1959), and in the Kootenay Trench region of extreme se British Columbia could belong to either the Pacific Flyway Population or the Central Valley Population.

1.3.3. WINTER RANGES OF MIGRATORY POPULATIONS.

1.3.3.1. *Eastern Flyway Population.* Until the 1980's most of the Eastern Flyway Population of sandhill cranes wintered in peninsular Florida and se Georgia (Walkinshaw 1973, Lewis et al. 1977, Crete and Toepfer 1978). The number of cranes wintering in Florida has recently declined, while numbers wintering in Georgia and other se states have increased, such that there are now a few thousand wintering in Louisiana (J. Linscombe, unpublished data). Recent wintering has shifted north with several hundred to a few thousand sandhill cranes now wintering in Indiana (Castrale and Bergens 2001), e Tennessee (i.e. at Hiwassee Wildlife Refuge, by late 1990s wintering cranes exceeded 10,000 and by 2009 numbered around 14,000; Aborn et al. 2008, Kruse et al. 2012), and Kentucky (e.g., Barren River Lake State Resort Park; Kruse et al. 2012). Some birds even stay along s Ontario on Lake Erie (Ad Hoc Eastern Population Sandhill Crane Committee 2010). These shifts may be in response to changes in agricultural practices or regional climate.

1.3.3.2. *Mid-Continent Population.* The Mid-Continent Population winters in the plains and along the gulf coast of Texas and Louisiana (Tacha et al. 1984, Drewien et al. 1996). Satellite transmitters indicate 82% of tagged cranes of the Mid-Continent Population use wintering grounds in Texas, with the remaining birds wintering in Oklahoma, Kansas, New Mexico, Arizona, and the Mexican states of Chihuahua, Coauila, and Tamaulipas (Krapu et al. 2011). Small numbers of cranes also winter in c Mexico, in the states of Zacatecas and San Luis Potosi (Llanes 2012, Lpez-Saut et al. 2011). Following the subpopulation delineation suggested by Krapu et al. (2011), the ec Canada-Minnesota subpopulation concentrates along the upper Texas Gulf Coast, and Tamaulipas. Individuals from the ec Canada-Minnesota subpopulation have used these same wintering grounds for many decades

(Tacha and Tacha 1985, Drewien and Lewis 1987, Krapu et al. 2011). The wc Canada-Alaska subpopulation winters primarily along the lower Texas Gulf Coast, with minimal overlap (Krapu et al. 2011). The n Canada-Nunavut subpopulation winters in w Texas. The w Alaska-Siberia subpopulation has the largest spread of wintering area locations, including w Texas, c and s New Mexico, se Arizona, throughout Chihuahua, and n Coauila. When winter weather is not severe, birds of the w Alaska-Siberia winter at more northern latitudes, such as those found on the Queen Charlotte Islands, Vancouver Island and the lower Fraser River valley (Campbell et al. 1990); this suggests overlap with the Pacific Flyway Population. The greatest overlap among all subpopulations occurs where wintering w Alaska-Siberia and n Canada-Nunavut subpopulations co-occur in nw Texas.

Within New Mexico, *G. c. canadensis* winter primarily along the lower Pecos River Valley, with the majority at Bitter Lake National Wildlife Refuge (Walkinshaw 1949, Boeker et al. 1961, Montgomery 1997). Another major wintering area is Grulla National Wildlife Refuge in Roosevelt County (Boeker et al. 1961). Some cranes of the Mid-Continent Population also winter in the middle Rio Grande Valley. The majority of cranes wintering in Mexico do so in the n highlands of Chihuahua and Coauila (Boeker and Baer 1962, Drewien et al. 1996). The nesting range of cranes wintering in Louisiana is unknown, but likely consists of birds from the Eastern Flyway and Mid-Continent Populations (King 2008).

1.3.3.3. *Rocky Mountain Population.* The Rocky Mountain Population winters primarily in the middle Rio Grande Valley of wc New Mexico, concentrating from the Albuquerque-Los Lunas region in Bernalillo and Valencia Counties s to Bosque del Apache National Wildlife Refuge in Socorro County (Bailey 1928, Drewien and Bizeau 1974, Drewien et al. 2000). Because over 50% of the Rocky Mountain Population winters annually at Bosque del Apache, it is considered the Rocky Mountain Populations most important wintering location (Drewien and Bizeau 1974). A smaller portion of the Rocky Mountain Population winters in sw New Mexico, within the Hatch and Uvas Valleys of Sierra and Dona Ana counties, Pecos Valley, Las Vegas National Wildlife Refuge, the Deming-Columbus area in Luna County, and the upper Gila River, in Grant County (Drewien and Bizeau 1974, Lewis et al. 1977, Drewien et al. 2000). In recent winters a small but increasing number (>1,000) have wintered in western Colorado in the Colorado and Gunnison River Valleys (Drewien and Bizeau 1974, Drewien et al. 1987, 1999). Another small group of cranes winters in the Sulphur Springs Valley in Arizona. An estimated 10% of the Rocky Mountain Population winters in the Mexican states of Durango and Chihuahua; most of these birds winter in northern Chihuahua (Drewien et al. 1996). Laguna de Babicora of Chihuahua is considered the most important wintering area in Mexico. Cranes of the Rocky Mountain Population and Mid-Continent Population overlap on wintering grounds, but there is no known pairing of birds across populations (Krapu et al. 2011).

1.3.3.4. *Lower Colorado River Valley Population.* This population winters along the lower Colorado River in w Arizona, the Gila River in sw Arizona, and in Californias Imperial Valley (Lewis et al. 1977, Drewien et al. 1987). Ninety-percent of this population is believed to winter in and around Cibola National Wildlife Refuge in sw Arizona, Sonny Bono Salton Sea National Wildlife Refuge in s California, and along the Gila River in sw Arizona (Kruse et al. 2012, Drewien et al. 1976, Rawlings 1992).

1.3.3.5. *Central Valley Population.* The Central Valley Population shares wintering areas with the Pacific Flyway Population in the Central and Imperial Valleys of California (Lewis et al. 1977, Littlefield and Thompson 1979). Much of the population is thought to use the

Sacramento Valley s to the San Joaquin-Sacramento Rivers Delta (Pogson and Lindstedt 1991), concentrating near Chico, s to Delano (Littlefield and Thompson 1979). Some 70% of *G. c. tabida* of the Central Valley Population winter in the Sacramento Valley (n Central Valley) from Gridley n to near Chico, with another wintering concentration on the San Joaquin-Sacramento Rivers Delta ssw of Sacramento. During unfavorable conditions some individuals retreat s to the Delta-Grizzly Island area of California (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983). Specific wintering areas considered important for *G. c. tabida* of the Central Valley Population are Stone Lakes National Wildlife Refuge, and Staten Island and Brack Tract of California (Ivey et al. 2003). The southern extreme of the winter range for *G. c. tabida* is Pixley National Wildlife Refuge, nw of Delano, California. Some individuals may winter on Sauvie Island and in neighboring sw Washington with members of the Pacific Flyway Population. A few individuals have wintered as far north as coastal British Columbia (Littlefield et al. 1994); likely of the subspecies *G. c. rowani*.

1.3.3.6. *Pacific Flyway Population.* All members of this population winter in the Central Valley of California. Merced is thought to be the most important wintering area in the Central Valley, supporting large concentrations of cranes (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983). Large concentrations also occur in San Joaquin County, extending s into Tulare County (formerly Carrizo Plains, San Luis Obispo County). *G. c. canadensis* winter primarily in the San Joaquin Valley (s Central Valley) and on the San Joaquin River Delta. About 12% of *G. c. canadensis* of the Pacific Flyway Population winter in the n Sacramento Valley, primarily in two areas, a coastal area from se of Red Bluff to sw of Chico along the Sacramento River, and an inland area from nw of Lodi s to the Carrizo Plaines se of McKittrick, and Pixley National Wildlife Refuge nw of Delano (Littlefield and Thompson 1982, Pogson and Lindstedt 1991). There is no known mixing in breeding areas of these two co-wintering populations (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983). Wintering *G. c. rowani* belonging to either the Pacific Flyway Population or Central Valley Population occur s into Butte County (sw of Chico), n into Tehama County, and if food becomes limited, may move as far s as the San Joaquin River Delta (CDL).

1.3.4. HISTORICAL CHANGES IN DISTRIBUTION. Following European expansion through North America, loss of habitat due to draining wetlands for agriculture (Samson and Knopf 1994) and uncontrolled hunting led to sharp declines in sandhill crane populations throughout all major breeding populations in the contiguous United States (Walkinshaw 1949; Drewien et al. 1975, Johnson 1976, Drewien and Lewis 1987; See Conservation and Management). By the 1930's, several local populations had been extirpated or reduced to very low numbers of breeding adults (Drewien and Lewis 1987, Henika 1936). Sandhill cranes in what is now the Mid-Continent Population were extirpated from the majority of their breeding range throughout the prairie pothole region (Drewien and Bizeau 1974, Walkinshaw 1949, Johnson 1976). Damming and inundation of bottomlands exacerbated impacts by eliminating important staging areas used during fall migration (Johnson 1963, Buller and Boeker 1965).

Though populations are now increasing, the sandhill cranes breeding range in North America was formerly more extensive. The Eastern Flyway Population, which has had the most successful recovery, is thought to have reoccupied a major part but not all of its historic range in the Midwest U.S. (Meine and Archibald 1996a) despite predicted losses of > 90%

of habitat in those areas (Tiner 1984). The Mississippi Population's historical distribution is unknown, but is thought to have been part of a contiguous population across the Gulf Coastal Plains of Louisiana, Mississippi, and Alabama (Walkinshaw 1949, Valentine and Noble 1970, Meine and Archibald 1996a). The historic Rocky Mountain Population extended throughout the c and n Rocky Mountains and the Great Basin, similar to today, except that the population once occupied now vacant areas in w Colorado and nw Arizona (Drewien and Bizeau 1974, The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007). The Mid-Continent Population once occupied areas throughout the prairie pothole region (across North and South Dakota e of the Missouri River, s Saskatchewan, and sw Manitoba) that are now mostly unoccupied. The lack of recolonization of these areas may have to do with high breeding site fidelity (see Breeding), and a disproportionately large, ongoing hunting harvest of the w Canada-Alaska and e Canada-Minnesota subpopulations (Krapu et al. 2011).

Historical wintering habitat also once included now vacant areas s to Arizona (Mearnes 1890), Baja California in Mexico, c Mexico, the Yucatan Peninsula and Lake Texaco near Mexico City (Cooke 1914, del Campo 1944, Walkinshaw 1949, Leopold 1965, Littlefield and Ryder 1968). Early accounts of sandhill cranes wintering in Mexico mentioned concentrations in the Northern Highlands (San Luis Potosi) s to Pueblo (El Carmen lagoon; Cooke 1914, Leopold 1965). Most were found in Chihuahua and northern Durango (Goldman and Goldman 1935, Leopold 1959, Goldman 1942). More recent counts indicate 97.4% of sandhill cranes wintering in Mexico occur in the Northern Highlands, with few s of Zacatecas (Drewien et al. 1996). Loss of wintering areas in e, c, and s, Mexico are thought to have been driven by changes in agricultural practices and habitat loss (Llanes 2012).

1.4. SYSTEMATICS

1.4.1. PHYLOGENY. Sandhill cranes were first described in 1750 by George Edwards from a specimen collected along the Hudson Bay (Houston 1994). It was originally named *Grus fusca canadensis* but later changed by Carolus von Linnaeus to *Ardea canadensis* in 1758 (Ridgway 1941). The genus was changed back to *Grus* in 1760 (Brisson 1760), and then to *Megalornis* in 1921 (Oberholser 1921). The genus was again returned to *Grus* only a few years later (Peters 1925) and was subsequently accepted by the American Ornithologists Union in 1931.

Fifteen crane species are currently recognized, all in the gruiform family, Gruidae. Within Gruidae, phylogenetic analyses indicate two monophyletic clades, the Balearicinae (crowned cranes) and the Gruinae (anatomically derived cranes; Krajewski and Fetzner 1994, Krajewski et al. 2010). The primary morphological separation is based on the furculae fusing to the sternum, and the trachea coiling posterior to the neck in Gruinae species. These features are absent in Balearicinae species. The Balearicinae clade includes a single genus, Balearica composed of two species (*B. pavonina*, *B. regulorum*). The Gruinae clade includes Anthropoides (*A. virgo*, *A. paradisea*), Bugeranus (*B. carunculatus*), Leucogeranus (*L. leucogeranus*), and *Grus* species (*G. americana* [whooping crane], *G. antigone*, *G. canadensis* [sandhill crane], *G. grus*, *G. japonensis*, *G. monachus*, *G. nigricollis*, *G. rubicunda*, and *G. vipio*; Krajewski et al. 2010) Based on DNA-DNA hybridization, *G. canadensis* appears to be from an old lineage and not closely related to the other species of the *Grus* genus (Krajewsku 1989, Krajewski et al. 2010).

1.4.2. FOSSIL HISTORY. The crane lineage is among the oldest living avian genera. The earliest possible fossil crane in the genus *Grus* is *G. conferta* (Miller and Sibley 1942), though Olsen (1985) questioned whether it truly is a *Grus* species. This specimen from the late Clarendonian NALMA (North American Land Mammal Ages; 9-10 mybp [million years before present]), was unearthed in Contra Costa County, California, and is the size of a modern-day *G. canadensis.* Also from late Clarendonian are two unspecified *Grus* specimens from the Love Bone Bed in Alachua County, Florida (Becker 1987). One specimen is the size of *G. canadensis*, and the other is the size of the larger *G. americana.* Another fossil of a crane-like bird that may be a direct relative of the sandhill crane was found in Uinta County, Wyoming and was deposited 10 mybp (Cracraft 1973).

A *Grus nannodes* (Wetmore and Martin 1930:62) exists from the late Hemphillian period of the NALMA (4.5 to 6 mybp), Sherman County, w Kansas. This species is known only from the holotype, a partial carpometacarpus that is smaller than that of *G. c. canadensis.* Also from the late Hemphillian, are two undescribed fossil species found at Lee Creek in Beaufort County, North Carolina. One of these is the size of *G. canadensis*, and another larger specimen is the size of the largest living crane, the sarus crane, *G. antigone*, of se Asia, (Bickart 1990). In 1870, O. C. Marsh named *G. haydeni* from late Tertiary beds along the Niobrara River, Nebraska, based on the distal end of a tibiotarsus. Both Wetmore (1928) and Brodkorb (1967) considered *G. haydeni* a synonym of *G. canadensis*, and a Pleistocene record. Recently, in his study of fossil birds from the Big Sandy Formation, late Hemphillian, Mohave County, Arizona, Bickart (1990) resurrected *G. haydeni* and reported it from the Big Sandy paleo-avifauna. If correct, this would extend this species back in geologic time almost 3 mybp. Understanding of *G. haydeni*, other fossil crane species, and their connection to sandhill cranes would benefit greatly from a comprehensive review and a rigorous phylogenetic analysis.

The earliest unequivocal fossil record for *G. canadensis* is from the late Blancan NALMA (2.5 mybp) Macasphalt Shell Pit in Sarasota County, Florida (Emslie 1992). More recent fossil deposits in the size range of the living subspecies *G. c. canadensis* occur from the Pleistocene (1.8 mybp) where prehistoric records for *G. canadensis* are numerous, with a broad geographic distribution from Alaska to Mexico, and from San Miguel Island, California to Florida (Brodkorb 1967, Parmalee 1977, Campbell 1980, Guthrie 1980, Lundelius et al. 1983, Emslie 1985, Emslie and Heaton 1987, Parmalee 1992).

1.4.3. Recognized Subspecies. Six subspecies are recognized, including three non-migratory: Cuban (*G. c. nesiotes*), Florida (*G. c. pratensis*), and Mississippi (*G. c. pulla*), and three migratory: Greater (*G. c.tabida*), Lesser (*G. c. canadensis*), and Canadian (*G. c. rowani*). For side-by-side drawings comparing subspecies, see Lower Columbia Fish Recovery Board (2004) and Pogson and Lindstedt (1991). These subspecies designations have developed from a series of revisions. The American Ornithologists Union (1886) originally recognized two subspecies, *G. c. canadensis* and *G. c. mexicana*, though the later was considered a species until 1918 (Oberholser 1918) and then later abandoned, in favor of *G. c. tabida* (Peters 1925). Sandhill cranes living in Cuba were originally identified as a species in the mid-19th century (Poey 1854) then later re-classified as the subspecies *G. c. nesiotes* in 1905 (Bangs et al. 1905). *G. c. pratensis* (Florida sandhill crane) was first described in the late 18th century (Meyer 1794), but was not recognized by the American Ornithologists Union until 1931, along with the subspecies *G. c. tabida* (Greater sandhill crane). In 1965 and 1972, the subspecies *G. c. rowani* (Canadian sandhill crane) and *G. c. pulla* (Mississippi sandhill crane) were recognized, respectively (Walkinshaw 1965, Aldrich 1972). Based on genetic and molecular analysis, there is some question as to the validity of the subspecies *G. c. rowani* (Rhymer et al. 2001, Glenn et al. 2002, Petersen et al. 2001, Petersen et al. 2003), *G. c. pulla* (Rhymer et al. 2001; Jones 2003, Henkel 2009) or *G. c. pratensis* (Rhymer et al. 2001).

Differentiating subspecies that overlap in distribution is possible through genetic (Jones et al. 2005a, 2005b, 2005c) and morphometric analyses when birds are captured. Multivariate statistical analysis of cranes of the Mid-Continent Population (see Distribution) indicated culmen, tarsus, and wing chord measurements could be used to identify subspecies with an error rate of $< 4\%$ when the sex of the individual was known (Johnson et al. 2005). Without knowing the sex, classification errors tripled and subspecific designations became unreliable.

Though culmen, tarsus, sex, and wing chord are best used simultaneously to discern subspecies, in general *G. c. tabida* and *G. c. rowani* have larger and more similar culmen and tarsus lengths than *G. c. canadensis*. *G. c. canadensis* and *G. c. rowani* have more similar and shorter wing lengths than *G. c. tabida* (Johnson et al. 2005). There also are relatively large differences between *G. c. canadensis* and *G. c. rowani* in culmen and tarsus length, while differences between *G. c. tabida* and *G. c. canadensis* are largest in wing chord.

Without capturing birds, differentiating subspecies that overlap in distribution can be difficult (Stephen et al. 1966), but is possible in certain areas. Because *G. c. tabida* and *G. c. pratensis* only overlap in wintering areas, any sandhill crane observed in Florida and Georgia between April and September can likely be assumed to be *G. c. pratensis*; otherwise, these subspecies cannot be distinguished. *G. c. tabida* and *G. c. canadensis* can be distinguished by gross morphological characteristics because *G. c. tabida* have longer and more massive bills in relation to head length, sloping foreheads compared to more round foreheads, lower-pitched calls, lighter gray plumage in late fall and winter, and are 25-33% taller and more massive (Drewien et al. 1995, Crossley 2011). Measurements from the posterior edge of the ball of the foot to, but not including, the nail of the anterior end of the mid-toe can also be used to distinguish *G. c. tabida* from *G. c. canadensis* and from most *G. c. rowani*. Specifically, in the Rocky Mountain Population, *G. c. tabida* have mid-toe ranges from 94-123 mm, *G. c. canadensis* have toes 95 mm long (range not reported), and *G. c. rowani* range from 89-103 (Drewien and Bizeau 1974, Guthery 1975a, Buller 1967, respectively). Alternatively, a novel method that characterizes vocal formant spacing has been shown to be effective in determining the subspecies composition of non-breeding sandhill crane populations (see Sounds; Jones and Witt 2012). Additional non-invasive and field ready methods to identify subspecies would add a significant improvement to future work to make inference to appropriate groups, include populations.

1.4.4. GENETIC AND MOLECULAR VARIATION OF SUBSPECIES. Within the Gruinae clade, *G. canadensis* appears most closely allied to the Australasian, Antigone species group (*G. antigone*, *G. rubicunda*, and *G. vipio*; Krajewski et al. 2010), not *G. grus* as previously assumed (Krajewski 1989, Krajewski and Fetzner 1994). Mitochondrial DNA analyses indicate little genetic foundation for most of the 6 subspecies. Rhymer et al. (2001) found molecular variance among all subspecies except *G. c. tabida* and *G. c. rowani*, which were indistinguishable and recommended *G. c. rowani* be abandoned. The greatest difference was detected between *G. c. canadensis* and all other posited subspecies (Rhymer et al. 2001). Genetic exchanges among subpopulations were also highly asynchronous, with no exchange between *G. c. canadensis* and other subspecies, moderate gene flow from *G. c. pratensis* to *G. c. tabida*, and greatest gene flow from *G. c. tabida* to *G. c. rowani* (Rhymer et al. 2001).

There is also no evidence of differential genetic variation in any subspecies, including those of small populations or of populations listed as endangered. However, overall nucleotide diversity is considered low for all subspecies, possibly due to the recent population reduction during European settlement across North America. Within the small bottlenecked population of *G. c. pulla*, microsatellite DNA analyses indicate low allelic richness and thus high similarity among captive and wild individuals (Henkel et al. 2012). The differentiation observed between *G. c. pulla* and all other subspecies is likely due to isolation and inbreeding in the last century and not differentiation (Jones 2003, Henkel et al. 2012). Rhymer et al. (2001) conclude the designation of Evolutionary Significant Units (sensu Moritz 1994) would only support two lineages, one of *G. c. candensis* and one of all other subspecies combined.

Differences described among the posited subspecies show relatively low genetic and molecular variability, suggesting size differences are clinal variation within a geographically widespread population (Rhymer et al. 2001, Jones et al. 2005a). Morphological differences are distinct, although there is a general gradient among migratory populations from smaller cranes in the north to larger cranes in the south (Johnson et al. 2005).

The findings of Rhymer et al. (2001) are consistent with later studies that were also unable to find genetic distinction between *G. c. rowani*, *G. c. tabida*, and *G. c. canadensis* (Glenn et al. 2002, Petersen et al. 2001, Petersen et al. 2003). Among non-migratory populations (subspecies), microsatellite DNA genotyping indicates gene flow occurs between the migratory Eastern Flyway Population and the non-migratory Florida Population. Genetically, the Cuban non-migratory population appears to be more like the Eastern Flyway Population than either of the other two non-migratory populations (Jones et al. 2005b).

1.4.5. Related Species. The sandhill crane belongs to the family Gruidae, in which 15 species are extant. Two subfamilies are currently recognized, Gruinae (typical cranes; 13 species) and Balearica (crowned cranes; 2 species; Krajewski et al. 2010). The only other North American crane is the whooping crane (*Grus americana*), the tallest bird of North America (1.5 meters, see Characteristics). Similarly to the sandhill crane, unregulated hunting and loss of habitat caused massive declines in whooping cranes populations, such that by 1941 there were only 16 migratory birds in the wild (U.S. Fish and Wildlife Service 1986, Lewis 1995). Other crane populations have also been affected by anthropogenic changes to the landscape (Sundar and Choudhury 2005, Miller et al. 2010, Shaw et al. 2010, Folk et al. 2013; see Priorities for Future Research).

1.5. Migration

1.5.1. Nature of Migration in the Subspecies. Populations in Cuba (*G. c. nesiotes*), Florida (*G. c. pratensis*), and Mississippi (*G. c. pulla*) are not migratory (Lewis et al. 1977). Migration occurs in all other populations (Eastern Flyway, Mid-Continent, Rocky Mountain, Lower Colorado River Valley, and Central Valley), subpopulations (see Distribution), and subspecies comprising those populations and subpopulations (*G. c. tabida*, *G. c. canadensis*, G. c rowani) are migratory. Cranes have major migration pathways within which large numbers of cranes travel annually. However, off-route migrating individuals could be observed almost anywhere throughout the continental United States.

1.5.2. Routes and Timing of Migration. Migration routes are described below for each population. Where breeding populations overlap at migratory stopover sites and where breeding area affiliations are poorly known, the origin of some individuals can be difficult to ascertain. For all populations, timing of fall migration, and thus arrival on the wintering grounds, is highly variable, depending on annual differences in winter severity. Non-breeding and unpaired cranes begin fall migration before families (pairs with young, Carlisle and Tacha 1983, Tacha et al. 1985a), but families with young arrive on wintering areas before unpaired cranes (Tacha and Vohs 1984), suggesting families migrate faster in fall than unpaired cranes. During mild winters, migration is later and migration distances can be shorter, with migration for the Mid-Continent Population truncated in the northern Great Plains of the United States for some individuals.

Timing of spring migration is more regular, enabling predictable viewing for researchers, managers and the public. For example, cranes of the Mid-Continent Population arrive with such regularity that Audubon Nebraska is able to host an annual spring Crane Festival in Kearny, Nebraska. During spring migration, pairs often arrive first on the breeding area, accompanied by offspring produced the previous year; unpaired birds will arrive a few weeks later (Drewien 1973, Littlefield 2001a, Campbell et al. 1990).

1.5.2.1. *Eastern Flyway Population.* The Eastern Flyway Population has recently expanded eastward from New Jersey to Maine. No data on migration are available from those areas (see Priorities for Future Research), so all information comes from sources west of that expansion. *G. c. tabida* breeding in Ohio, Michigan, Wisconsin, Minnesota, and s Ontario migrate through Georgia, Kentucky, Tennessee, Ohio, Indiana, and Illinois to winter in s Georgia and c Florida (Walkinshaw 1949, 1973, Williams and Phillips 1972, Lewis et al. 1977, Jones et al. 2005). The two major fall and spring stopover areas used by the Eastern Flyway Population are the Jasper-Pulaski State Fish and Wildlife Area in nw Indiana and the Hiawasse State Wildlife Refuge in se Tennessee (Crete and Toepfer 1978, Lovvorn 1980).

Fall migration can occur as early as Sep and as late as Jan, depending on winter severity (Ohio Division of Wildlife 2013). *G. c. tabida* often depart nesting areas from late Sep to Dec with peak departures in early Oct (Lewis et al. 1977, Toepfer and Crete 1979, Crete and Grewe 1982; Downs 2004; Ohio Division of Wildlife 2013). Peak numbers at Jasper-Pulaski State Fish and Wildlife Area occur in late Oct (Walkinshaw 1949, Toepfer and Crete 1979). The average fall stay is 9 d (range 6-12 d; Toepfer and Crete 1979). Fall migrants first arrive on Florida wintering areas in late Oct with most arrivals by mid-Nov to mid-Dec (Toepfer and Crete 1979). Migrant cranes depart Florida late Feb to early Apr, with most departures in the first 2 wk of Mar (Nesbitt 1975a). Spring migrants arrive at the Jasper-Pulaski State Fish and Wildlife Area in early Mar to mid-Apr (peak numbers late March; Walkinshaw 1949) and remain there an average of 12 d (range 1-17 d; Crete and Toepfer 1978). Members of the Eastern Flyway Population arrive on nesting areas primarily in early to mid-Apr (Walkinshaw 1949).

1.5.2.2. *Mid-Continent Population. G. c. tabida* breeding in nw Minnesota and s Manitoba migrate through w Minnesota, e South Dakota, e Nebraska, Kansas, and Oklahoma south to the Gulf Coast region of Texas (DiMetteo 1992, Guthery and Lewis 1979, Drewien and Lewis 1987, Krapu et al. 2011). Fall staging prior to migration occurs in c and w Saskatchewan (69%), North Dakota (16%), southwestern Manitoba (10%), and nw Minnesota (3%; Krapu et al. 2011).They arrive on the breeding grounds in nw Minnesota in late Mar and leave in Oct (Dimatteo 1992).

G. c. canadensis of the Mid-Continent Population migrate from breeding areas in Canada, Alaska, and Siberia to wintering areas in Texas, New Mexico, and c and n Mexico (Walkinshaw 1949, 1973, Lewis et al. 1977, Drewien et al. 1996). These cranes concentrate briefly at many scattered stopover areas during spring and fall migration (Buller 1967, Johnson and Stewart 1973, Lewis 1974), then concentrate up to 80% to 90% during a stop for up to 6 wk in spring in the North Platte and Platte River valleys of Nebraska (Walkinshaw 1949, 1973, Lewis et al. 1977, Krapu et al. 2014). Some *G. c. canadensis* of the Mid-Continent Population migrate through Colorado, stopping in the San Luis Valley with cranes of the Rocky Mountain Population; these are believed to be sandhill cranes from w Canada-Alaska and w Alaska-Siberia subpopulations (Benning et al. 1997, Krapu and Brandt 2008, Krapu et al. 2011).

The Western subpopulation of *G. c. canadensis* of the Mid-Continent Population (see Distribution) breeding in w and c Canada, w Alaska, and ne Siberia migrate through c Alberta, s Saskatchewan, portions of North and South Dakota, Nebraska, and Oklahoma, and e portions of Montana, Wyoming, and Colorado to wintering areas in w Texas, New Mexico, se Arizona, and c and n Mexico (Tacha et al. 1984). These cranes tend to stop in Saskatchewan, Alberta, and w North Dakota during fall migration, and in more western portions of the Platte River Valley and the North Platte River Valley. Large concentrations occur from North Platte, North Dakota to Grand Island North Dakota during spring migration (Boise 1979, Kessel 1984, Tacha et al. 1984).

G. c. canadensis of the Mid-Continent Population (see Distribution) breeding in e and n Manitoba, and n central Canada migrate primarily through Manitoba, e North and South Dakota, c Nebraska, Kansas, and Oklahoma to wintering areas along the Gulf Coast of Texas, Kansas and ne Mexico (Guthery and Lewis 1979, Melvin and Temple 1980, Tacha et al. 1984, 1986). These birds tend to stop in e North Dakota and s Saskatchewan during fall, and in c and more e parts of the Platte River Valley during spring (Melvin and Temple 1980, Tacha et al. 1984).

Cranes of the Mid-Continent Population nesting in Siberia, n Canada, and Alaska begin to leave breeding grounds starting late Aug (Walkinshaw 1981), with most having departed by early Oct (Walkinshaw 1949, Lewis 1977, Walkinshaw 1982). Fall migration through c Alaska primarily occurs in Sep, peaking in mid-Sep (Kessel 1984). Movement through se Saskatchewan occurs in early Aug to mid-Oct peaking in Sep (Stephen 1967, Tacha et al. 1985a). Migration through North Dakota occurs from Sep through Nov, peaking in mid-Oct (Melvin and Temple 1980, Carlisle and Tacha 1983). Peak migration through Oklahoma occurs in late Oct (Lewis 1974). Usually cranes arrive on Texas wintering areas from Oct to Jan (Melvin and Temple 1980, Tacha and Vohs 1984), with peak numbers in early Feb (Iverson et al. 1985a). Cranes depart Texas wintering areas in late Feb to early Mar (Walkinshaw 1949). Arrival on stopover areas (North Platte and Platte River valleys, Nebraska) occurs in late Feb where numbers peak from mid- to late Mar. Cranes depart Nebraska from early to mid-Apr (Walkinshaw 1949, Melvin and Temple 1980, Iverson et al. 1987). Spring migration through se Saskatchewan occurs in late Apr (Iverson et al. 1987), with arrival at nesting areas in Manitoba soon after (Melvin and Temple 1980), and in Alaska from early to mid-May (Walkinshaw 1949, Mickelson 1987, Tacha et al. 1987a). The earliest cranes arrive on the breeding grounds in Siberia is early May (Krechmer et al 1978).

1.5.2.3. *Rocky Mountain Population. G. c. tabida* nesting in nw and w Colorado, sc and e Idaho, w Montana, Utah, and Wyoming migrate through central and s Colorado and n New Mexico to winter primarily in the middle and lower Rio Grande Valley of New Mexico, se Arizona and s into n and c Mexico (Drewien and Bizeau 1974, Lewis et al. 1977, Drewien et al. 1996). Spring and fall stopovers are concentrated in the San Luis Valley of s central Colorado (Drewien and Bizeau 1974, Drewien et al. 1987, 1999). Other important spring and fall overnight stopover sites include Harts Basin and the Grande Valley of central w Colorado along the Green River, Ouray National Wildlife Refuge in Utah, and Cochiti and Jemez Reservoirs in New Mexico (Stahlecker 1992, Drewien and Bizeau 1974, Stahlecker 1997). Fall arrival in the San Luis Valley begins in late Aug and peaks in Oct when 90% of the population has arrived. Cranes begin to leave in Nov (Drewien and Bizeau 1974, Drewien et al. 1995, 1999) and arrive on the wintering grounds shortly thereafter in Nov and early Dec. Spring migrants arrive back in the San Luis Valley Feb-Mar, stay for about one month, then depart early to mid-Mar or early Apr (Peterson and Drewien 1997) and subsequently arrive on the nesting areas soon after. Notably, the percentage of cranes of the Mid-Continent Population among groups of birds stopping over in the San Luis Valley is not consistent between years, making it difficult to estimate the size of only the Rocky Mountain Population (Benning et al. 1997).

1.5.2.4. *Lower Colorado River Valley Population. G. c. tabida* breeding in ne Nevada and sw Idaho migrate through spring and fall stopover areas near Lund, Nevada (Lewis et al. 1977, Drewien et al. 1987, Rawlings 1992). Precise migration timing is unknown for this population, but is likely to follow other populations with fall migration beginning in Sep and spring migration beginning in Mar.

1.5.2.5. *Central Valley Population. G. c. tabida* of the Central Valley Population migrate from nesting areas in British Columbia, Washington, Oregon and ne California to winter in the Central Valley of California (Littlefield and Ryder 1968, Lewis et al. 1977, Littlefield and Thompson 1979). Cranes migrating through Washington often use Ridgefield National

Wildlife Refuge, Shilapoo-Vancouver Lake Wildlife Resource Area, and Sauvie Island as stopover areas (Littlefield 2001a). These cranes are believed to be the coastal nesting *G. c. rowani* of British Columbia and possibly Alaska, but may be a mix of subspecies (Ivey et al. 2005, Harding 2010). Malheur National Wildlife Refuge of Oregon is also an important fall stopover area for *G. c. tabida* of the Central Valley Population (Littlefield 2001a, Littlefield and Ivey 2002).

Fall migration usually occurs between Sep and mid-Oct (Pogson and Lindstedt 1991, Engler and Anderson 1998). Cranes leave their wintering areas in late Feb and early Mar and generally arrive on the breeding areas during the same months (earliest arrival documented at Malheur NWR is 7 February; Littlefield 1990). Those breeding in coastal British Columbia (*G c. rowani*) arrive on breeding areas in late Feb, whereas inland breeding (*G. c. tabida*) birds arrive in early Mar (Campbell et al. 1990).

1.5.2.6. *Pacific Flyway Population. G. c. canadensis* migrate from nesting areas in sw Alaska through Oregon and Washington to winter in the Central Valley of California (Lewis et al. 1977, Herter 1982, Littlefield and Thompson 1982, Mickelson 1987). Major stopover areas during spring and fall occur in both Oregon (i.e., Harney County) and Washington (Moses Lake and Ephrata, in Grant County, and near Mansfield in Douglas County; Littlefield and Thompson 1982). Cranes wintering near Red Bluff, California use the Sauvie Island in the Columbia River nw of Portland, Oregon (Littlefield 2001a) during both spring and fall migration. The route of cranes travelling through British Columbia is poorly known, however, stopover areas include White Lake, Lac Le Jeune, Bechers Prairie, Kispiox valley, Nig Creek, Liard Hot Springs, and the Okanagan Valley (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983, Cooper

1996). Cranes nesting further n than British Columbia use numerous stopovers including the Upper Cook Inlet, Gustavus flats, Stikine River Delta and e Copper River Delta areas of Alaska (Herter 1982, Mickelson 1987, Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983). Cranes depart nesting areas and arrive on Alaska staging areas late Aug to early Sep; peak numbers on staging areas occur from mid to late Sep (Herter 1982, Mickelson 1987). Thereafter, the Pacific Flyway Population migrates primarily in Sep and Oct, arriving in the Central Valley of California in Oct and Nov. Spring departure starts in late Feb (Littlefield and Thompson 1982) with arrival at Alaska spring staging areas beginning in mid-Apr, and peaking in late Apr-early May (Herter 1982; Mickelson 1987).

In both spring and fall, individuals of the Pacific Flyway Population of *G. c. rowani* migrate along the Pacific coast from se Alaska and coastal British Columbia to wintering areas in the n California Central Valley, with a major stopover area on Sauvie Island in the Columbia River (Littlefield 2001a). These cranes may belong to their own unique population, or be part of the Central Valley Population (Ivey et al. 2005). Cranes migrating along the Pacific coast often stopover in Vancouver, Canada, and the Ridgefield National Wildlife Refuge and Woodland Bottoms areas of Washington (Littlefield 2001a). These cranes are thought to be *G. c. rowani*, but which population they belong to has not been identified.

1.5.3. MIGRATORY BEHAVIOR. Sandhill cranes generally migrate with clear to partly cloudy skies and with a tailwind. To conserve energy, they rarely migrate against headwinds except when approaching wintering areas (e.g. from 21,736 cranes, 12,092 [55.6%] arrived against a headwind in nw Texas; Littlefield, 2010). Migration flights usually begin 1.5 to 5.0 h after sunrise and conclude for the day 2.0 h before to 0.25 h after sunset (110 h of flight), but andhill cranes will continue migration well after dark if they are near their destination (Nesbitt and Himtermister 1984). Sandhill cranes fly an average of about 250 km per day during migration at speeds of 23 to 83 km/h, depending on wind speed and direction (Melvin and Temple 1982). To conserve energy, sandhill cranes, similar to many raptors (Rappole 2013), often gain altitude by circling tightly in rising thermal air currents when conditions permit. When sufficient altitude is achieved, they glide on outstretched wings as they descend to an adjacent thermal, where they are again lifted high to repeat the process. Most flights involve linear (sometimes V) formations and occur at < 1600 m (75% between 150 and 760 m), though gliding flights between thermals, and powered flights made when thermals are unavailable, can occur at altitudes of up to 4,600 m.

1.5.4. Control and Physiology of Migration. Fall migration usually begins with clear skies, strong nw (tail) winds, and cool temperatures. Spring migration departures are greatest with clear skies and se winds (Melvin and Temple 1982), or sw winds in nw Texas, New Mexico (RCD) and the Central Valley of California (CDL). The final stimulus to migrate often comes from preflight posturing, takeoff of nearby birds, and seeing or hearing flocks of cranes passing or circling overhead. False migration attempts during fall and spring are common in the Rocky Mountains when birds depart along migratory paths only to return hours later.

1.6. HABITAT

Sandhill cranes are native to the wetlands and grasslands of North America (Tacha et al. 1994). Cranes generally primarily breed in open freshwater wetlands and shallow marshes, but each population uses a broad range of habitats, including bogs, palustrine wetlands, riparian wetlands, sedge meadows, fens, open grasslands, pine savannahs, and agricultural lands through the annual cycle.

1.6.1. NON-MIGRATORY POPULATIONS.

1.6.1.1. *Cuban Population. G. c. nesiotes* on w Cuba and the Isla de la Juventud (Isle of Youth) are unique, nesting in dry upland habitat and occasionally occupying rocky, mountainous terrain (Walkinshaw 1949, Tacha et al. 1994, Aguilera et al. 2005). Drinking water comes from small streams, springs, and rain-filled pools. Most territories are in areas with sparse shrubs and trees, sometimes park-like and flat, and dotted with small clusters of pine trees (*Pinus cubensis*) or palm trees (*Acoelorrhaphe species*). Grasslands, hammocks, and savannahs are used for feeding, roosting, nesting, and rearing young (Walkinshaw 1949, Tacha et al. 1984, Faanes 1990), and some individuals in the Cuba Population may never visit a marsh (Walkinshaw 1949). In at least some individuals, habitat selection appears to depend on breeding status. During the breeding season, breeding pairs use semi-closed habitats and non-breeders concentrate in open savannas (Aguilera 2002). During the non-breeding seasons, all cranes of the Cuban Population use similar savannah habitat.

1.6.1.2. *Florida Population. G. c. pratensis* primarily use freshwater marshes adjacent to grassy uplands, emergent paustrine wetlands, pasture, and forest-pasture transition areas (Tacha et al. 1994, Nesbitt and Williams 1990). Agricultural areas are heavily used during the winter and early spring (Tacha et al. 1994). Cranes around Okefenokee Swamp use open herbaceous marsh areas throughout the year (Bennett 1989b). Within the nesting season, cranes have higher nesting density with higher herbaceous cover (Bennett 1989a). Prairies, pastures, other open (low growth) uplands, and herbaceous wetlands are favored along with transition areas between wetlands and upland habitats (Nesbitt and Williams 1990). Peanut and corn fields, and other agricultural areas (feed lots, dairy farms, etc.) are favored in winter and early spring. Forested edges surrounding these habitats are also used for shade during midday loafing in summer.

1.6.1.3. *Mississippi Population. G. c. pulla* habitat includes pine savannas dominated by wiregrass, marshes, and pine plantations (Wilson 1987). Cranes nest in wet areas of open savannas, along wetland edges, pine plantations, and forest edges. Roosting occurs in freshwater and slightly brackish marshes, artificial ponds, and savannas (Valentine and Noble 1970, Gee 2005). Cranes at the Mississippi Sandhill Crane National Wildlife Refuge use the same area throughout the year but exhibit some seasonal movement between wetlands in summer and uplands in winter (Valentine 1981). In fall and winter, cranes roost mainly in Pascagoula Marsh and fly to small cornfields or pastures to feed (Valentine 1981). Daily back-and-forth movements from nocturnal roosts to foraging areas are associated with high collision risks with fences and overhead power lines in some populations (see Conservation and Management, and Priorities for Future Research). Some birds fly to crop fields to feed, and some spend the day feeding in swamps and savannas within the breeding range.

1.6.2. MIGRATORY POPULATIONS (BREEDING RANGE).

1.6.2.1. *Eastern Flyway Population. G. c. tabida* nest in isolated, open marshes or bogs, surrounded by shrubs and forests or expansive grasslands (Walkinshaw 1973). They also use wet marshy hay meadows or burned-over aspen stands in grass succession, with small but frequent pools or ponds of shallow water or streams, sandy and peat soils. Recent re-colonizers of Maine are using areas dominated by sphagnum moss (Sphagnum species), American woollyfruit sedge (*Carex lasiocarpa*), and scattered leatherleaf (*Chamaedaphne calyculata*; Melvin 2002). In s Hudson Bay lowland, Ontario, cranes use mixtures of open grasslands, open low shrubs, and low shrub physiognomic groups mixed with fens and fen pools. Non-breeders use more open grass sites. The most important characteristics are diverse compositions of perennial aquatic vegetation supported by seasonally stable water levels. In the Upper Peninsula of Michigan, sandhill cranes nest in remote bogs and loaf and feed in bogs and adjacent upland openings and forest edges (Walkinshaw 1978). Upland openings and adjacent park-like forest stands are used increasingly as summer progresses. In c Wisconsin, sandhill cranes use floating sedge bogs, shallow grass and cattail marshes, and flooded aspen forests (Hamerstrom 1938). Sandhill cranes also breed in forested floodplains along the upper Mississippi River in Minnesota, Wisconsin, and Iowa (Knutson 1997).

1.6.2.2. *Mid-Continent Population.* From behavioral observations around nests at Agassiz National Wildlife Refuge, Minnesota, habitat use by *G. c. tabida* of the Mid-Continent Population is 67% wetland and 33% mixture of grassland, brushland, woodlots, and a small amount of cropland (DiMatteo 1992). More northerly *G. c. canadensis* nest in arctic tundra (Boise 1976, Mallory 1987, Safina 1993). Sandhill cranes nesting in c Alberta use open, wet sedge marshes adjacent to wooded areas (Carlisle 1982). In British Columbia, nesting occurs in mixtures of shrubs and herbaceous cover, including hardhack (*Spiraea douglasii*), sweet gale (*Myrica gale*), willows (*Salix* species), sedges (*Cyperacaeae*), and Labrador tea (*Rhododentron* species; Campbell et al. 1990). In the Northwest Territories, *G. c. canadensis* nest along eskers (long winding ridges of glacial sand and gravel), with 75% lichen cover, dominated by bryocaulon lichen (*Bryocaulon divergens*), and others (*Flavocetraria nivalis*, *F. cucullata*; Mallory 1987). *G. c. canadensis* breeding further north in the Yukon-Kuskokwim Delta, Alaska, typically nest in wet marshes, small ponds, or sedge meadow areas of tundra (Boise 1976). Broods spend most of their time in taller Elymus vegetation along slough banks, heath tundra, short-grass meadows, and in similar habitats in tundra areas of n Canada (Walkinshaw 1973). Sandhill cranes nesting in Siberia use moderately wet tundra island mounds of hummock surrounded by open water (Watanabe 2006). The nesting habitat of *G. c. rowani* in the Mid-Continent Population has not been described specifically, but is likely similar to other Mid-Continent Population subspecies, and to *G. c. rowani* in other populations.

1.6.2.3. *Rocky Mountain Population. G. c. tabida* nest in isolated, well watered river valleys, marshes, and meadows at elevations above 1,500 m (Drewien 1973, Drewien and Bizeau 1974). From behavioral observations and marking individuals, these birds mostly nest along marsh edges in wet meadow-shallow marsh zones. In n Utah and sw Wyoming, sandhill cranes use pastures (55%), small grain fields (19%), riparian areas (8%), alfalfa fields (6%), corn fields (3%), and a mix of other communities (9%; McIvor et al. 1992, McIvor et al. 1994a).

1.6.2.4. *Lower Colorado River Valley Population.* This population of *G. c. tabida* uses flat river valleys and basins. Habitat is often a mixture of wet meadows, marshes, riparian areas, and cultivated farmland. (Great Basin Bird Observatory 2010).

1.6.2.5. *Central Valley Population. G. c. tabida* nest in flooded meadows and marshes in the Great Basin and Cascade, Blue, and Sierra Nevada Mountains of Oregon, Washington, and California (Littlefield and Ryder 1968, Littlefield et al. 1994). Breeding occurs in marsh vegetation (Ivey 2007, Ivey and Dugger, 2008) with emergent vegetation including broadleaf cattail, hardstem bulrush (*Scirpus acutus*), cattails (*Typha* species), and broadfruit bur-reed (*Sparganium eurycarpum*; Littlefield 1995a). In e Oregon, sandhill crane breeding habitat includes wetlands adjacent to big sagebrush (*Artemisia tridentata*), Douglas fir (*Pseudotsuga* *menziesii*) and ponderosa pine (*Pinus ponderosa*; Littlefield 1999a). In ne California, breeding habitat includes wet meadows with grasses, sedges, rushes (*Juncus* species), spikerush (*Eleocharis* species), hardstem bulrush, and broadleaf cattail (Littlefield 1995b). In Washington state, sandhill cranes use wet meadows with sedges, willows, hair grass (*Deschampsia cespitosa*), and timber oatgrass (*Danthonia intermedia*). In coastal British Columbia, nesting habitat is on heavily vegetated bulrush marshes in rangelands, and marshes and meadows with nearby coniferous forests (Cooper 1996) with foraging on sheltered shorelines near estuaries, bogs, marshes, fens, and lakes (Roessingh and Penn 2010). *G. c. rowani* along the coast of British Columbia may belong to the Pacific Flyway Population or their own unique population (Ivey et al. 2005; see Distribution, and Priorities for Future Research).

1.6.2.6. *Pacific Flyway Population.* On Vancouver Island in s British Columbia, nesting occurs in open lightly forested sheet-bogs, and in isolated bogs, swamps, and marshes in remote rugged areas of the Coastal Western Hemlock bio-geoclimate zone (Campbell 1990, Cooper 2006). Though atypical, one nest found on Queen Charlotte Island was near the top of a mountain in the middle of logging slash, and adults with young were found deep in mature Sitka Spruce-Western Hemlock forest (Campbell 1990). Sandhill cranes of the Pacific Flyway Population staging in the e Copper River Delta, Alaska roost primarily in wetlands associated with medium shrub and intertidal mudflat habitats, and feed primarily in wet meadow habitats (Herter 1982).

Individuals of the subspecies *G. c. rowani*, which may belong to the Central Valley Population or to their own unique population (Ivey et al. 2005) nest along the nw Pacific Coast using islands and adjacent inland sites from se Alaska sw along the coast to s British Columbia. Breeding habitat is primarily coastal boreal bogs (Harding 2010).

1.6.3. Migratory Populations (Spring and Fall Migrations). High quality stopover habitat is critical to the successful migration of avian populations, and thus to the long term persistence of migratory species, including sandhill cranes (see Conservation and Management). Spring and fall migration stopover areas are critical sites between breeding and wintering areas where sandhill cranes briefly pause in migration to rest and acquire the necessary energy to continue. Historically, inter-annual fluctuations in productivity of natural prairies likely dispersed cranes widely during migration. In the past half-century, industrial scale agriculture has increased the density and predictability of high energy waste grains, and reduced the number and variability of natural wetlands. Stopover areas now occur primarily near croplands where waste cereal grains are available adjacent to a permanent water body (Tacha et al. 1985a, Iverson et al. 1987), perhaps leading cranes to develop strong fidelity to particular areas and supporting concentrations that would likely exceed the carrying capacity of natural landscapes. Equally as important during migration is the availability of wetlands, which are used for roosting, loafing, and drinking. Critical protein and calcium are replenished by foraging on macro-invertebrates (Krapu and Johnson 1990, Reineke and Krapu 1986). Because cranes can be densely concentrated at stopover areas, geographically restricted dangers have the potential to affect many individuals. In particular, overhead power lines can pose substantial collision risks as birds move in flocks back and forth between roosting and foraging areas (see Conservation and Management). As wind resource areas are developed in migration areas, interactions with wind turbines may also become important (see Priorities for Future Research, Figure 1.10).

1.6.3.1. *Eastern Flyway Population.* In Michigan, *G. c. tabida* concentrate in autumn on large marshes with little human intrusion (Walkinshaw 1973). Cranes roost in shallow water at night and use agricultural areas diurnally. They feed in alfalfa, pasture, or hay fields until wheat fields are harvested. Cranes later feed in newly planted fall wheat, until waste corn becomes available. In Indiana, roost sites are isolated, characterized by water 20 cm deep over a firm bottom (Lovvorn and Kirkpatrick 1981), and appear to be selected based primarily on cranes ability to sight human encroachment from the roost site, rather than proximity to human habitation. Fall migrants forage on winter wheat, waste corn and fallow-pasture but avoid soybeans (Lovvorn and Kirkpatrick 1982a). Spring migrants prefer unplowed corn stubble and fallow pasture.

1.6.3.2. *Mid-Continent Population.* Fall-staging cranes in se Saskatchewan roost in shallow, open wetlands and feed in small grain fields (Stephen 1967). In e North Dakota, cranes roost in shallow lakes and marshes, feed in harvested grain fields, and loaf in hayfields and pastures (Melvin and Temple 1983). In w North Dakota cranes roost in sites with large expanses of shallow water, with a soft substrate, away from bare shoreline, and forage in agricultural fields (Soine 1982, Krapu et al. 1984).

Optimum habitat complexes for spring migrants (*G. c. tabida*, *G. c. rowani*, and *G. c. canadensis*) staging in the North Platte River Valley include a river or shallow wetland roost site, an interspersion of 30% to 70% corn stubble, 5% to 40% pasture, 13% alfalfa, and 1 wetland within 4 km of the roost site, as indicated by a combination of behavioral observations and telemetry (Iverson et al. 1987). Roosting areas along the river are characterized by having water channels 0.1 to 21 cm deep and up to 48 m wide, with no visual obstructions within 25 m (Folk and Tacha 1990). Adjacent corn fields are used during daily foraging, but use of a particular field depends on proximity to roost sites (closer fields are used more), the specific agricultural practices used, and the stage (i.e., recently harvested) of that agriculture field (Sudgen et al 1988, Anteau et al. 2011). Cranes are most likely to use fields that are mulched and least likely to use tilled fields. Cornfields adjacent to large wet grasslands are typically selected (Anteau et al. 2011).

Sandhill crane habitat use of the North Platte River Valley changed between 1980 and 1989, with increased use of corn fields (45.6-57.2%) and pasture (27.1-40.4%), and decreased use of Alfalfa (20.2-0.2%) and wetlands (7.1-2.2%; Folk and Tacha 1991). Roost space apparently does not limit abundance of these cranes during spring staging in Nebraska (Folk and Tacha 1990). Rather, lack of wet-meadow habitats near rivers are most limiting in the North Platte and Platte River Valleys, underscoring the need to preserve and manage complexes of essential habitats identified by Iverson et al. (1987). Distances between roost sites and foraging areas have increased over time, causing them to expend additional energy (Krapu et al. 2014).

In spring, northbound cranes stopping in se Saskatchewan roost in shallow wetlands and selectively use wheat stubble during the day (Iverson et al. 1987). Birds staging in c Alaska also roost in shallow wetlands and selectively use barley fields.

1.6.3.3. *Rocky Mountain Population. G. c. tabida* of the Rocky Mountain Population use the San Luis Valley, Colorado as their primary stopover area during spring and fall migrations. Within the San Luis Valley, most cranes use wetland areas along the Rio Grande River between Monte Vista and Alamosa National Wildlife Refuges (Drewien et al. 1995). Both refuges and surrounding private lands are used for feeding on cereal grains (barley, wheat, oats; Drewien and Bizeau 1974, Laubhan and Gammonley 2001). Primary loafing and roost sites are wet meadows, the Rio Grande River, the Monte Vista National Wildlife Refuge and Higel State Wildlife Area (Laubhan and Gammonley 2001).

1.6.3.4. *Lower Colorado River Valley Population.* This population of *G. c. tabida* uses the area surrounding Lund, Nevada as a major stopover site. Specifics have yet to be described, but their habitat is known to include barley fields and nearby wetlands for roosting.

1.6.3.5. *Central Valley Population.* Migratory *G. c. tabida* using Malheur National Wildlife Refuge forage on grain fields (barley, oat, rye, and wheat) and roost and loaf in shallow ponds, sloughs, lakes, and canals (Littlefield 1986).

1.6.3.6. *Pacific Flyway Population.* Migration habitats are poorly described for this population, but are likely to be similar to that of other populations. Cranes migrating through Harney County, Oregon use native-grass meadows (Pacific Flyway Study Committee 2012).

1.6.4. MIGRATORY POPULATIONS (WINTER RANGE). The wintering range for sandhill cranes is a critical area that is perhaps in significant need for conservation efforts.

1.6.4.1. *Eastern Flyway Population.* Wintering habitat for the Eastern Flyway Population of *G. c. tabida* is crop lands, and to a lesser extent pastures in proximity ($\leq$10 km) to roost sites. The acres of land under agricultural that had supported most of the wintering cranes of the Eastern Flyway Population have declined since Wenner and Nesbitt (1987) described habitats and movements of migratory cranes wintering in Florida. Sandhill cranes are expanding their wintering range into areas of Georgia and other se states (see Distribution). These habitats have yet to be described, but cranes likely use a mix of wetland areas for roosting and agricultural areas and open pastures for foraging.

1.6.4.2. *Mid-Continent Population.* Sandhill cranes of the Gulf Coast subpopulation wintering along the Texas Gulf Coast roost in shallow open water marshes, with the highest density of cranes in estuarine intertidal areas, while feeding occurred among a variety of wetland areas (Anderson et al. 2000). Habitats used by *G. c. tabida* are primarily rice growing areas of the Texas Gulf Coast (DiMatteo 1992, Guthery and Lewis 1979, Drewien and Lewis 1987).

All three subspecies (*G. c. tabida*, *G. c. canadensis*, *G. c. rowani*) of the Western subpopulation use habitat similarly, roosting on $<$ 20 saline pluvial lakes in w Texas, and concentrating in particular at lakes with at least 1 freshwater spring (Iverson et al. 1985a). Over 95% of the variation in use of these lakes can be explained by the number of freshwater springs and percentage of surrounding area in sorghum stubble. Saline lakes are the only available roosting sites in the area, so fresh water from natural springs is needed for drinking water (Iverson et al. 1985a). These cranes selectively use sorghum stubble and salt lakes with freshwater springs nearby, while only minimally using cotton stubble, plowed fields, and brush lands (Iverson et al. 1985b, 1985c). In New Mexico, birds roost in shallow river or lake areas and spend most of the day in irrigated croplands and pastures (Walker and Schemnitz 1987). In se Arizona, cranes roost in shallow playa lakes, loaf in grasslands or wetlands, and feed on grain fields, especially corn (Perkins and Brown 1981).

1.6.4.3. *Rocky Mountain Population.* Wintering *G. c. tabida* in New Mexico frequent areas of livestock ranching, irrigated pastures, and crop land (Lewis et al. 1977). In the Rio Grande Valley, cranes frequent federal and state refuges and management areas, dairy farms with grains, and other private agricultural lands.

1.6.4.4. *Lower Colorado River Valley Population.* Sandhill cranes wintering in Arizona and se California use wetland areas of the Wellton-Mohawk and Imperial-Coachella Valleys, the Mohave and Colorado River Indian Reservations, and the Cibola National Wildlife Refuge (Ohmart et al. 1985). Occupied wetlands include those with shallow water roosting areas with little vegetation, playa lakes, and sandbars along shallow rivers. Wintering areas are often closely associated with harvested grain fields, particularly corn fields. Foraging habitat also includes non-irrigated alfalfa, plowed, and milo fields (Ohmart et al. 1985).

1.6.4.5. *Central Valley Population.* This population of *G. c. tabida* shares a winter range with the Pacific Flyway Population in the Central and Imperial Valleys of California (Lewis et al. 1977, Littlefield and Thompson 1979). Roosting occurs in a variety of wetland habitats, including pooled agricultural areas, while foraging primarily occurs on agricultural fields.

1.6.4.6. *Pacific Flyway Population.* Historically (in the 1920's) cranes of the Pacific Flyway Population wintered near Red Bluff, Tehama County, California and were reported by local residents to feed on blue oak (*Quercus douglasii*) acorns they found on and around the edges of open prairies (Grinnell et al. 1930). From behavioral observations, for 14,755 *G. c. canadensis* in Merced County, California (their major wintering area) in 1969-1970 field use percentages were: alfalfa 51%, corn 19%, milo 17%, grasslands 9%, wheat stubble 5%, and cotton 0.4% (Littlefield 2008). Roost sites were in a variety of wetland habitats including rain-pooled agricultural fields, shallow freshwater lakes and ponds, alkaline lakes, and shallow river channels (Littlefield 2008). Both *G. c. canadensis* and *G. c. rowani* consume waste grains in winter. Corn and wheat predominate, but milo, rice, barley, and oats, are also consumed when available. At Merced National Wildlife Refuge in California, feeding habitats include burned grasslands, pastures, mowed unharvested corn, unaltered and tilled corn stubble, recently planted winter wheat, alfalfa, disked barley, ungerminated trapper peas, clover, and burned rice fields.

1.7. Food Habits

1.7.1. Feeding. Sandhill cranes are omnivorous, gleaning prey from the surface of the ground and capturing subsurface food by probing firm bottoms of lakes, and soft soils and mud with their bills (Walkinshaw 1949, 1973, Mullins and Bizeau 1978, Tacha 1987). They feed primarily on land or in shallow marshes with emergent vegetation, and often forage on waste grain in harvested fields, particularly during fall migration. Grit sites are important when cranes are feeding on waste grain.

Sandhill cranes of the Mid-Continent Population spend 1.4% to 6.4% of their diurnal time searching for food, 0% to 17.1% gleaning surface foods, and 17.9% to 60.4% probing for subsurface foods (Tacha et al. 1987a). The frequency of these foraging activities does not vary among age, sex, or social classes, but juveniles spend 25% more time foraging than adults, and females 2% more time foraging than males. Adult pairs and family units spend 14% more time foraging than lone adults (Tacha 1987), presumably because solitary birds must constantly check for predators where birds in groups can partially rely on the vigilance of nearby birds (Krause and Ruxton 2002).

1.7.2. Diet. Sandhill cranes are opportunistic, omnivorous foragers that consume a variety of plant materials, small vertebrates, and invertebrates (Walkinshaw 1973, Mullins and Bizeau 1978, Ballard and Thompson 2000). Crane diet has likely changed substantially in the last century with the loss of natural prairie systems, substantial wetland drainage, and the development of large-scale agriculture. Cranes exact diet varies considerably by season and location (Walkinshaw 1949, 1973), but cultivated grains are a major food item wherever available (Table 3.3, Figure 1.11). Details of sandhill cranes diet are still poorly documented, except among hunted populations where funding is provided for research programs that will help inform management. Overall, animal prey comprises a low percentage of a cranes overall diet (≈5-10%), but is thought to be important in providing essential amino acids and calcium (Reineke and Krapu 1986). Animal prey includes insects, crayfish, earthworms, eggs and nestling birds, snakes, mice, and lemmings (Drewien 1973, Walkinshaw 1949, 1973, Bennett 1978, Mullins and Bizeau 1978, Reed 1988, Archibald and Lewis 1996).

Non-migratory subspecies eat insects and their larvae, snails, reptiles, amphibians, nestling birds, small mammals, acorns (*Quercus* spp.), berries, and tubers (*Cyperus* species, *Hydrocotyle* species, *Nymphaea* species, and *Sagittaria species*; SAN), and agricultural waste grains.

Among migratory populations, foods vary widely depending on what is available in various seasons and locations (Walkinshaw 1949, 1973). During breeding seasons, cranes consume primarily plant material, but have a diverse diet that is dependent on the breeding area of a given population and the nest-site location within that breeding area.

During breeding seasons in n Michigan, cranes of the Eastern Flyway Population primarily consume berries and insects during summer. Diets of adults and young in se Wisconsin include invertebrates and some small mammals and reptiles during early brood rearing. Non-breeding adults in se Wisconsin eat mostly tubers of aquatic plants in spring and early summer, and cultivated grains in late summer (Walkinshaw 1973).

G. c. tabida of the Rocky Mountain Population consume 73% plants by total volume, and 27% insects and earthworms (Mullins and Bizeau 1978). Mullins and Bizeau (1978) found sandhill cranes eating primarily corn and insects during summer in Idaho. In Alaska, breeding cranes eat assorted berries and small mammals during the breeding season (Walkinshaw 1949). Cranes approaching breeding areas eat mostly tubers (*Cyperacesae* species) and gastropods (Iverson et al. 1982).

Sandhill cranes of the Central Valley Population feed on mostly plant material along beaches with abundant cover of rockweed (*Fucus* sp.) and among salt marsh with sedges (*Carex* sp.), mudflats, and Pacific silverweed (*Potentilla anerina pacifica*; Roessingh and Penn, 2010).

Waste grains from agricultural crops, such as corn, barley, and wheat are the most important source of energy during migration and wintering (Stephen 1967, Lockman et al. 1987, Walker and Schemnitz 1987, Clark and Sugden 1990, Iverson et al. 1987, Tacha et al. 1985a; Table 3.3). Cranes of the Mid-Continent Population staging along the Platte River Valley in Nebraska and consuming agricultural grains increase body mass by 17% and 20% for adult females and males, respectively, during fall migration (Krapu and Johnson 1990) and by 30% and 34%, respectively, during spring migration (Krapu et al. 1985). However, there is likely significant variability in the rate cranes increase body mass due to arrival to the staging area, food availability, local weather, competition with migratory waterfowl, and the number of cranes in the area (Krapu and Johnson 1990).

Agricultural grains comprise most of the diet of cranes wintering in Texas, except for those in the South Texas Plains where cranes predominately eat nut-grass, chufa (*Cyperus* species), and tubers (Guthery 1975b, Ballard and Thompson 2000). Cranes wintering in the Gulf Coast of Texas at the Aransas National Wildlife Refuge consume high quantities of acorns and wolfberry, which are high in important ascorbic acids, iron, calcium, and essential amino acids not available in grain crops (Hunt and Slack 1989). How cranes in other wintering areas obtain these nutrients has not been identified. Diets during migration and wintering are roughly similar among age, sex, and social classes (Reineke and Krapu, 1986, Ballard and Thompson 2000). One comparison found cranes feeding in cornfields consume $> 99\%$ corn while cranes feeding on native grasslands and alfalfa fields consume 79 to 99% invertebrates (Reineke and Krapu 1986). In Texas, cranes winter diet includes 5% animal matter. Wintering *G. c. canadensis* of the Mid-Continent Population in n and c Mexico consume many grains, but especially corn (Llanes 2012). These birds corn consumption is consistent despite changing availability, suggesting preference or specialization; instead of switching diets, cranes moved when corn availability became low (Llanes 2012). While not easily quantified, sandhill cranes wintering in New Mexico also consume below-ground foods, often in flooded areas; in one study chufa (*Cyperus esculentus*) was most consumed (Taylor and Smith 2005).

1.7.3. NUTRITION AND ENERGETICS. Animal matter is important in crane diet, presumably because it provides essential amino acids and calcium rarely available in grain (Reineke and Krapu 1986). Protein content of adult cranes of the Mid-Continent Population varies little throughout the year (Iverson 1981, Krapu et al. 1985). Lipid reserves, an index to body condition, do vary however. These were measured in Mid-Continent Population cranes prior to fall migration from Last Mountain Lake, Saskatchewan, and again throughout their migration. Levels varied dramatically at key times of year, with the lowest levels occurring in mid-Aug, suggesting a period of relatively poor physical condition (Tacha et al. 1985a). By later in the fall, individuals gained an average 9 g lipid/d while eating high-energy grains. Lipid levels did not vary from when cranes departed Saskatchewan, through staging in Oklahoma and wintering in w Texas, to spring arrival at stopover sites in Nebraska (Iverson 1981, Tacha et al. 1985a, 1987a). Individuals deposited an average 12.8 g lipid/d while in Nebraska and maintained these lipid levels through spring migration while crossing Saskatchewan and c Alaska to nesting areas in w Alaska. They then lost 4 g/d during pre-nesting (Iverson 1981, Krapu et al. 1985, Tacha et al. 1987a).

The accumulation of lipids during fall in Saskatchewan and spring in Nebraska was possible because high-energy food resources (grain) were concentrated and accessible (Tacha et al. 1987a). Lipids levels were maintained during later stages of spring migration through regular stops at grain fields along the migratory route. Losses of lipids during pre-nesting were due to increased energy expenditures associated with low food availability, territorial defense, and egg production. Krapu et al. (1985) hypothesized that availability of cultivated grain allows cranes of the Mid-Continent Population to transport maximum lipid levels to nesting areas. Once there, lipids are used for early reproduction, allowing increased productivity compared to pre-agricultural development in the Great Plains and Alaska.

While protein is necessary for normal growth and maintenance, too much of it during development can cause skeletal abnormalities (Nairn and Watson 1972, Hedhammar et al. 1974, Serafin 1982). An experiment involving chick-rearing of *G. c. tabida* and *G. c. pratensis* found *G. c. tabida* grew faster on a high protein diet (32% by volume), but were afflicted by leg disorders (17%) and abnormal wing development (25%). *G. c. pratensis* grew more slowly than *G. c. tabida*, regardless of diet, but developed no abnormalities on a high protein diet. Additional information on protein intake from wild cranes is unknown, but would be especially important in developing future bio-energetic models.

1.7.4. DRINKING. Sandhill cranes drink water with salinities up to 20 ppt (Haley 1987) by submerging the lower mandible to fill the beak, then raising the head to swallow (Tacha

1988). About 0.2% of daily time budgets are spent drinking. This does not vary among age, sex, or social classes. Drinking water appears mostly opportunistic and is not particularly to specific types of water bodies. Although, no specific investigation has been done. However, like many wild animals, cranes may discern between certain types of water bodies, which may provide important and naturally occurring minerals.

1.8. SOUNDS

1.8.1. VOCALIZATIONS.

1.8.1.1. *Mechanics.* The calls of sandhill cranes are described as trumpeting, bugling, rattling, or croaking, but these adjectives do not fully convey the volume or quality of the sound produced by a mature sandhill crane. Several physiological adaptations enable cranes to vocalize as they do. These include tracheal elongation and coiling (see diagrams in Gaunt et al. 1987), tracheal reverberations with the sternum, and enlargement of the syrinx, the focal organ located at the base of the trachea (Gaunt et. al 1987, Klenova et al. 2007, Niemeier 1979). Tracheal elongation and coiling into the sternum is an anatomical feature of all species of the genus Grus, and of some members of the closely related genus Anthropoides. The elongated trachea of cranes allows them to manipulate their formant frequency (frequencies at which the air vibrates or peaks of acoustic energy in a frequency spectrum) such that vocalizations are not typical of an animal of the cranes size, but of that of a larger bird (Fitch, 1999). Tracheal elongation and subsequent manipulation of formant spacing may also provide acoustic indicators of individuals, and of a birds sex, sexual maturity, and age (Fitch and Kelly, 2000, Jones and Witt 2014). This information, if communicated, may help birds distinguish high quality mates. Since formant frequency dispersion is inversely related to body size or trachea length, it can also be used by researchers and managers to identify subspecies (Jones and Witt 2012).

Deliberate shortening of the trachea dramatically reduces the intensity (loudness) of a vocalization (Gaunt et al. 1987). Simultaneous tracheal coiling reduces the intensity even further, allowing cranes to moderate the intensity of their calls. Cranes can also adjust the pitch of their calls by moderating air flow through the syrinx (Goller and Suthers 1996). The syrinx allows cranes to generate low frequencies (Fitch, 1999) which travel further and with less distortion when produced among dense vegetation (such as occurs at a nesting site).

1.8.1.2. *Development.* Beginning a day or so preceding pipping and continuing until about 9 to 10 mo of age, young cranes produce three distinct calls: Pipping Calls, Contact Calls, and Stress Calls (Voss 1976). The Pipping Call is made up of trills and peeps and is the first call to develop. The Contact Call can be described as a yelp, consisting of 3 or more high-pitched, broken notes and a sustained following note. The Stress Call consists of loud rapid slurred notes covering a wide frequency range, and lasting < 5 s (Nesbitt and Bradley 1997). The change to the Unison and Guard Rattle Calls of adults is preceded by a protracted process of tracheal elongation and intrasternal coiling concurrent with the first uses of Purrs. The adult voice is acquired thereafter at about 10 months (Tacha 1988).

1.8.1.3. *Vocal Array.* Very young cranes produce Trills and Peeps. Adult calls are more varied, but fit in 3 categories: soft Purrs, loud Rattle Calls, and other calls, which together may exceed a dozen vocalizations.

1.8.1.4. *Trills and Peeps.* Trills are the first vocalization to develop. The pre-hatching Trill is slow, with a lower fundamental frequency than those given later. Trills continue as contact calls after hatching, sounding like a steady trill lasting 0.2 to 0.4 s, and given 1-2/s.

The Peep is a short, sharp stress call, first heard during pipping. Peeps are loud ascending calls lasting about 0.2 s. Peeps are low frequency and given only during pipping.

1.8.1.5. *Purrs.* Various Purrs are given in many situations (e.g., pre-flight, feeding, aggression). They are low amplitude, low intensity, and used for short distance communication within a flock or family group. In adults, Purrs are 4 to 12 muffled click-like sounds delivered at a rate of 12-20/s (Nesbitt and Bradley 1997). The Flight Intention Purr is a 2-part call with a rising inflection given during a preflight behavior (e.g., wing flapping, leaping; Tacha 1984) and immediately prior to an unforced flight (Voss 1976). It is not given when startled or following others to take off; thus its absence when a crane takes flight may be a cue to others to do the same. The Feeding Purr is the slowest of the Purrs and is almost constantly given when feeding. The Growl Purr is an aggressive signal given as part of the Low Bow display (see Behavior; Voss 1976, Nesbitt and Archibald 1981). This Purr is low frequency and low intensity, carrying only a few meters. Pre-copulation Calls are given in a series of calls, gradually rising in volume, and preceding copulation (Voss 1976). The Nesting Call is a Purr given at or near a nest during building, incubating, and brooding (Voss 1976). The loudest, highest-pitched, most rapidly delivered Purrs are Flight Purrs that occur only while in flight (Nesbitt and Bradley, 1997). For sonograms of Purrs, see Nesbitt and Bradley (1997).

1.8.1.6. *Rattle Calls.* Rattle Calls are 7 to 20 very loud notes delivered at rate of about 15/s (Nesbitt and Bradley 1997). The mean fundamental frequencies for Rattle Calls are approximately 0.56 KHz for males and 0.93 KHz for females (Weekley 1985), and can be heard up to 4 km away. In flight, these calls have rising or falling inflections with a higher fundamental frequency than those given on the ground. Rattle Calls may be either Unison Calls or Guard Calls.

Unison Calls, are a sexually stereotypic duet call generally given en route to and from feeding, loafing, and roosting locations (Nesbitt and Bradley 1997). The male part is lower pitched and more drawn out than the females staccato tuck-a-tuck-a-tuck-a.

Guard Calls are often used in conjunction with Tall Alert Postures wherein the crane gives a slow even rattle when disturbed (Walkinshaw 1949, Archibald 1975), or are used in unison by a pair or family group as an aggressive display when advertising or defending a nesting territory. The Rattle Call has a distinct antiphonal quality when delivered in flight as a pair flies over a defended territory. Older chicks ($>$ 9 wk of age) participate in both Guard Calls and Unison Calls with their parents (SAN). A chicks Guard Call is a high-pitched, broken sound first ascending then descending in pitch, lasting about 0.45 s (Voss 1976). During migration (day or night) Rattle Calls are given by cranes on the ground in response to flying (often nonvisible) cranes also emitting Rattle Calls. This allows arriving individuals to locate cranes on the ground, especially at night. For sonograms of Rattle Calls, see Nesbitt and Bradley (1997).

1.8.1.7. *Other Calls.* Adults also give several other calls, reported here in order of increasing intensity. Snores have been reported from cranes on roosts (L. H. Walkinshaw, pers comm.) and are produced by orally tranquilized cranes (SAN). A shrill, diminuendo tremolo with a descending inflection is given by cranes in distress, as when captured. A short Purrt, 4 notes rising in pitch separated by unequal intervals, triggers an alert state in others in a flock and may be given as birds take flight or land. Yelps consisting of 3 or more high-pitched, broken notes and a sustained following note may serve as location calls (see Voss 1976) or to maintain or reestablish contact between flock or pair members separated by a greater distance than can be bridged by Purr Calls (Nesbitt and Bradley 1997). Moans and goose-like Honks are often interspersed among Rattle Calls and are intermediate between the full-voiced Rattle Call and a Purr. During aggressive behaviors, sandhill cranes produce a series of loud rapid slurred notes covering a wide frequency range, and lasting < 5 s (Nesbitt and Archibald 1981, Nesbitt and Bradley 1997, see Behavior). Also during aggressive behaviors, both among conspecifics or when mobbing a potential predator, the attacking bird delivers a loud Hiss inserted among other vocalizations.

1.8.1.8. *Social Context.* Unison Calls and Guard Calls are used in Duets to advertise territorial occupancy and boundaries and serve to avoid conflict among territorial adults. In other aggressive situations, Rattle Calls are used by dominant territorial pairs or individuals to intimidate intruding birds and drive them away. The Guard Call also is given also when birds (individuals, pairs, or flocks) mob a potential predator (Nesbitt and Bradley 1997; See Behavior).

1.8.1.9. *Phenology.* Territorial advertisement calling via Rattle Calls increases with the onset of nesting season and declines through incubation. Other social calling increases during late summer and fall, as cranes become more gregarious. Calls are produced year-round from breeding seasons, through fall migration, winter, and spring migration, but are context specific. I.e., loud calls on breeding territories likely serve to maintain spacing, while loud calls during migration and wintering likely serve to bring cranes together.

1.8.1.10. *Daily Pattern of Vocalization.* Sandhill cranes are most vocal from about 30 min before sunrise through mid-morning. They are relatively quiet during mid-day, then become vocal again during late afternoon feeding, and when arriving at roosts or pre-roost gatherings. This pattern is observed throughout the year.

1.8.1.11. *Nonvocal Sounds.* None known.

1.9. BEHAVIOR

1.9.1. LOCOMOTION. Sandhill cranes are primarily active during day light (i.e., diurnal). Night-time hours are mostly spent resting with little movement (<5%; Tacha et al. 1987a), except during migration when individuals approaching stopover sites may complete the days journey in darkness (see Migration).

From the Mid-Continent Population unless otherwise noted (see Priorities for Future Research). The relative proportion of cranes most common activities during wintering, migration, and pre-nesting (e.g., feeding, flying, resting, and being social) differ with location and season (breeding area, stopover site, wintering area), and time of day (Tacha et al. 1987a, Fox et al. 1995). About 7% (range 2-9%) of the day and 5% of the night is spent in locomotion other than foraging (flying, walking) with males moving about 50% more than females (Tacha et al. 1987a). *G. c. canadensis* in the North West Territories spend more time in locomotion during pre-nesting, at 15.4% of daytime hours (Fox et al. 1995). Daily flight time differs depending on distances between roosts and foraging areas. For example, cranes in breeding areas prior to nesting in Saskatchewan fly 2.8%, and cranes in Alaska 4.8%. Cranes at a migration stopover site in Nebraska spend 4.2% of their time in flight, and cranes wintering in w Texas spend 9% of the day flying. There are also minor differences in activity budgets among age groups and between sexes; juveniles spend 25% more time foraging than adults, females 2% more time foraging than males, and adult pairs and family units 14% more time foraging than lone adults (see Food Habits). Male cranes nesting in the Northwest Territories spend more time alert (16.3% vs. 9.6%) and forage less than females (26.8% vs. 40.2%; Fox et al. 1995). Bathing and swimming are rare behaviors, collectively accounting for $< 0.1\%$ of diurnal activity.

During most of the year, non-migratory flight does not involve soaring unless cranes are traversing long distances. In the San Luis Valley of Colorado, soaring can occur daily in fall and especially in spring, if daily weather conditions favor migration. Often after morning feeding, groups will soar for 15 min to one hour and then return to regularly occupied foraging and roosting areas for the remainder of the day.

1.9.2. SELF MAINTENANCE. Descriptions of self maintenance mostly come from the Mid-Continent Population, unless otherwise noted. Tacha (1984, 1987a, 1988) described and documented frequency, duration, and percent of time allocated to various behaviors during nesting, migration, and wintering. Cranes spend the majority of the day, regardless of the time of year, foraging or engaged in maintenance activities (preening, stretching, loafing, and sleeping; Tacha et al. 1987a, Fox et al. 1995, for drawings see Tacha 1987). The single most prevalent daytime and nighttime activity is resting, generally occupying 14-38% of the day and 95% of the night. During nesting, resting is reduced (14%), and is split fairly evenly between loafing and sleeping; nocturnal resting is primarily sleeping (Tacha et al. 1987a). Adults spend 50% more time loafing than juveniles, and males spend 50% more of the day loafing than females, while females forage (Tacha et al. 1987a).

Cranes of the Mid-Continent Population spend 3-10% of their time in grooming activities (preening, head rubbing, head scratching, body shaking; for drawings see Tacha 1987), with more time spent grooming in Texas (10%), Nebraska (7%), and Saskatchewan (6%) than in

Alaska (3%; Tacha et al. 1987a). About 95% of time spent grooming is preening. Adults without mates or young spend twice as much time preening as adults in pairs or families (Tacha et al. 1987a). Time spent doing comfort activities (preening and stretching) varies by age, sex, and location (range: 9.9 to 2.8% of daytime activity; Tacha et al. 1987).

1.9.3. AGONISTIC BEHAVIOR. Intra-specific agonistic behaviors begin almost immediately upon hatching. Siblings are aggressive toward each other and conflicts are frequent. Intense sibling aggression begins within 2 d of hatching and then wanes after about 3 mo (Miller 1973, R. C. Erickson pers. comm.) when a dominant sibling emerges (Drewien 1973, Layne 1982b). Sibling aggression may be one reason why even though cranes typically lay 2 eggs, often only 1 bird is raised to fledging (Miller 1973). Sibling aggression is mediated by food (Quale 1976) with more pairs raising 2 young in years of abundant food.

In adults, sandhill crane display behaviors can be interpreted following Happ (2012). Seven agonistic behaviors are known: 3 non-directional threat displays (Low Bow, Ruffle Bow, and aggressive calls, i.e., Guard Call), and 4 target-specific aggressive behaviors (Choke, Upright Forward, Upright Stab, Upright Kick; Voss 1977, Nesbitt and Archibald 1981, Tacha 1988, for drawings see Tacha 1988 or Happ 2012).

1.9.3.1. *Low Bow.* This behavior is observed after a crane lands within a flock. It is performed by lowering the head toward the ground, arching the neck, and causing the crown to expand and become bright red (see drawings in Tacha 1988). The Low Bow is performed equally by both sexes for an average of 4.1 seconds (Tacha 1988); use among different ages may vary by population.

1.9.3.2. *Ruffle Bow.* This behavior is the same as Low Bow with the addition that all feathers are ruffled and shaken, while wings are held against the body. Some authors have also referred to this as a Generalized Body-Wing Shaking (Voss 1977, Nesbitt and Archibald 1981, Tacha 1988).

1.9.3.3. *Aggressive Calls.* I.e., Guard Call (see Sounds).

1.9.3.4. *Choke.* During this behavior, the head and neck are extended forward toward a targeted opponent, while feathers of the neck and body are ruffled and the crown is expanded and bright red. It occurs on average for 3.6 seconds and does not differ among ages or sexes (Tacha 1988).

1.9.3.5. *Upright Forward.* This behavior has also been referred to as the Spread Wing Display (Voss 1977), where a crane stands erect with the wings fully or partially spread open and facing an opponent (see drawings in Tacha 1988). It is often observed in response to a Choke display for an average duration of 7 seconds; this behavior does not vary by age or sex.

1.9.3.6. *Upright Stab.* This behavior is similar to the Upright Forward behavior except that the head and neck are drawn backward, while the bill is thrust forward (see drawings in Tacha 1988). This behavior occurs on average for 7.7 seconds and does not vary by age or sex (Tacha 1988).

1.9.3.7. *Upright Kick.* This behavior is similar to the Upright Forward and the Upright Stab, but also includes kicking of the feet towards the head and body of target bird, predator, or other intruder, while also leaping and flapping the wings (see drawings in Tacha 1988).

Non-directional and target-specific agonistic behaviors protect space around individuals or social units to displace other cranes (Tacha 1988) or intimidate potential predators. Adults spend 1.5 times more time in agonistic behaviors (0.23%) than juveniles (0.15%), and males 4.5 times more than females. Male *G. c. pratensis* direct more aggression toward other males than toward females (67% versus 33%), and females direct more aggression toward other females than males (83.5% versus 16.5%; Nesbitt 2005). Paired and parent adult males use the highest intensity aggressive displays, typically when defending territories or young. Within flocks, dominance is associated with the use of high-intensity aggressive displays, cheek patch color (more white vs. gray), age, and reproductive status. Agonistic encounter rates are highest when flock densities are highest, particularly during spring migration, and lowest after nesting territories are established. Displays typically associated with reproduction (e.g., Bill Up display [described below] and even copulatory mounting) are sometimes given outside of reproductive context, and may serve as a territorial display. Agonistic behaviors have yet to linked with activity of stress hormones, but could be important in understanding the links between aggression and successful rearing of chicks.

1.9.4. SEXUAL BEHAVIOR. Sexual behavior consists of a collection of linked or isolated behaviors between a pair.

1.9.4.1. *Courtship.* Eight courtship displays are recognized. Three of these are limited to paired adults and likely function in pair bond maintenance, synchrony of reproductive development, and egg fertilization (Bill Up, Copulation, non-aggressive calls). Five displays are exhibited by all social classes and serve as a courtship display; three of these are to attract attention (Upright Wing Stretch, Horizontal Head Pump, Vertical Toss), while two are part of a sequence of courtship displays that are collectively referred to as Dancing (Bow, Vertical Leap; Tacha 1988). For drawings, see Tacha 1988.

1.9.4.2. *Bill Up.* In the Bill Up display, the neck is arched forward and the bill is pointed approximately 45 degrees from horizontal (see drawings of Tacha 1988). It is performed by both sexes prior to and after multiple copulations.

1.9.4.3. *Copulation.* Following a Bill Up behavior, the male will circle the female and approach from the rear. The female lowers the wings, allowing the male to mount while being supported by her wings. The male grasps the nape of the female and crouches to make cloacal contact. This behavior averages 4 seconds (Tacha 1988).

1.9.4.4. *Upright Wing Stretch.* Males combine an erect posture with raising their wings to about 60 degrees above the body, presumably to attract a female audience (see drawings in Tacha 1988).

1.9.4.5. *Horizontal Head Pump.* This behavior begins with the neck vertically erect then the neck curves backward, bringing the top of the head back toward the body, the wings open, and the bill points downward. Lastly, the wings are folded and the neck stretches forward until moving into a standing upright position (see drawings in Tacha 1988). The duration of this behavior varies by age and sex, with adult females averaging 8.9 sec, adult males 2.0 sec, and juveniles 3.6 sec.

1.9.4.6. *Vertical Toss.* A usually male crane begins with an erect posture, grabs a small piece of vegetation or clump of soil in the distal ends of the mandible and tosses the object into the air while extending the neck vertically. This behavior is not obviously oriented towards another crane but generally in a flock. However, because the Vertical Toss can precede the Dance behavior of courtship (described below), Vertical Toss may be intended for a particular observer even if other cranes are nearby.

1.9.4.7. *Bow.* This behavior is similar to the forward neck stretch done in the Horizontal Head Pump but differs in that it is oriented towards a partner and held for 3 to 8 seconds (see drawings in Tacha 1988).

1.9.4.8. *Vertical Leap.* This behavior begins in a semi-crouched position. The crane then springs upward with the wings fully extended. The head is held high during this behavior and while in the air, the wings are flapped two to five times (see drawings in Tacha 1988).

1.9.4.9. *Dancing.* Dancing is perhaps the behavior people most associate with sandhill cranes. Dancing by males is often preceded by an Upright Wing Stretch and Horizontal Head Pump, and then one or more Vertical Tosses. Once a male has attracted the attention of a female, the dance begins with a Low Bow by both sexes. The male then throws back his head, touching his body (repeat of Horizontal Head Pump), and gives a deep Unison Call (see Sounds). The female responds by orienting her head backward about 45 degrees and emitting a call that is higher pitched and shorter than the Unison Call. First the male and next the female then leap many times into the air (Vertical Leap), while running and flapping their wings.

Though Dancing is associated with courtship, Dancing occurs year-round while courtship seems more limited. Thus, Dancing may not necessarily be associated with mate selection. Notably, Dancing can spread throughout a flock, but why this is so has not been investigated. Courtship activities are stimulated by changes in day length that trigger hormonal release (Tacha et al. 1987b). Courtship behavior and mate selection criterion are for the most part poorly understood.

1.9.4.10. *Pair bonds.* Pairs of sandhill cranes are socially monogamous, often with long-term pair bonding (Tacha 1988, Nesbitt 1989) and extended biparental care of young, though extra-pair copulation and fertilization occurs (Wisconsin: Hayes et al. 2006, 2007, Oregon: CDL, Idaho: RCD). Mate pairing and subsequent nesting can occur as young as 3 years of age, but is atypical until 5 or 6 years, and practically all birds are paired by age 8 (Tacha et al. 1989, Lewis et al. 1977). In the Mid-Continent Population, only 20% of cranes age 4 are likely to be paired, but by age 7, 90% are paired (Tacha et al. 1989). Sandhill cranes are generally thought to maintain life-long pair bonds (Tacha 1988). However, younger *G. c. tabida* and *G. c. pratensis* of the Eastern Flyway Population commonly break pairings following nest failure. One study over a period of 20 years found that of pairs that do not produce young, 53% broke the pairing (Nesbitt and Tacha 1997). Re-pairing without loss of the nest or the mate is infrequent (Littlefield 1981a, Nesbitt and Wenner 1987, Nesbitt and Tacha 1997). Pair bond stability may be fostered by reproductive success (Nesbitt and Tacha 1997). *G. c. pratensis* banded in Florida form persistent dyad relationships from as early as 14 months of age and as late as 3 years of age (Nesbitt and Wenner 1987).

In Mid-Continent sandhill cranes, pair bonds are most commonly initiated during spring migration (Tacha 1988). However, pair formation can occur at any time of year, particularly following nest failure. When pair bonds are broken, with or without mate loss, re-pairing occurs without extended courtship and sometimes within a few hours (Nesbitt et al. 2001). Replacements presumably come from non-breeding flocks if cranes follow general avian patterns (Newton and Rothery 2001, Penteriani et al. 2008), but this has not been investigated explicitly. Mutually given behaviors associated with territory acquisition and defense and brood rearing may serve to maintain pair bonds outside the breeding season.

1.9.5. SOCIAL AND INTERSPECIFIC BEHAVIOR. Banding studies have enabled identification of age, sex, and social class in individuals, and allowed description and quantification of social behaviors and relationships. Social behaviors account for about 5% of diurnal time (Tacha 1988). Pending additional information, social and interspecific behaviors other than flocking are presumed similar across populations and subspecies. Flocking behavior appears to differ by population. Family groups in the Eastern Flyway Population are often in small flocks, whereas non-breeding birds are more often in larger flocks (Lovvorn and Kirkpatrick, 1982b). Among cranes of the Rocky Mountain Population, flocking differs by season. Larger flocks occur on wintering grounds than on the fall staging area in the San Luis Valley (Drewien et al. 1995). Family units tend to maintain some distance from other cranes when in a large flocks, leading families to be most often on the edges of flocks (Drewien et al. 1995). Implications to predation have not been explored. Among *G. c. canadensis* in Saskatchewan, individuals in flocks have a mean distance from nearest neighbor of 1.75 ± 0.05 m, and on the whole, are often uniformly distributed when feeding in cultivated fields (Miller and Stephen 1966).

1.9.5.1. *Preflight and Alert Postures.* Sandhill cranes appear to signal their intention to fly with a preflight Neck-stretch Display. Such preflight displays facilitate coordinated takeoff of pairs and family units, and prevent unnecessary escape behaviors in flock members triggered by sudden flights.

1.9.5.2. *Neck-stretch Display.* In this behavior, the neck is arched forward, such that the head and neck are slightly angled upward toward the sky (see drawings in Tacha 1984).

1.9.5.3. *Alert Investigative Posture.* This behavior occurs when a crane is not obviously alarmed but may be inquisitive about something nearby. The body is erect, legs are tall and straight, and the neck is vertical, bringing the bird to maximum height. The head is often rotated and not looking forward (see drawings in Tacha 1988), apparently to allow the bird to carefully focus the center of the field of vision of one eye on the object of interest (see Martin and Shaw (2010) for a description of related Blue Cranes (*Anthropoides paradise*).

1.9.5.4. *Tall Alert Posture.* This behavior is simply when the body is held erect and the head is elevated to its maximum extent. The bill is held parallel with the ground, while feathers are flattened against the body. No movement occurs or sound emitted (see drawings in Tacha 1988). Tall Alert Posture is used when alarmed (Tacha 1988) and is taken up rapidly by nearby cranes until the entire flock is alert; loud Rattle Calls are often used in conjunction with Tall Alert Posture (Archibald 1975, JFD; see Sounds).

Adults spend nearly twice as much diurnal time in alert postures (4.7%) as juveniles (2.7%), and males spend five times as much time in alert postures as females. Adults in pairs or family units spend four times as much time alert as adults without mates or young. Alert behavior becomes progressively more common as cranes migrate from wintering to breeding areas.

1.9.5.5. *Relationships.* The most stable relationships among sandhill cranes during migration and wintering are mated pairs and family units (Tacha 1988), regardless of population. Among non-migratory *G. c. pratensis*, families break up between 12 Jan - 1 Mar (average 3 Feb), and the mean age when offspring depart from their parents is 327.4 ± 26.1 days (Nesbitt et al. 2002). Juveniles gain substantial advantages from remaining in family units, including more loafing and feeding time, fewer agonistic encounters, less alert time, and higher body lipid levels than juveniles without parents. No costs in time or energy have been attributed to being a parent during winter and early spring.

Family size of *G. c. canadensis* in the Mid-Continent Population is 1.14 ± 0.02 SE (Drewien et al. 1995). Family units stay together from hatching through the following March, when 90% of juvenile cranes of the Mid-Continent Population are still with parents (Tacha 1988). Family size for *G. c. tabida* of the Rocky Mountain Population in the fall is 1.25 ± 0.02 SE, with most young departing from their parents from late February-early April (9-10 months) along the migration route (RCD, Drewien et al. 1999). Extended family relationships can persist after the first year, however, siblings and parents will temporarily rejoin in later years (e.g., two male 20-yr old siblings and their mates formed a group). This may have been an example of individual recognition). Similar examples are known from wintering grounds, during migration, and on breeding areas among Rocky Mountain Population *G. c. tabida* (RCD). In Oregon, young cranes leave their parents in March and early April (CDL).

1.9.5.6. *Organization.* Sandhill cranes form groups composed of breeding pairs, families, paired non-breeders, groups of unpaired non-breeders, and mixtures of all of the above (Tacha 1988). Breeding pairs often persist year-round until one of the mated individuals dies (see Breeding). Family units are typically composed of a breeding pair, their most recent offspring, frequently their 2-year olds, and sometimes much older offspring from previous broods. Paired non-breeders can remain as a discreet social unit for multiple years. Unpaired non-breeders form nomadic flocks during breeding seasons, presumably to avoid conflict with territorial breeding birds. They aggregate in roosting and feeding flocks with breeding pairs, families, and paired non-breeders at staging areas prior to fall migration, and remain in these mixed groups through wintering and spring migration. Aggregations may persist through migration and over winter but are unstable in the long term, such that associations across population do not persist.

1.9.5.7. *Interspecific.* Cranes often roost and feed near ducks and geese (Walkinshaw 1949, 1973), and in Florida, near cattle (JFD). Few conflicts arise in these groups but when competitive interactions do occur cranes typically are dominant over other birds, but yield to ungulates. Few studies have investigated conflict behavior between cranes and other species. Particularly relevant are better undering conflict behaviors near nesting and feeding sites, including the proportional time cranes are winners and losers, when fighting over a resource.

1.9.6. Predation. Sandhill cranes are potentially predated upon by a plethora of species, depending on their location, but it is likely there are only a few dominant predators.

1.9.6.1. *Types of Predators.* Predation pressure varies annually within populations (Littlefield 1976, 1995a, c, 2003), and likely also varies among populations and seasons, but specifics describing this variation are unavailable. Coyotes (*Canis latrans*), Common Ravens (*Corvus corax*), Raccoons (*Procyon lotor*) and Mink (*Neovison vison*) are generally the most common predators of sandhill cranes (Ivey & Scheuering 1997, DesRoberts, 1997, Littlefield 2003). Less often, cranes are predated upon by a long list of species. The following are grouped by taxa and then listed in alphabetical order by common name, Mammalia: Badgers (*Taxidea taxus*), Bobcats (*Lynx rufus*), Red Foxes (*Vulpes vulpes*), Wolves (*C. lupus*), Aves: American Crows (*Corvus brachyrhynchos*), Golden Eagles (*Aguila chrysaetos*), Great Horned Owls (*Bubo virginianus*), gulls (Laridae species), Northern Harriers (*Circus cvaneus*), Red-tailed Hawks (*Buteo jamaicensis*), and other raptors (Walkinshaw 1949, Johnsgard 1983, Walkinshaw 1973, Tacha et al. 1994, Ellis et al. 1999, Littlefield 2003).

The Cuba and Florida Populations face unique nest predators, Alligators (*Alligator mississippiensis*) and American Crocodiles (Crocodylus acutus, which are not encountered by other breeding populations. American Crocodiles (*Crocodylus acutus*) prey on pre-fledged young and adults in Cuba, particularly sick or injured individuals (Walkinshaw 1949, 1973). Eggs are likely taken by all of these predators, except for perhaps Crocodiles since cranes in Cuba tend to breed in uplands. Alligators may occasionally eat eggs (Folk et al. 2015).

To minimize egg predation during the incubation period, the non-incubating crane may be more secretive than usual, even when not near the nest. When disturbed, breeding cranes often crouch to hide among tall vegetation, rather than walking or flying away. In pre-fledged *G. c. pratensis* chicks, 82% of known mortalities were due to predation. Avian predators (Hawks and Owls) took youngest chicks (0-19 days) and mammalian predators (Bobcats and Coyotes) took older (> 19 days) chicks (Nesbitt et al. 2008a). Flighted (healthy) adult or juvenile cranes may be taken by Golden Eagles and Bobcats. For 56 nests in ne California, Coyotes were the main predator, taking 17 (30.4%), while Common Ravens took 6 (10.7%), and Raccoons 5 (8.9%; Littlefield 1995b).

At Modoc National Wildlife Refuge in ne California, DesRoberts (1997) found when predator control of Coyotes was implemented in 1990 and 1992, 4 of 28 radioed chicks (14%) were lost to Mink and 3 (11%) to Coyotes. For 1,096 *G. c. tabida* clutches assessed at Malheur National Wildlife Refuge in se Oregon, 214 (20.1%) were destroyed by Coyotes, 100 (8.8%) by raccoons, and 165 (15%) by Common Ravens during 1966-1989 (Littlefield 1995a). A telemetry study at Malheur National Wildlife Refuge, in 1983 and 1984 (during a period of no predator control) found that of 39 radioed chicks, 17 were lost to predators; Coyotes took 13, Great Horned Owls 2, a Raccoon 1, and a Domestic dog 1 (Littlefield and Lindstedt 1992). When predators were controlled at Malheur National Wildlife Refuge (1991-1998; particularly Coyotes), out of 219 chicks radioed, predators were responsible for the loss of 109 (61%); Mink took 29%, Coyotes 21%, Great Horned Owls 17%, Golden Eagles 9%, one was lost to a Northern Harrier and one to a raccoon (Ivey and Scheuering 1997). At Sycan Marsh, in s central Oregon, 339 nests were assessed, of which 72 (61%) were destroyed by Coyotes and 25 (21.2%) by Common Ravens or gulls (Stern et al. 1987). In e Oregon, of 63 nests monitored in 1976 and 1986, Coyotes destroyed 12.7%, Common Ravens 11.1%, and perhaps a gull destroyed one nest (Littlefield 1999b).

1.9.6.2. *Response to Predators.* Sandhill cranes threatened by avian predators will use the Upright Forward, Upright Stab, and the Upright Kick behaviors. When confronted by a mammalian predator, the typical response is an Upright Forward behavior where the wings are partially or fully spread and the bill oriented toward the predator. If the predator does not retreat, an Upright Stab behavior is used in combination with the leaping and kicking of the Upright Kick behavior. When attacked, cranes launch into Upright Kick behavior, vaulting into the air and throwing their feet towards the predator.

1.9.6.3. *Distraction Display.* The Distraction display is a stiff-legged wing-dragging movement away from the nest or nestlings. The adult feigns injury, accompanying the movements with hissing (Yosef 1994). When predators are near the nest, adults will attempt to lead the predator away by performing a Distraction Display.

Sandhill cranes will also mob a predator, as individuals, pairs, or in flocks. Guard Calls are vocalized repeatedly during mobbing (see Sounds; Nesbitt and Bradley 1997). There are several references to cranes giving Guard Calls (see Sounds) and approaching Caribou (*Rangifer tarandus*), Moose (*Alces alces*), Mule Deer (*Odocoileus hemionus*) and Cattle (*Bos primigenius*), when these animals come close to the nest (Altman 1960, Walkinshaw 1965, Miller and Broughton 1973, Drewien 1973). Cranes will also attack potential predators (Badgers, Coyotes, Red Foxes, and raptors) when these animals approach (CDL, RCD, SAN). To do so, sandhill cranes attempt to use their beaks in and Upright Stab to spear predators. For example, R. Rigby (manager Bosque Refuge NWR) observed a crane kill an attacking Coyote by stabbing it through the eye during the winter of 1976 (RCD).

During winter in the sw U.S. and n Mexico, Golden Eagles and occasionally Bald Eagles (*Haliaeetus leucocephalus*), approach mixed flocks of Rocky Mountain Population *G. c. tabida* and Mid-continent Population *G. c. canadensis* and *G. c. rowani* on the ground. When Golden Eagles attack, responses often differ by subspecies. The smaller and more agile flying *G. c. canadensis* will usually take flight, whereas the much larger *G. c. tabida* typically remain on the ground, quickly forming a tight group with their bills all pointed skyward. This behavior proved successful in several observed incidents where Eagles left without successfully attacking the group (RCD). Eagle attacks of single cranes are normally more successful, resulting in capture and consumption of a crane.

During attacks by Golden Eagles on cranes of the Rocky Mountain Population in flight, the targeted crane will break flight formation and initiate a steep dive in an attempt to elude the eagle. Such aerial attacks by Golden Eagles were observed relatively frequently during fall migration studies conducted in the Rocky Mountains (RCD). When attacks are successful, Golden Eagles typically detach the cranes head from the body immediately upon subduing the crane (RCD).

1.10. BREEDING

1.10.1. PHENOLOGY. Breeding pairs establish territories 2-4 weeks prior to building a nest and laying eggs (Drewien 1973). Earliest eggs are laid by individuals in non-migratory populations. In Florida, eggs are laid as early as December and as late as August (Bent 1926), though most eggs are laid January to May (Walkinshaw 1973, Nesbitt 1988). Average laying dates are 22 to 24 February in sc Florida and 12 March in nc Florida (Walkinshaw 1982). Estimated laying date by flightless individuals undergoing molt in late summer in

Florida from 1972-2009 averaged 9 June; all were likely re-nestings (M. Folk. pers. Comm.). In migratory populations, mean nest initiation dates range from early Apr to late May (Walkinshaw 1973). Boise (1976) reported hatch dates in Alaska as 27 May to 1 Jun with a 16 Jun average hatch date for Banks Island, Northwest Territories (Walkinshaw 1973). At Malheur National Wildlife Refuge, Oregon, nesting begins in early Apr, with peak nest initiation occurring about 21 April (Littlefield 1990; range = 25 Mar to 18 Jun). At other Great Basin nesting sites in e Oregon, eggs are laid between mid-Apr and early May, and in late Apr to late May in mountainous regions (Littlefield 1999a). In ne California, egg-laying begins in mid-Apr (earliest 11 Apr) with most in late Apr (latest 11 May), though one chick found on 9 Aug must have hatched between 15-21 Jun (Littlefield 1995a).

1.10.2. Renesting. Renesting can occur up to 3 times per yr, as noted across the species range from Florida to the Sycan Marsh National Wildlife Refuge in Oregon (M. Stern pers. comm.) and Grays Lake, Idaho. The average interval between clutches is 19.5 d in Florida (Nesbitt 1988). Renesting in *G. c. tabida* is known only among pairs that lose their nests during the first half of the incubation period with an interval between clutches for one pair of 15 d (Drewien 1973). More recently, 2 pairs of the Rocky Mountain Population were observed renesting after losing hatched young < 1 week old (RCD).

1.10.3. Nest Site. A nesting territory usually has several potential nesting sites that may be used. Which sex, if either, controls nest site selection is unknown. In se Oregon, *G. c. tabida* males frequently initiate nest construction, but females rarely use a site the male selects. Once a nest site is selected, one bird, usually the female, stands on the nest mound and arranges nest material provided by both birds. Unfinished nest foundations or alternate nest starts often occur near active nests. These may represent an abandoned site or an intentional addition to the nest area that provides several elevated platforms for brooding and feeding the young. Most extra nest platforms are built by males (RCD). In Florida, Idaho, and Oregon, regardless of sex, when one member of a breeding pair dies, the surviving member retains the nesting territory with a new mate (Nesbitt and Tacha 1997, RCD).

In Michigan, *G. c. tabida* select nest sites in or near seasonally flooded emergent (non-woody) wetlands, while avoiding forested uplands (Baker et al. 1995). In Mississippi, water distribution and levels influence nest site selection within an area of otherwise apparently homogeneous habitat (Smith and Smith 1988). Sites chosen are usually marshes, bogs, or swales. These sites may abut open water or exist in small, isolated wetlands. Nests in expansive wetlands are usually within 300 m of the edge. The mean distance between nests in emergent vegetation and open meadows at Malheur National Wildlife Refuge, Oregon was 40 m (range = 0 to 345 m, n = 515; Littlefield 2001b).

Throughout most of the species range, the presence of standing water with emergent aquatic vegetation is an important characteristic of the nest site. Measured water depths under active nests have ranged up to 99.1 cm for nests built over open water (Thompson 1970). Mean water depth was 26.7 cm at 100 nests in central Florida (Dwyer 1990), 21.2 cm at 110 nests in s Michigan (Walkinshaw 1973), 20.0 cm at 187 Idaho nests (Drewien 1973), 18.0 cm at 274 nests at the Sycan National Wildlife Refuge in Oregon (Stern et al. 1987), and 25.8 cm (range = 0 to 105 cm) for 881 nests a Malheur National Wildlife Refuge in Oregon (Littlefield 2001b).

Although cranes typically nest over water in either attached or floating nests, they will also nest on dry ground (Layne 1982a), particularly *G. c. nesiotes* and arctic-nesting *G.*

c. canadensis (Walkinshaw 1973, Drewien 1973, Valentine 1982, Nesbitt 1988). *G. c. nesiotes* nest on nearly level, dry grasslands (Walkinshaw 1953, Walkinshaw 1973, Aguilera et al. 2005), with nearby vegetation of scattered tropical pines (*Pinus tropicalis*), palmettos (*Acoelorraphe wrightii*), and bushes. The height and density of vegetation increases further away from *G. c. nesiotes* nests (Ferrer Sanchez et al. 2010). In Mississippi, nut-rush (*Scleria baldwinii*) is almost always found near nests, such that it could be used as an indicator of potential crane nesting (Valentine 1982). Cattails and sedges (*Carex* species and/or *Scirpus* species) predominant around nests in s Michigan; in the Upper Peninsula 12 of 13 nests were in sphagnum (*Sphagnum* species) bogs (Walkinshaw 1973). Rocky Mountain Population *G. c. tabida* nesting in Idaho usually nest in grassy areas that include *Juncus balticus* and *Carex* sp. (Drewien 1973). Oregon nests are typically in stands of burreed (*Sparganium eurycanpum*) and hardstem bulrush (*Scirpus acuta*; Littlefield and Ryder 1968, Littlefield 2001b). Alberta nests are in open sedge marshes (Carlisle 1982). Alaska nests are in Sphagnum species or various grasses and sedges (Boise 1976). Nests on Banks Island and other areas of n Canada and Alaska are in sand dunes 3 to 10 m high, completely dry with scattered dune grasses, or in marshes dominated by sedges and grasses (Walkinshaw 1973, Reed 1988).

1.10.4. Nest. Sandhill cranes most commonly construct nests in water where floating piles of aquatic vegetation, grass, mud, sticks, and moss separate vulnerable eggs and chicks from terrestrial predators (Lewis et al. 1977; see Behavior). In emergent aquatic sites, cranes collect nest material from the immediate surroundings and toss it over their shoulder, eventually forming a mound at the site with a characteristic vegetation-free pluck-zone surrounding the nest. Larger material forms the foundation, with a distinguishable egg cup formed and lined with smaller stems or twigs. Early in the nesting season, birds use the dried residue of the preceding seasons growth to initiate nest construction. Later in the season, green material is added to the nest. When nesting occurs on dry ground, nests have minimal construction and no egg cup. Regardless of the substrate, both sexes participate in construction that may last 1 d to 2 wk (Littlefield and Ryder 1968).

1.10.4.1. *Dimensions.* Nest size varies with substrate; nests built over standing water are considerably larger than nests built on dry sites. Floating nests are usually built up 10 to 16 cm above the water surface, with birds compensating for small increases in water levels by adding material to the nest. Length and width measurements vary from 98 x113 cm in Michigan (Walkinshaw 1973), to 111 x 127 cm in Oregon (Littlefield 2001b), and 80 x 86 cm (SD = 31 x 36) in Idaho (Drewien 1973).

Throughout incubation, the sitting bird (particularly males) may add small amounts of material and continually rearrange the nest. The nest may adjust (float) to slight increases in water level, but pairs may select a new site for renesting if water levels change substantially. Successive nests in Oregon (within or between seasons) are usually near each other if water levels permit. The average distance between within-season renesting is 183 m (n = 6; CDL), though use of the same nest for a within-season renesting also occurs (Dwyer 1990). Mean distance between first nests and renests in Idaho was found to be 148 m (SD = 131, range 33-351 m, n = 4; Drewien 1973).

1.10.5. EGGS. Sandhill crane eggs are sub-elliptical to long oval; their average size is 93.1 x 59.1 mm with an average mass of 161.2 g, but these measurements likely vary among subspecies and regions. Shell thickness ranges from 0.397 mm for *G. c. pratensis* to 0.550 mm for *G. c. canadensis* (Baldwin 1977). Color is variable but generally pale brownish buff to light olive, irregularly marked with darker brown, reddish brown or pale gray. White, unpigmented eggs have also been reported (Radke and Radke 1988). The egg surface is semi-glossy to flat and smooth to irregularly grainy, with grain size sometimes quite large.

Sandhill cranes lay 1-3 eggs per clutch, at 2 d intervals (Littlefield and Ryder 1968, Drewien 1973), with a mode of 2 eggs and a mean from several populations and subspecies of 1.90 (range = 1.76 to 1.98; Boise 1976; Walkinshaw 1973). Smaller clutch sizes are more common in northern breeding populations (Nesbitt 1989, Tacha et al. 1994). One 4-egg clutch, produced by a *G. c. tabida* was observed in Oregon (Littlefield and Holloway 1987), but has never been elsewhere.

1.10.6. INCUBATION. Incubation begins with laying of the first egg and continues until the second egg hatches or is abandoned (usually 1 or 2 d after hatching of the first egg). Cranes will continue to incubate an addled or infertile clutch 10-15 d beyond the normal incubation period (Nesbitt 1988). An incubation patch develops in both sexes on each side of the sternum. The mode for the incubation period is 30 d and a mean of 30.2 (range 29-32, n = 14, Drewien 1973). Males and females share incubation duties equally during daylight hours, but only females incubate at night, and thus females perform about 70% of the total incubation (Littlefield and Ryder 1968, Drewien 1973, Walkinshaw 1985, Nesbitt 1988). Nests are usually attended constantly. Throughout the species range in the contiguous U.S., incubating birds may occasionally leave the nest unattended for periods of $\leq$1 h during cooler parts of the day (morning or evening), or depart briefly if the mate is late arriving for nest exchange. Nest exchanges occur several times during the day. If male does not arrive within 2 hours before sunrise the female often does not return to relieve him until evening (CDL). Studies in Idaho of individually marked *G. c tabida* of the Rocky Mountain Population revealed nest attentiveness was related to the age of breeding individuals. Older, more experienced breeders were more attentive, rarely leaving nests unattended. In contrast, younger individuals more frequently left nests unattended for extended periods (RCD). During mid-day, the non-incubating bird may be found loafing near the nest, but usually roosts away from the nest at night.

Early in incubation, eggs can survive only brief cooling (snow with low wind-chill factor; RCD, CDL). The tolerance of eggs to temperature fluctuations improves after 2 weeks of incubation. By the last week of incubation, eggs can survive longer periods of neglect, provided they are not exposed to the heat of the day or direct solar radiation, and have not yet pipped (SAN, CDL, RCD). Laboratory investigations of heat and cold tolerances have not been preformed, which would help to understand the connection between phenotypic deformities and egg development.

1.10.7. HATCHING. Up to 72 hrs before hatching, parents give Purrs (see Sounds) in response to young vocalizing in the egg; this may help stimulate hatching (Archibald and Viess 1979, Hartman et al. 1987). Hatching begins with pipping where the young bird breaks the egg from inside. Hatchlings produce 3 distinct calls during pipping; the Contact Call, Pipping Call, and Stress Call (Voss 1976; see Sounds). The older embryos calls are believed to stimulate the younger embryo to begin pipping. Thus, the second egg frequently hatches after 29 days of incubation, not the usual 30 days. Within 20 h of pipping, the chick begins rotating counter-clockwise and breaks the shell (Hartman et al. 1987). An average of 7.3 h elapse between the beginning of rotation and emergence. Mean period between the first break in the shell (pipping) and emergence is 26.5 h (range 11 to 48 h; Archibald and Viess 1979, Hartman et al. 1987). In a 2-egg clutch, the eggs hatch at one day intervals (Walkinshaw 1973, Drewien 1973).

Parents may help break the shell of hatchlings when hatching is protracted. Upon emergence, parents may offer the chick small pieces of the shell and/or consume some of the shell themselves. Parents commonly carry the shell and membrane away from the nest (CDL, RCD, C. B. Kepler, P. W. Sykes Jr., pers. comm.), though some fragments and occasionally large pieces of shell and the membrane may remain.

1.10.8. YOUNG BIRDS. Hatchlings are nidifugous (i.e., they leave the nest soon after hatching). Their down dries 2 to 3 h after hatching, by which time their eyes are open, they can sit up on their tibiotarsi, and sometimes even stand feebly. Shortly afterward they stand well. If necessary, young can leave the nest on foot or by swimming within 8 h after hatching (Walkinshaw 1973). More often, young leave the nest within 24 h of hatching. Mean weight for 15 *G. c. tabida* chicks at hatching was 114.2 g, a bill length 22.7 mm, tarsus length of 44.2 mm, and a wing cord of 33.7 mm (Walkinshaw 1973).

1.10.8.1. *Growth and development.* Chicks begin feeding within 24 h of emergence (Figure 1.12). *G. c. tabida* chicks (n =13) 1.0 to 1.5 d after hatching increase body mass by an average of 1.9 g, bill length by 1.2 mm, tarsus length by 3.7 mm, and wing cord length by 1.7 mm (Walkinshaw 1973). By 12 to 13 d of age, 3 *G. c. tabida* chicks from Idaho averaged 315 g (Drewien 1973). By 20 to 30 d of age, young acquire about half of their adult leg and wing length, though mass increases more slowly (Baldwin 1977). Thirty-five days after hatching, *G. c. tabida* and *G. c. pratensis* increase body weight by 14.0 to 14.5 times; *G. c. rowani* and *G. c. canadensis* by 17 times (Archibald and Viess 1979). Forty d after hatching, legs are almost full grown and by 60 d, bill and wings are nearly adult size (Baldwin 1977). Growth is not complete until up to 10-12 months of age when birds reach adult mass (Walkinshaw 1949). In yearling *G. c. pratensis*, adult mass can be attained at about 270 days, more than 6 mo after long bone growth is completed (Nesbitt et al. 2008b). The two most northerly nesting subspecies (*G. c. rowani* and *G. c. canadensis*) develop the fastest, while *G. c. tabida* and *G. c. pratensis* (more southerly nesters with the longest nesting seasons) develop more slowly (Baldwin 1977).

The acquisition of homeothermia (warm-bloodedness) is correlated with nesting range. *G. c. pratensis* (and presumably *G. c. pulla* and *G. c. nesiotis*), the three populations that are non-migratory, are poikilothermic at hatching (cannot regulate their body temperature). These subspecies require about 24 h to become fully homeothermic. *G. c. tabida* are heterothermic (partially able to regulate body temperature) at hatching and fully homeothermic after 9 h. *G. c. rowani* and *G. c. canadensis* are homeothermic when hatched (Baldwin 1977). These data were collected from limited locations within subspecies range. A broader sampling might indicate range related differences to be greater than subspecies differences. For example, more northerly nesting birds of all subspecies may be the most quickly homeotermic. However, additional surveys would be beneficial.

1.10.9. Parental Care. Young are brooded intensively after hatching, principally by the adult female (Walkinshaw 1973). Chicks may be brooded on the back or under the wings (especially in n populations), and if the parent stands and begins walking chicks may remain in place to be briefly transported, but extensive parental carrying of young does not occur. The frequency and duration of brooding declines with age, such that brooding is infrequent 3 wks after hatching (longest observed was 23 d; CDL).

1.10.9.1. *Feeding.* Both parents feed young (Walkinshaw 1973) and generally keep them separated, perhaps to reduce sibling aggression, but perhaps also to minimize the likelihood that one predator could get both chicks. During the first 10 d or so after hatching, chicks are mainly fed bill-to-bill by parents. Food items too large for a chick to take whole (particularly animal items) may be broken by a parent and fed in pieces. Young become more self-feeding after half grown. Food items may be dropped at the feet of young by adults leading them to feeding opportunities. Food begging by young continues sporadically until independence though occasionally parents will offer food to the chick, even without begging (Tacha 1988). These behaviors may be more socially (parent/chick bond) or physiological (hormonally stimulated) than nutritionally necessary.

1.10.9.2. *Nest Sanitation.* Adults do not defecate at the nest (Walkinshaw 1973). Young leave the nest soon after hatching, so post-hatching nest sanitation does not occur.

1.10.9.3. *Parental Care for Young.* Perhaps because chicks are aggressive toward each other (see Behavior), when 2 chicks hatch, each is tended separately by one adult. Typically, but not universally, within 24 hours of hatching, the adult female leaves with the first hatchling, and the adult male leaves with the second (Drewien 1973). For the first 10-14 d after hatching, the area used by a pair with young is restricted to within a couple hundred m of the nest (Drewien 1973). Range increases daily, and by fledging may encompass the total nesting territory.

1.10.10. COOPERATIVE BREEDING. Cooperative breeding has never been noted to occur for any subspecies or population.

1.10.11. BROOD PARASITISM. Thought to be generally uncommon, although inter- and intra-specific nest parasitism has occurred (Littlefield 1981c, Littlefield 1984). The rate at which this occurs is unknown.

1.10.12. FLEDGLING STAGE. Fledging usually occurs at seven weeks for *G. c. canadensis*. *G. c. tabida* of the Rocky Mountain Population fledge at 9.5-10 weeks (Drewien 1973, Boise 1979). Juveniles generally remain with the parents for 9-10 months, from nesting through fall migration, wintering and the first spring migration (Tacha et al. 1989, Drewien et al. 1999, see Behavior). In captive-reared young, mean age of first flight 53.4 d ± 2.4 SD (means ranged from 50.6 d for *G. c. canadensis* to 56.4 d for *G. c. pratensis*; Baldwin 1977). First flight in the wild is at 66 d for *G. c. tabida* (Oregon, CDL), and up to 75 d for *G. c. pratensis* and *G. c. tabida.*

1.10.13. IMMATURE STAGE. Young become strong fliers soon after their first flight. Though young can care for themselves, they still depend on parents for feeding opportunities and protection from aggressive (territorial) conspecifics and predators (Tacha 1988; see Behavior). Independence usually occurs during the first spring migration, or 30 to 60 d before the parents next clutch. In *G. c. pratensis*, mean age of independence is 295 d, (range 248-321 d, n = 16; Nesbitt 1992a). Young sandhill cranes begin associating with their peers in a non-breeding flock soon after leaving their parents (see Behavior), provided this opportunity exists. Young birds remain in these flocks until pairing begins. In *G. c. tabida*, yealings will remain in pre-breeding flocks during their 2nd summer, but these groups rarely persist during migration or over winter. Yearlings 12-15 months old do not pair in these summer flocks (RCD). Young non-breeders are the most mobile social class and are generally more nomadic and gregarious than adults (Nesbitt and Williams 1990). Very little to no information is available on the non-breeding proportion of sandhill crane population. Most important is the age-of-first reproduction and age-of-first successful fledgling. However, there is additionally no empirical information whether sandhill cranes skip-breeding in certain years, and if so, what the mechanism is that would drive these events.

1.11. DEMOGRAPHY AND POPULATIONS

1.11.1. MEASURES OF BREEDING ACTIVITY.

1.11.1.1. *Age at First Breeding; Intervals Between Breeding.* Sandhill cranes most commonly begin breeding at 2 to 3 yrs of age, but though they nest and lay eggs, most first-time breeders fail to produce young that survive to independence. Once a pair attains reproductive status they usually attempt breeding annually, though if nesting conditions are unfavorable pairs may delay or forego nesting that year. When management of threatened species is based exclusively on nesting, this behavior can place breeding territories at risk (e.g., Dwyer et al. 2012b).

In Florida, *G. c. pratensis* associate with between 3.6 and 6.0 potential mates before attaining breeding status (Nesbitt and Wenner 1987). Breeding efforts in *G. c. pratensis* may begin at 2 yr in males and 3 yr in females; 2-yr old males are rarely successful; the mean age of first successful reproduction is 5.2 yr. In contrast, *G. c. tabida* of the Eastern Flyway Population have a mean age of first reproduction of 4.3 yr (Nesbitt 1992a). In the Mid-Continent Population, successful reproduction may begin at 5 yr of age, but mostly ($>$ 75%) occurs in birds $\geq$ 8 yr old (Tacha et al. 1989), though this seems unusually delayed compared to other subspecies (CDL, SAN, RCD). *G. c. tabida* of the Rocky Mountain Population generally do not breed successfully before 3 yr of age (Drewien et al. 1995); however, a color-marked 2-year old female *G. c. tabida* in the Central Valley Population did nest successfully at Modoc National Wildlife Refuge, California (Radke and Radke 1986) and a 2-year old male nested at Conbay Lake National Wildlife Refuge, Washington (Washington Department of Fish and Wildlife 2002).

1.11.1.2. *Annual and Lifetime Reproductive Success.* Annual reproductive success averages 0.35 young/yr raised to the age of independence in the Eastern Flyway Population in particular, and in general for any *G. c. pratensis* in any population (Nesbitt 1992a). Lifetime reproduction in the Eastern Flyway Population in particular, and in general for any *G. c. pratensis*, is estimated at 1.86 (± 0.16 SE) young for any adult, and 2.70 (± 0.16 SE) young for an established breeder (one that reproduced successfully at least once before; Nesbitt 1992a). In the Eastern Flyway Population of *G. c. tabida*, 64% of adults reproduce successfully, and 74% of *G. c. pratensis* succeed; 26% of these adults produce 52% and 62% of the young, respectively (Nesbitt 1992a). Cranes of the Rocky Mountain Population nesting at Grays Lake National Wildlife Refuge, Idaho had an apparent mean nest success from 1998 through 2000 of 60%.

Once young have hatched, survival to fledging at 10 weeks is about 32.4% (Fox 2011), with the age of a chick the greatest predictor of its survival to fledging (Nesbitt 1992a, Bennett and Bennett 1990). Specifically, the older a chick is, the more likely it is to fledge. Following fledging, the annual percentage of juveniles in various populations averages 11%, with a range of 6.6 to 18.3% (Tacha and Vohs 1984, Tacha et al. 1986, Bishop 1988, Bennett and Bennett 1990, Nesbitt 1992a).

Among game birds in North America, sandhill cranes have the lowest annual recruitment of any species (Drewien et al. 1995). Annual recruitment across populations varies considerably spatially and annually from as low as 2.4% to as high as 21% (Johnson and Kendall 1997). Recruitment specific to populations is described below.

Across populations, predation is likely the most common source of nest failure (Sargeant and Arnold 1984, McWethy and Austin 2009), strongly impacting annual and lifetime reproductive success. Cranes rely on the water surrounding their nests to protect eggs from predators (See Behavior). Deep water limits the mobility of mammalian predators, and thus predators chance of encountering crane nests (Littlefield 1995a, Ivey and Scheuering 1997, DesRoberts 1997, Maxson and Riggs 1996, McWethy and Austin 2009). Water levels must be stable to be effective. In the Eastern Flyway Population, nest success varies by year, where higher water depth has a positive effect on daily nest survival (Austin et al. 2007). When water levels are shallow, predator control has benefited breeding success of sandhill cranes and whooping cranes (Littlefield 2003, Drewien et al. 1985, Drewien and Bouffard, 1990). The same has been observed for cranes of the Rocky Mountain Population nesting in riparian and palustrine wetlands, where nest success was 69% when water levels were high and stable (McWethy and Austin 2009). For *G. c. pratensis*, precipitation may be an important factor determining productivity of young. Winter rainfall is related to increased reproductive productivity, possibly due to improved feeding conditions, while high rainfall in early spring appears to reduce productivity, likely due to increased loss of eggs or young to flooding (Layne 1983).

Across the species range, other factors influencing reproductive success are vegetation surrounding the nest (Drewien 1973, Littlefield and Ryder 1968, Stern et al. 1987, Urbanek and Bookhout 1992), nest concealment (Littlefield 1995a, Maxson and Riggs 1996), land-use practices (Littlefield and Paullin 1990, Ivey and Dugger 2008, but see Austin et al. 2007), and weather (Ivey and Dugger 2008). The relative importance and interactive effects of these factors is not clear.

1.11.2. SURVIVORSHIP AND LIFE SPAN. Survival during post-hatching to fledgling is poorly understood, but believed to be affected primarily by predation (see Behavior). Annual survival probability for adult sandhill cranes is generally high at 0.91 - 0.95 (Drewien et al. 1995, 2000, BDG) but varies by population and can range from 0.82 - 0.96 (Johnson and Kendall 1997). In the Eastern Flyway Population (mostly not hunted) of *G. c. tabida*, annual survival probability, based on mark-re-sighting data, for post juvenile ($\geq$ 1 yr) cranes (all age classes combined), is 0.874 for males and 0.858 for females; for *G. c. pratensis* the rate is 0.884 for males and 0.918 for females (S. A. Nesbitt and C. T. Moore, unpubl. data). In the Rocky Mountain Population, survival probability of juveniles from summer to winter increases with increasing body condition and was higher during a non-hunting period (1969-1981) than during a hunting period (1982-1992; Drewien and Kendall, unpublished data). The largest difference between pre- and post- hunting survival occurs between poorly conditioned juveniles. A population model for sandhill cranes indicated dynamics of the Gulf Coast subpopulation of the Mid-Continent Population were highly influenced by population size and recruitment rate (Johnson and Kendall 1997). Future modeling efforts should incorporate age and spatial structure (i.e., migration) as these are likely the dominant life-history traits most affecting the population trajectory of cranes. Future models should also incorporate hunting as hunting pressure builds with increasing populations sizes (BDG, see Priorities for Future Research).

Mean life expectancy for any crane that reaches the age of independence is 7 yr (S. A. Nesbitt and C. T. Moore, unpubl. data). Maximum age in the wild is 21.6 yr for *G. c. pratensis* in Florida (SAN), and 19.4 yrs for a bird from the Mid-Continent Population (Klimkiewicz and Futcher 1989). A few color-marked *G. c. tabida* at Malheur National

Wildlife Refuge, Oregon have lived beyond 30 yrs (CDL). Maximum ages of banded cranes of the Rocky Mountain Population in Idaho include birds of 35.5 and 37 years old (Drewien et al. 2008). As of summer 2010, 4 cranes, all banded as flightless juveniles were aged as follows recovered or last observed: 1) 35.5 years old when last observed at Bosque del Apache National Wildlife Refuge, NM; 2) 36.5 years old when found dead of avian cholera at Bosque del Apache, NM; 3) 37.5 years old when shot during hunting season in Bernardo, NM, and 4) 40 years old and paired during summer 2010 when observed at Grays Lake, ID (RCD). Age records are updated by the U.S. Geological Surveys Breeding Bird Laboratory as bands are recovered by hunters and researchers. Thus, additional up-to-date age records may be viewed at:http://www.pwrc.usgs.gov/bbl/longevity/Longevity_main.cfm.

1.11.3. MORTALITY AND DISEASE.

1.11.3.1. *Bacterial, fungal, and viral diseases.* Diseases most significant in mortality of adult sandhill cranes are avian botulism (*Clostridium botulinum*) and avian cholera (*Pasteurella* sp). Avian tuberculosis (*Mycobacterium avium*) is less important but remains a potential mortality factor (Windingstad 1988). Aspergillosis has occasionally caused deaths but is usually secondary to other factors (Forrester and Spalding 2003). Serum samples from over 700 individuals in the Mid-Continent Population showed $< 2\%$ had positive indicators of exposure to Salmonella species or Type A Influenza, while 11% showed exposure to Newcastle disease (Haley et al. 1984).

No particular diseases or parasites have been associated with the nest, except that prefledged young of the Florida Population have been found debilitated or moribund from infections of coccidia (*Eimeria gruis* and *E. reichenowi*; Forrester and Spalding 2003). *G. c. pratensis* have tested positive for the infectious bursal disease virus serotype 2, which can cause death and is suspected as the cause of high mortality of captive-reared Whooping Cranes (*Grus americana*) released in Florida (Forrester and Spalding 2003). This virus may reduce survival of sandhill crane chicks. One occurrence of Highlands J virus has been identified as the cause of death for a single *G. c. pulla* (Ip et al. 2014).

1.11.3.2. *Parasites.* Twenty-four species of parasites have been associated with *G. c. tabida* and 22 with *G. c. pratensis* (Forrester el al. 1974, 1975, 1977, Forrester and Spalding 2003), though few are associated with documented pathology. Significant protozoans are *Haemoproteus antigonis*, *Leucocytozoon grusi*, and *Eimeria* species. Several species of trematodes have also been found, the most common being *Orchipedum jolliei.* One study found *Leucocytozoon grusi* in 11% of wintering sandhill cranes in Florida (Forrester and Spalding 2003). Among chicks of the Florida Population, parasites have varying levels of prevalence: *Leucocytozoon grusi* in 10% of chicks, *Haemoproteus antigonis* in 7%, *Haemoproteus balearicae* in 3%, and *H. balearicae* in $< 1\%$ (Dusek et al. 2004).

The most common nematodes associated with cranes are *Tetrameres grusi*, *Strongyloides* species, and *Syngamus trachea.* Four species of biting lice have been found: *Estiopterum brevicephalum*, *Gruimenopon canadense*, *Heleonomus assimilis*, and *Saemundssonia sagulata.* Helminth parasites (Iverson et al. 1983) and feather mites (Atyeo and Windingstad 1979) also have been reported. Infections with *Eimenia* species are occasionally significant, and cases of disseminated visceral coccidiosis have been reported (Carpenter et al. 1984, Forrester and Spalding 2003).

1.11.3.3. *Exposure.* Blizzards, hail storms, and lighting have caused the deaths of a substantial number of cranes. In 1966, a spring blizzard killed many migrating cranes of the Mid-Continent Population in Nebraska, but the exact number is unknown (Wheeler 1966). In

1979, a large hailstorm in Oklahoma is thought to have killed about 600 cranes of the Mid-Continent; hail fractured skulls and caused internal hemorrhaging (Heflebower and Klett 1980). In 1960, approximately 1000 wintering cranes of the Rocky Mountain Population were discovered dead in New Mexico following a 30 minute severe hailstorm (Merrill 1961). An adult and juvenile *G. c. pratenesis* in Florida were killed by lightning when standing near a wire fence during a storm in 1995 (Spalding and Forrester 2003), and ninety cranes in Nebraska were thought to be killed by lightning in 1978 (Windingstad 1988). Additional lightning strikes killing cranes have occurred, but can not be confirmed. It is unknown to what affect these lightening strike kills have on behavior of cranes that were not killed, but in close proximity.

1.11.4. RANGE.

1.11.4.1. *Initial Dispersal from Natal Site.* In the Florida Population, males are more philopatric than females; mean natal dispersal distance for male *G. c. pratensis* is 3.94 km (SD = 2.77, range 0.8-9.6), and for females is 11.58 (SD = 11.16, range 0.40-48.3). In one study, the direction animals dispersed did not differ from random and orientation was unaffected by sex (Nesbitt et al. 2002). Because males are strongly philopatric, the species is relatively slow colonizing new habitat more than 10 or 20 km from occupied habitats (Nesbitt et al 2005).

1.11.4.2. *Fidelity to Breeding Site.* Sandhill cranes have a high site fidelity to their breeding location. When water and vegetative conditions favoring breeding success are consistent, a breeding pairs nest may be within 100-200 m of previous years site. Cranes of the Florida Population consistently nest annually in the same territories. For example, 15 Florida sandhill crane nesting territories monitored from 1980 through 2005 were occupied for a total of 132.3 crane nesting years (range = 4.9 to 10.6) and went through 26 changes among the mated pairs (mean 1.7, SD = 1.6, range = 0 to 5). Despite the frequency of change in occupants, territory boundaries remained virtually unchanged (Nesbitt and Schwikert unpublished data).

Among migratory populations, randomly sampled cranes of the Mid-Continent Population all returned to within < 8 km (median distance = 1.6 km) of the activity center of the previous breeding season, including 38% of birds which returned to < 1 km (Krapu et al. 2011). Direct observations of marked birds and recovery data spanning 31 years for *G. c. tabida* of the Rocky Mountain Population also demonstrate strong fidelity to breeding areas (Drewien et al. 1999, 2000). Nests of *G. c. tabida* in the Central Valley Population on Malheur National Wildlife Refuge, Oregon and at Grays Lake National Wildlife Refuge, Idaho that were in isolated emergent stands were sometimes within 5 m of nests used in previous years (CDL, RCD).

1.11.4.3. *Fidelity to Winter Range.* In migratory subspecies, individuals (particularly established pairs) consistently return to the same wintering sites (Tacha et al. 1984, Wenner and Nesbitt 1987, Drewien and Bizeau 1974, Drewien et al. 1999). For example, the same color-marked individuals of *G. c. tabida* returned annually to the same roost sites and feeding areas in the Central Valley of California, and Rio Grande Valley, NM. Similar patterns occur at wintering areas in Florida (CDL, SAN, RCD).

1.11.4.4. *Home Range and Territory Size.* In Florida, year-round home ranges (area used by an individual or adult pair throughout the year but not always exclusively) average from 657 ha (SD = 299 ha, n = 6, Bishop 1988) to 1,366 ha (SE = 393, n = 20, Nesbitt and Williams 1990), with nesting territory size (the area defended by a pair for their exclusive use during the nesting and brood rearing) 71% of overall territory size (Nesbitt and Williams 1990). Annual home ranges in the Okefenokee Swamp of Georgia were 93 ha (SE = 26, n = 15, Bennett 1989b).

In the Lower Peninsula of Michigan, home ranges of cranes of the Eastern Flyway Population were 53.5 ha (n = 76), while in Upper Michigan they were 85 ha (n = 13; Walkinshaw 1973). The territory size of cranes of the Mid-Continent Population nesting on Banks Island, Northwest Territories was on average 90 ha (Reed 1988). In the Central Valley Population, nesting territories in Idaho averaged 17 ha (range = 10 to 23 ha, n = 5; Drewien 1973). At Malheur National Wildlife Refuge, Oregon territory size varied, depending on pair density, from 1.2 ha to 68 ha and averaged 25 ha for 8 territories (Littlefield and Ryder 1968); at high density sites, 8 territories averaged 9 ha (CDL). Nine pairs at Conbay Lake National Wildlife Refuge, Washington occupied territories averaging 140 ha (range = 58 to 218 ha; Washington Department of Fish and Wildlife 2002).

Sandhill cranes tend to remain on breeding territories throughout the breeding season. However, cranes of the Florida Population with nesting territories in relatively poor or declining habitat left their territories and moved to share undefended areas of better quality with other cranes (Nesbitt and Williams 1990). Because this usually occurred after fledging, it is similar to the staging behavior of migratory populations. In one instance a pair with 2 pre-fledged (< 30 days old) siblings walked to a shared area 8 km away (SAN). Navigation to the flock might be explained if flocks use the same areas annually, or if the adults moved more widely in flight while foraging, but this has not been explored.

In migratory populations, generally both members of each pair remain on breeding territories throughout the season. However, males in the Central Valley Population at Malheur

National Wildlife Refuge in Oregon may occasionally fly up to 3.2 km to feed in a grain field. Similar behavior has not been observed in females (CDL). In Idaho, family units frequently walk daily from territories into undefended higher elevation uplands to forage on invertebrates, which are more available earlier in the season in uplands than at marsh locations. This is especially true of grasshoppers.

1.11.5. POPULATION STATUS. Sandhill cranes are the worlds most abundant crane. Population estimates and trends (Tables 1.1 and 1.2) based on direct counts and interpolations dividing habitat by home range, indicate that among non-migratory populations, only the Florida Population is declining (Nesbitt and Hatchitt 2008). Among migratory populations, all populations appear stable or increasing where estimates have been attempted.

1.11.6. NON-MIGRATORY POPULATIONS.

1.11.6.1. *Cuban Population.* The *G. c. nesiotes* population was estimated at 526 individuals in 2002 (Aguilera and Chavex-Ramierz 2010). This population appears to be stable, but nonetheless are listed as Critically Endangered (Endangered Species Act, 1973) because it persists in a small isolated population (Meine and Archibald 1996a, 1996b), which is vulnerable to land use changes, genetic isolation, and hurricanes.

1.11.6.2. *Florida Population.* In the 1970s, the *G. c. pratensis* population was estimated at 4,000 to 6,000 and believed increasing (Lewis et al. 1977). A 2003 estimate, based on available habitat and known range of occurrence was 4,594, indicating a 35.7% decline from 1973 (Nesbitt and Hatchitt 2008). Habitat loss is a concern for other grassland birds in Florida (Dwyer 2010, Dwyer et al. 2012a, 2012b), and likely is responsible for the decline of the Florida Population. Another ± 400 *G. c. pratensis* occur in Georgia, mostly in the Okefenokee Swamp (Abler and Nesbitt 2001).

1.11.6.3. *Mississippi Population.* This population is listed as Endangered (Endangered Species Act, 1973), and would likely be declining without annual supplementation of captive raised young and active habitat management. Breeding programs started in 1965 at Patuxent Wildlife Research Center and in 1994 at White Oak (http://www.whiteoakwildlife.org) have increased the total population of *G. c. pulla* from 30 birds in the mid-70's to over 100 birds currently. A winter 2008 population study estimated 110 to 125 cranes, including 25 nesting pairs (Hereford and Grazia 2008) based on direct counts of 101 individuals. The average count for the preceding years (1999-2007) was 112.5 (± 9.1 SD; S. Hereford pers. com.). The most recent count indicated 105 individuals (Henkel et al. 2012). Thus, the population appears stable, but low heterozygosity (Dessauer et al. 1992) and high predation are apparently responsible for poor breeding success in the wild (Olsen 2004).

1.11.7. MIGRATORY POPULATIONS.

1.11.7.1. *Eastern Flyway Population.* Throughout the range of the Eastern Flyway Population, regional and statewide surveys indicate the population has grown substantially over the past 30-40 years and is becoming more widely distributed. A survey in 1973 estimated the population between 8,000-10,000 (Lewis et al. 1977), while a 1981 U.S. Fish and Wildlife Service survey counted 11,943, and a 2012 survey counted 87,796 (Ad Hoc Eastern Population Sandhill Crane Committee 2010, Kruse et al. 2013). The current survey is coordinated by the U.S. Fish and Wildlife Service during late-October to early November and covers historic migratory staging areas. This survey is not a complete count and thus represents an index to the population. The largest proportion of the Eastern Flyway Population of *G. c. tabida* nests in the Great Lakes states, primarily Wisconsin (24,372, 2009 population index), Michigan (24,320, 2009 population index), and Indiana (10,979, 2009 population index; Ad

Hoc Eastern Population Sandhill Crane Committee, 2010). Recruitment (% of the population that are juveniles) of the Eastern Flyway Population during the fall of 1979 and 1980 at Jasper-Pulaski Fish and Wildlife Area in Indiana varied by roosting area and year, but was generally between 10-13% (Lovvorn and Kirkpatrick 1982b). More generally, recruitment throughout the Eastern Flyway Population has averaged 12% (range = 9.2-14.3%; (Drewien et al. 1995) and most recently has been estimated as high as 16% (Kelly et al. 2011). The U.S. Fish and Wildlife Services management objective for the Eastern Flyway Population is to maintain a 5-year average population index of 30,000-60,000 sandhill cranes (Ad hoc Eastern Population Sandhill Crane Committee 2010).

1.11.7.2. *Mid-Continent Population.* This population of *G. c. canadensis*, *G. c. rowani*, and *G. c. tabida* is the most abundant of all crane populations in North America ($> 500{,}000$). For Mid-Continent *G. c. canadensis* using the San Luis Valley during fall migration, mean recruitment has been estimated as 11.2% ± 0.34 SE (Drewien et al. 1995). The Mid-Continent Population is monitored by a spring survey in the central Platte River Valley of Nebraska that has been ongoing annually since 1974. The majority of this population ($>$ 90%) is assumed to be in this area by the end of March each year. Starting in 1982, aerial transects using photography to correct counts of cranes not identified by observers has been employed (Central Flyway Webless Migratory Game Bird Technical Committee 2006). The average annual photo-corrected ocular spring population index has varied considerably in the last three-decades; for example the 2011 estimate was 519,397 cranes, and the 2012 estimate was 356,742 (Kruse et al. 2013). Thus, one particular count may not be as accurate as hoped, but analysis of counts over many years may still be a reasonable indicator of population trajectory. A recent assessment found that the MCP survey generally corresponded to when the peak of the population was present and that adjusting the timing of the survey would offer no improvements (Pearse et al. 2015). The current management objective for this population is to maintain a stable spring population index of 349,000-472,000 birds, as determined by an average of the three previous and reliable surveys (Central Flyway Webless Migratory Game Bird Technical Committee 2006). Additional management objectives include maintaining the geographic and temporal distribution of the population similar to the 1982-2005 range, and to maximize subsistence and consumptive recreational use of cranes, while still meeting conservation and management objectives. Recruitment in the Mid-Continent Population is difficult to measure given their expansive breeding areas. However, migrating cranes through Saskatchewan in 1972-1973 were observed to have a low recruitment of 3.5% and 5.3%, respectively, suggesting a decrease in annual recruitment with more northerly nesting cranes (Miller and Hatfield 1974).

1.11.7.3. *Rocky Mountain Population.* This population of *G. c. tabida* is monitored by pre-migration fall surveys that include > 60 areas throughout their breeding grounds. Annual fall surveys began in 1995 after spring counts in the San Luis Valley, Colorado were found unreliable due to mixing of subspecies and populations (Benning et al. 1997; The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007). The initial motivation for spring counts was that the entire population was thought to be present during this time (Johnson et al 2001). The fall count is a cooperative survey by the Pacific Flyway Subcommittee on the Rocky Mountain Population of Greater sandhill cranes, state natural resource agencies, and the U. S. Fish and Wildlife Service. In the mid-1940's, this population was estimated at only 400-600 cranes (Walkinshaw 1949). The Rocky Mountain Population has increased from approximately 10,000 in 1970 to 1971 (Drewien and Bizeau 1974), 11,000 in 1972 (RCD unpubl data), 17,000 in 1987 to around 20,000 since 2000 (Drewien et al. 2008), but has recently dropped to 17,992 (2011) and 15,417 (2012; Kruse et al. 2013). The percent distribution by states during September 2011 was Idaho = 28.7%, Montana = 38.0%, Wyoming = 17%, Utah = 8.6%, and Colorado = 7.7% (Kruse et al. 2012). Mean recruitment for the Rocky Mountain Population over 37 years was 8.0% (range = 3.4 to 12.1, Drewien 2008) as measured during Oct surveys in the San Luis Valley, Colorado. Recruitment of *G. c. canadensis* and *G. c. tabida* wintering in the state of Chihuahua, Mexico was estimated at 10.1% and 6.5% from 1986-1990, respectively (Drewien et al. 1995).

The current U.S. Fish and Wildlife Service management objective is to maintain the Rocky Mountain Population at numbers and distribution that will provide maximum direct benefits to the public and for the intrinsic values of the birds themselves (The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007). Specific objectives are to maintain a stable population index of 17,000-21,000 cranes, as determined by an average of the three previous and reliable pre-migration fall surveys. It is thought that a Rocky Mountain Population exceeding 21,000 may increase the probability of large-scale crop damage and the proliferation of disease and overcrowding in their wintering range. However, density-dependent process have yet to be empirically investigated.

1.11.7.4. *Lower Colorado River Valley Population.* This population of *G. c. tabida* is the smallest of the migratory sandhill crane populations. Winter counts thought to represent > 90% of the population, but not corrected for cranes present and unseen during the count, appear to be stable at 2,000-3,000 birds (Kruse et al. 2011). The most recent count from 2013 is 3,078 cranes (Kruse et al. 2013). Recruitment is estimated at 8.1% (2012; Pacific Flyway Study Committee 2012) to 9.36% (2011; Kruse et al. 2011). This population is annually counted via a coordinated aerial winter survey at Cibola National Wildlife Refuge, the Colorado River Indian Tribes wetland areas, Sonny Bono Salton Sea National Wildlife Refuge, and along the Gila River, which are located in Arizona and California (Kruse et al. 2012).

1.11.7.5. *Central Valley Population.* This population of *G. c. tabida* numbered around 8,000 in 1993. Low recruitment at some Great Basin breeding sites may be hindering growth in local segments of this population. Currently nesting numbers and breeding range are expanding in the Sierra Nevada Range of the Cascade Mountains, but there are no data to indicate an increase in the breeding populations in British Columbia (Cooper 1996). The most recent count of this population, conducted in November of 2000, and corrected for mixed subspecies, estimated a population of *G. c. tabida* at 13,940 (West Coast Crane Working Group 2000). The U.S. Fish and Wildlife Services objective is to maintain an estimated 20,000-25,000 birds in the wintering population in California (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983).

For the Central Valley Population of *G. c. tabida* at Malheur National Wildlife Refuge, Oregon, percent annual recruitment for paired adults ranged from 0.4 to 12.7 from 1970 through 1989 (Littlefield 1995c). From 1970 through 1989, 66.5% to 98.8% of young were lost between hatching and fledging (Littlefield 1995c). The number of young fledged per 100 adults ranged from 3.1 to 28.9 during 8 years when some predator control occurred, and 0.8 to 19.9 during 12 years when no predator control occurred (Littlefield 2003).

1.11.7.6. *Pacific Flyway Population.* There is no systematic survey of this population, either in its winter or summer range. In the 1982, approximately 25,000 *G. c. canadensis* wintered in the Central Valley of California (Littlefield and Thompson 1982). On British

Columbia islands and the nearby mainland, residents report that after disappearing in the early part of the last century, nesting cranes began returning about 30 years ago (North American Working Group, 2007). The coastal segment of *G. c. rowani* wintering primarily in the Sacramento Valley and adjoining foothills of Northern California, is estimated to be 2,200. The U.S. Fish and Wildlife Service objective is to maintain an estimated 20,000-25,000 birds in the wintering population in California (Subcommittee on the Pacific Flyway Population of Lesser Sandhill Cranes of the Pacific Flyway Study Committee 1983).

1.11.8. Population Regulation. Perhaps the most important factor regulating sandhill crane populations is habitat availability. As open habitats are lost to development, especially in Florida and the sw U.S. wintering range, or converted to land use practices that do not foster sandhill crane occupancy, populations decline (see Conservation and Management). By contrast, a generally warming climate may be allowing pairs in the Mid-Continent Population to successfully reproduce at higher elevations and more northern latitudes, and reduce migration distances, but there are no crane-specific studies in w or n Arctic and subarctic deliberately designed to evaluate this possibility. Nesting effort and success, and survival of young, correlate directly with the amount and quality of nesting habitat. Mortality associated with hunting also regulates the size of the Mid-Continent Population (Sharp and Vogel 1992). Predation continues to be a particular problem for *G. c. tabida* in some breeding areas of the Central Valley Population, and during drought conditions, predation can exacerbate habitat loss by dramatically reducing chick survival. However, w coast *G. c. tabida* and *G. c. rowani* are reoccupying historic breeding sites where habitat remains intact or has been restored (e.g., Conbay Lakes National Wildlife Refuge, Washington). There are no data available on factors regulating the Pacific Flyway Population of *G. c. canadensis*, which rebounded after the elimination of market hunting, which decimated the California population it the late 1800s and early 1900s.

1.12. Conservation and Management

Sandhill crane populations endured dramatic population declines throughout North America during the first half of the twentieth century, primarily due to habitat loss, human presence in remaining habitat, and hunting (Walkinshaw 1973, Meine et al. 1996a). Only the Florida population is known to remain in decline (Nesbitt and Hatchitt 2008). By contrast, the Eastern Flyway Population is increasing, and all other populations are either stable or their trajectories are unknown (Aguilera and Chavex-Ramierz 2010, Henkel et al. 2012, Kruse et al. 2012).

Due to the sandhill cranes wide distribution and relatively large populations, the International Union for the Conservation of Nature currently lists the sandhill crane as ''least concern" (IUCN 2012). Nevertheless, concerns for the future persist, particularly because low annual recruitment limits the ability of the species to rebound rapidly from declines (Drewien et al. 1995, see Demography), and changes in crop types and agricultural practices pose a continual threat to food supplies, particularly for the three migratory subspecies.

Consequently, small isolated populations, including *G. c. pulla* in Mississippi and *G. c. nesiotes* in Cuba are listed as endangered under the U.S. Endangered Species Act (Endangered Species Act 1973). Supplementation with captive-reared birds continues to be necessary to maintain the Mississippi Population (Ellis et al. 1992), where 75% to 80% of the current population was produced in captivity. Outside of endangered populations, hunting is legal, or under consideration in many areas of the U.S. Canada lists *G. c. tabida* as “Not at Risk”. However, the *G. c. tabida* population across Canada has not be assessed since 1979 (COSEWIC 2011), and no other subspecies have ever been assessed, so more objective evaluation of the species is warranted. Mexico has listed sandhill cranes as threatened due to existing and future impacts regarding habitat loss and other anthropogenic factors. Additional information on land-use in Mexico is necessary to be understand how habitat loss is affecting cranes.

1.12.1. Effects of Human Activity. Sandhill cranes are affected by human activity primarily through habitat loss, displacement by human presence, and hunting. Complicating factors include collision risks with stationary objects, exposure to pesticides, oil and biotoxins, ingestion or contact with lead, plastic, or other objects, and stress. As human activities increase across wild lands, greater numbers of cranes will be exposed to these factors, and thus vulnerable to displacement, loss of breeding opportunities, and mortality (Krapu et al. 1984). Additional long-term banding of cranes could help better understand how these threats impact cranes at the species and population level.

1.12.2. Habitat Loss. All sandhill crane populations and subspecies are vulnerable to habitat loss. In breeding areas, wintering areas, and along migratory routes, changes in agricultural production or outright loss of farmland to the effects of global climate change, oil and mineral extraction, and development are all potential long-term risks to crane populations (Krapu et al. 2011). In many cases, habitat may not substantially change, yet a new disturbance may prevent cranes from using what otherwise appears to be high-quality habitat. For example, one study in the short grass prairies of Texas found cranes avoided wind farms by up to 8 km (Navarrete 2011). Reasons for this avoidance may have been due to a mixture of conditions, such as presence of turbines, increased noise, and increased road and human traffic. With growing demand for renewable energies in the United States, there is potential for considerable and accumulating habitat losses.

1.12.3. Non-migratory Populations.

1.12.3.1. *Cuban Population.* Breeding habitat of *G. c. nesiotes* is being lost to sugarcane and rice cultivation, damming of rivers (Aguilera 2002), and woody plant encroachment due to fire suppression and agricultural development (Aguilera and Chavez-Ramirez 2010).

1.12.3.2. *Florida Population.* Grassland specialists in Florida face ongoing habitat loss as wetlands and agricultural areas are converted to more lucrative non-habitats such as urban areas (Dwyer 2013). Between 1974 and 2003, potential sandhill crane habitat declined by an average of 16.6% per year (Nesbitt and Hatchitt 2008). Today, much of the sandhill cranes habitat is under private ownership, increasing the challenges of implementing a state-wide conservation strategy. The Comprehensive Everglades Restoration Plan (CERP) may offset some habitat loss as managers work to reinstate the natural hydrology of south Florida (USACE 1999), but will likely not completely compensate for habitat concurrently lost to development. Loss of habitat has resulted in a major component of cranes in se Florida now using urban areas (Toland 1999). The productivity of these individuals is relatively low, especially at altered sites such as golf courses, lawns, intensively used agricultural lands, and urban created wetlands. Problems are exacerbated when individuals become habituated to humans, particularly as a result of direct hand feeding. Habituated cranes become quite bold and aggressive. Thus, colonization of urban areas is unlikely to relieve constrictive pressure on the Florida Population.

1.12.3.3. *Mississippi Population.* Habitat loss has likely contributed to the decline of *G. c. pulla.* From the 1950's to present, habitat for *G. c. pulla* has declined substantially, with savannas declining from 74% to 14% around Jackson County, while woodland increased from 18% to 70%, agricultural land from 8% to 9%, and urban lands from a trace to 6% (Smith and Valentine 1987).

1.12.4. Migratory Populations. For many migratory populations, the expanding distribution of invasive plant species poses a significant risk, as non-native plants alter wetland species compositions and flow dynamics, potentially impacting sandhill crane nesting and roosting habitat. In particular, the common reed *Phragmites australis* significantly impacts native plant and animal species (Randall et al. 2008) and may reduce the quality or availability of sandhill crane habitat (Kessler et al. 2011). As with most migratory species, high quality stopover areas are critical to the persistence of populations (Gill 2006). Sandhill crane stopover habitats have changed, and are likely to continue to change (Kruse et al. 2013) due to local human activity and to global climate change. These affects are population-specific and require detailed investigations to understand local impacts to sandhill crane population dynamics.

1.12.4.1. *Eastern Flyway Population.* This population of sandhill cranes is currently less affected by ongoing habitat loss, likely because habitats which persisted unoccupied through the 1900's as a result of hunting losses (see Hunting below), are now being re-occupied (Kruse et al. 2012).

1.12.4.2. *Mid-Continent Population. G. c. tabida* breeding in wetlands are frequently threatened by drainage of habitat and conversion to agricultural croplands. Remote wetland breeding areas for *G. c. canadensis* and *G. c. rowani* in Alaska, Canada, and Siberia seem fairly secure, though there is potential for disturbance, pollution, and habitat loss from oil/natural gas and mineral exploration and development. Threats to wintering habitats also are ongoing, particularly in Mexico where urbanization, and thus the potential for disturbance to roosting areas, is increasing (Lopez-Saut et al. 2011).

The Mid-Continent Population migrates through the Platte River Valley (see Distribution) where sandhill cranes pause to gorge on waste corn (see Food Habits). There is considerable variability from year to year in the availability of corn during spring migration. This may significantly affect the ability of sandhill cranes and other waterfowl to gain the mass required for successful migration (Pearse et al. 2010). Between 1978 and 1996, cranes with below average fat levels were observed during spring migration, presumably caused by a combination of reduced waste corn and increasing competition with arctic-nesting geese (Krapu et al. 2005a, 2005b). The inability of individuals to gain necessary body fat may put the population at risk for future declines. Reductions in mass result from reductions in waste grain, occurring as a consequence of increased harvest efficiency and recently changed post-harvest practices (Sherfy et al. 2011, Krapu et al. 2004). Future reductions of corn in the Central Platte River Valley by 25% are predicted to increase daily foraging distances by between 27 and 38% (Pearse et al. 2010).

Changes in food availability may be exacerbated by loss of roosting habitat as expansion of Common Reed (*Phragmites australis*) in the central Platte River Valley may decrease roosting habitat to less than 1% of what is currently available (Kessler et al. 2011, Kessler et al. 2013). Changing hydrologic regimes may also compound the effects of changes in food availability. Outcomes of ongoing debate over water resources in the western U.S. could further impact hydrological regimes of important waterways used by sandhill cranes, such as the Platte Rivers in Nebraska where changing water depths and water velocities are important components of roosting habitat (Kinzel et al. 2009).

1.12.4.3. *Rocky Mountain Population, and Lower Colorado River Population.* Agricultural practices are changing (Krapu et al. 2004) and important food crops used by cranes, including thousands of hectares of small grain agriculture (particularly corn and milo) have recently been converted to cotton, soybeans, and chili peppers, Conservation Reserve Program (CRP) grasslands, or other crops little used by cranes. Continued residential expansion in e Idaho, w Wyoming, and sw Montana are negatively impacting important pre-migration staging areas (Drewien et al. 2008). Local alterations of hydrology, such as pumping groundwater for crop irrigation can lower the water table, diminishing surface waters, and leading to a loss of roosting sites (Winter 1988).

These changes can affect breeding areas, stopover areas, and wintering areas. For example, lowering of the water table in the San Luis Valley has resulted in the loss of foraging habitat (The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007). In another example, at Muleshoe National Wildlife Refuge in Texas, 53,968 ha of croplands surrounding the refuge were converted to CRP grasslands between 1986 and 2000 (CDL). Mean wintering crane numbers at Muleshoe National Wildlife Refuge for the years 1971 to 1984 were 57,743 (SD ± 26,767), but declined during the 1985 to 2000 period to 7,707 (SD ± 6,633). Similar declines in cranes wintering in the Pecos Valley, New Mexico occurred as corn was replaced with alfalfa and other crops (Montgomery 1997), but reversed when corn planting increased (Montgomery 2008).

1.12.4.4. *Central Valley Population and Pacific Flyway Population.* These populations face many of the same challenges as those encountered by the Mid-Continent, Rocky Mountain, and Lower Colorado River Populations (Meine et al. 1996b). For example, $>$ 95% of California wetlands have been destroyed or modified (Gilmer et al. 1982); only 115,000 ha remained in 1987 (Heitmeyer et al. 1989), challenging cranes to find suitable breeding, stopover, and wintering areas. Changes in agricultural practices in the California Central Valley (e.g., conversion from grain crops to vineyards and orchards, increased autumn tillage, stubble flooding, post-harvest burning) may result in food shortages in many California wintering locations (Littlefield 2002). Ongoing efforts by researchers in California, including Gary Ivey, will hopefully help clarify how changes agriculture are affecting wintering cranes in California.

1.12.5. Collisions with Stationary or Moving Objects.

1.12.5.1. *Power Lines.* Anthropogenic structures can lead to habitat loss even if the footprint of the structures themselves are relatively small. Overhead power lines and buildings can pose such a scenario for sandhill cranes. For more than six decades, sandhill crane mortality resulting from collisions with high voltage transmission lines has been documented. The first record was of 10 dead *G. c. canadensis* found by Walter J. Breckenridge near a line south of the North Platte River in Lincoln County, Nebraska on 28 March 1945 (Walkinshaw 1956). Since then mortalities have been documented in states ranging from California, Colorado, Florida, North Dakota, Oregon, Texas, and Washington.

Specific reports, in order of increasing number, are: 22 *G. c. tabida* on one foggy morning in the Central Valley of California in the mid-1980's (Schlorff 2005), 45 in south-central Nebraska from 1988 to 1990 (Morkill and Anderson 1991), 51 at a transmission line across the Platte River east of Kearney, Nebraska on 31 March 1981 (Windingstad 1988), 52 during one foggy afternoon near Mound Lake, Texas on 9 February 1978 (Tacha et al. 1979), and 90 in the San Luis Valley of Colorado from 1988 to 1991 (Brown and Drewien 1995). From 1980 to 1982, Faanes (1987) found 633 dead birds beneath a mix of 230kV and 400kV transmission lines in North Dakota; 9.8% were sandhill cranes. Drewien (1973) reported 37% of mortalities of *G. c. tabida* from the Rocky Mountain Population resulted from collisions with power lines. In California, collisions are the most common mortality factor for cranes wintering in the Central Valley. Generally, power line collision mortalities were associated with inclement weather (e.g., strong winds, fog, dust storms, blizzards), but collisions can also occur at night if roosting sites are disturbed naturally by predators, or unnaturally by waterfowl hunters arriving near roost sites in the predawn hours.

Entanglements with barbed-wire fences also have been recorded, primarily on breeding grounds. Of 135 deaths of color-marked *G. c. tabida* from the Rocky Mountain Population, eight (4.5%) died from collision or entanglement (Drewien, unpublished data.). Unusually, two Florida sandhill cranes that died from electrocution were found beside a barbed-wire fence which had conducted electricity from a lightning strike (Folk et al. 2001). Dozens of *G. c. pratensis* also are injured or killed annually on roads. Of 122 cranes assessed in Florida, 15 (12.3%) had been hit by vehicles (Folk et al. 2001).

1.12.5.2. *Wind Turbiness.* To date, only two collisions of sandhill cranes with wind turbines have been reported (Navarette and Griffis-Kyle 2013). However, only Navarette and Griffis-Kyle (2013) have deliberately conducted crane-focused research within a wind resource area. With numbers of cranes and wind turbines increasing, particularly in the migration corridor of the Mid-Continent Population, additional conflicts are likely to arise. Collisions may become more likely not only for sandhill cranes, but also for endangered whooping cranes (Navarette and Griffis-Kyle 2013).

1.12.6. HUNTING. Concerned with the potential extinction of sandhill cranes in the early 20^{th} century, the United States and Canada instituted a general closure of hunting in 1916 under the Migratory Bird Treaty Act. After 44 years (1916 to 1959) without legal hunting seasons, hunting was resumed in 1959 in Saskatchewan (Drewien et al. 1975), and sandhill cranes are now hunted in 2 Canadian provinces (Saskatchewan and Manitoba), 14 U.S. states, and in Mexico. Justification for the hunting program evolved from an experimental tool for reducing local crop depredation (Lewis et al. 1977) into a management strategy to regulate crane numbers more broadly. Over the years, as interest in sandhill crane hunting has increased, so have season lengths, number of crane hunters, and numbers of cranes harvested (Kruse et al. 2012). While illegal hunting may be ongoing, it is likely less common than it was in the 1960's and 1970's when cranes were regularly shot in the San Luis Valley of Colorado and the Central Valley of California (Littlefield and Ivey 2002).

The age structure of a population can be influenced by many processes, including hunting, if different aged birds are more or less vulnerable to harvest. Juvenile sandhill cranes are more susceptible to hunting (Johnson 1979, Tacha and Vohs 1984). Specifically, the use of decoys by hunters can double the percentage of juveniles harvested compared to hunting without decoys (Tacha and Vohs 1984), which may impact population structure. Hunting also can cause severe disturbance; Montgomery (1997) reported 50% of all cranes wintering in the Pecos Valley of New Mexico left because of hunter disturbance. Walkinshaw and Hoffman (1974), Crete and Toepfer (1978), and Littlefield (1986) reported autumn departures of sandhill cranes on the opening days of waterfowl or pheasant hunting seasons. While there is no evidence to suggest density dependence may be limiting populations, such that hunting mortality is compensatory, it is possible given that cranes are highly territorial on breeding grounds.

1.12.7. Hunting: Non-migratory Populations.

1.12.7.1. *Cuban Population.* Sandhill cranes are legally protected in Cuba, but people nevertheless hunt them for food (Fernandez Montaner 1968, Garcia Montana 1987).

1.12.7.2. *Florida Population.* The Florida Population is not legally hunted.

1.12.7.3. *Mississippi Population.* The Mississippi Population is not legally hunted.

1.12.8. Hunting: Migratory Populations. All migratory populations of sandhill cranes are harvested in at least part of their range. The level of hunting and likely the total impact of anthropogenic harvest on each population is variable. All migratory populations are managed by state and federal agencies are subject to the Migratory Bird Treaty of 1918.

1.12.8.1. *Eastern Flyway Population.* As a result of the dramatic increase in sandhill crane numbers in the Eastern Flyway Population, the Atlantic and Mississippi Flyway Councils developed a cooperative management plan to allow hunting for the first time in Kentucky (Department of the Interior Fish and Wildlife Service 2011) and Tennessee. The plan initiated an experimental three-year hunt in Kentucky starting in the 2011 to 2012 season. A maximum of 400 permits were issued for a 30-day season with a season limit of two birds per person (Kentucky Department of Fish and Wildlife Resources 2010). In Tennessee, the first seasons occurred in the fall and winter of 2013, with 400 permits issued and a seasonal bag limit of 3 birds per person (http://www.tn.gov/twra/sandhillhunt.shtml).

1.12.8.2. *Mid-Continent Population.* Hunting of the Mid-Continent Population mostly occurs in the Canadian provinces of Saskatchewan and Manitoba, and the plains states of North Dakota, Kansas, Oklahoma, and Texas. However, hunting seasons are also currently held annually in portions of Colorado, Montana, New Mexico, South Dakota, Minnesota, and Wyoming (Kruse et al. 2011). Nebraska is the only state within the Central Flyway that does not have a hunting season for sandhill cranes. Annual harvests of the Mid-Continent Population are generally increasing (Kruse et al. 2012). Harvests of the ec Canada-Minnesota and w Canada-Alaska subpopulations (see Distribution) are disproportionately high in some years, relative to other subpopulations (Krapu et al. 2011). For the Mid-Continent Population of sandhill cranes, an annual hunting mortality rate of 5% (25,000 cranes) was initially recommended (Sharp and Vogel 1992). For the period of 1985 through 1990, hunting mortality estimates were near or slightly above the 25,000 level. From 1991 through 2002, annual hunting mortality exceeded the objective in 11 of 12 years; the greatest estimated mortality was 38,957 in 1998. A mean of 22,691 cranes were annually hunted from 1980 through 1989, but the annual mean increased to 30,411 from 1990 through 1999, with 84% of the hunters from two states, Texas (53%) and North Dakota (31%; Sharp et al. 2003). For the Mid-Continent Population, crippling-loss rate (number lost/(retrieved + lost)) was greater than 16% in 1975, but has declined to < 10% in the last few years (Kruse et al. 2011). While the crippling-loss rate of sandhill cranes remains important for setting harvest rates, it is less of a concern in recent years due to increased hunter efficiency.

1.12.8.3. *Rocky Mountain Population.* Legal hunting of the Rocky Mountain Population began in 1981 and remained very limited with < 200 cranes harvested annually through 1985. Annual harvests have generally been increasing since, with harvests in 2009 and 2010 estimated at > 1,000 individuals (Kruse et al. 2012).

1.12.8.4. *Lower Colorado River Population.* Following an Environmental Assessment, the U.S. Fish and Wildlife Service allowed a small harvest (approximately 30 cranes), as long as the 3-year average of winter counts exceeded 2,500 (Kruse et al. 2012). Since this ruling, the 3-year average count exceeded 2,500 in 2009 and 2010, but not 2011 or 2012.

1.12.8.5. *Central Valley Population.* Sandhill cranes of the Central Valley Population are hunted for sport and subsistence in Alaska (Pacific Flyway Study Committee 2012).

1.12.8.6. *Pacific Flyway Population.* Sandhill cranes of the Pacific Flyway Population are hunted in Alaska and possibly Russia. Subsistence hunting occurs in Alaska, but is generally thought to be low. Between 1971 and 1981, sport hunting was considered to be a very small proportion of the total population (Pacific Flyway Study Committee 2012).

1.12.9. PESTICIDES. In the 1970's, crane studies from several regions found pesticides in substantial quantities. Lewis (1974) reported that cranes collected in southern Texas had high residues of heptachlor epoxide, perhaps accumulated from areas treated for fire ant control. High levels of heptachlor also were found in muck soils from vegetable growing regions in Wisconsin. High levels of DDT, DDE (a metabolite of DDT), dieldrin, and heptachlor were found in 11 cranes collected at a Jackson County, Oklahoma wintering area. In fact, heptachlor residues had the highest levels ever analyzed at the Denver Wildlife Research Center. Jackson County was the county in Oklahoma most intensively sprayed with pesticides, where heptachlor was used to protect wheat seeds from predation by root beetle larvae. From the Pacific northwestern states, Mullins et al. (1979) reported *G. c. tabida* eggs collected from Malheur National Wildlife Refuge, Oregon, and Bear Lake and Grays Lake National Wildlife Refuges, Idaho, all contained lead, mercury, and DDE. DDT was present in all 35 eggs assessed, except for one at Grays Lake and three from Bear Lake. Dieldrin occurred in five eggs collected from Camas County, Idaho, and three of 10 from Bear Lake. Seven of 10 eggs from Malheur, three of 10 from Bear Lake, and two of 10 from Grays Lake had mercury residues, with Grays Lake eggs containing significantly higher levels. Other pesticides occurring less frequently included benzene hexachloride (BHC) found in four

Malheur eggs (1-6.4 ppb), one egg from Bear Lake (2.6 ppb), and one from Camas County (34.5 ppb). Heptachlor was found in one Bear Lake egg (9.1 ppb) and Ronnel in one egg each from Bear Lake (85.3 ppb) and Camas County (34.5 ppb). All of 20 cranes collected in Idaho contained DDT and DDE in adipose tissue and feathers. Dieldrin occurred in adipose tissue of three, mercury in all brain and feather samples, 15 of 20 muscle tissue samples, 17 of 20 liver samples, and 17 of 20 kidney samples. Older breeding cranes had significantly greater amounts of DDT, DDE, and dieldrin than younger birds, whereas younger cranes had significantly more lead. Why lead levels were higher in young cranes has not been identified (Mullins et al. 1979).

1.12.10. OIL AND BIOTOXINS. Ingestion of refined oil is reportedly more toxic to birds than crude oil, though feather oiling can be a serious threat at crude oil spill sites (Fleming et al. 1982). In the playa lakes region of northwestern Texas, southeastern New Mexico, and western Oklahoma, open pits or tanks containing crude oil and oil field waste killed approximately 100,000 birds of various species annually (Flickinger 1981). This area has one of the greatest winter concentrations of *G. c. canadensis* in North America, and the potential exists for serious losses. Exclusion netting over open pits is critical to protecting wildlife in oil fields. Similar threats from northern Alaskan oil producing regions are not known, but few sandhill cranes occur there. However, proposed development in the Bristol Bay region of southwestern Alaska may pose a problem in the future as a large numbers of *G. c. canadensis* from the Pacific Flyway Population breed there.

Biotoxins have killed numerous cranes. Specifically, mycotoxins produced by fungi (e.g., Fusarium species) growing on waste peanuts have caused serious *G. c. canadensis* losses in some years. Cranes lost to biotoxins were first noted in the mid-1940's near Portales, New

Mexico. Though the causative agent was not identified, in February 1946, almost 95% of 174 cranes assessed had consumed peanuts from a recently plowed field, implicating myctoxins as the causative agent (Muleshoe National Wildlife Refuge files). Recurrent large-scale die-offs from mycotoxins on waste peanuts were first diagnosed in February 1982 in Gaines County, Texas, when over 500 sick and dead cranes were discovered. Approximately 5000 died in late January to early February 1985 in central Texas. A sample of these cranes was necropsied, and of 120 crane gizzards assessed, 95% contained peanuts (Nelson et al. 1990). Other sources of biotoxins also occur. For example, 30 sandhill cranes died from aflaticosis along the Texas coast during November and December 1979; moldy corn was the suspected source (Windingstad 1988).

1.12.11. Ingestion or contact with lead, plastic, or other objects. Little information is available on sandhill crane contact with foreign objects, except perhaps a few accounts of cranes ingesting lead. Folk et al. (2001) reported only three of 212 (1%) cranes assessed in Florida had consumed metal. Elsewhere, one *G. c. tabida* dying of avian cholera at Monte Vista National Wildlife Refuge, Colorado, in March 1984, was also suffering from lead poisoning, with five well-worn lead shots found in the gizzard. Lead poisoning was diagnosed for a moribund *G. c. canadensis* found near Grand Island, Nebraska, in April 1984; two lead shots and a lead bullet had been ingested (Windingstad 1988). Wallace et al. (1983) collected 125 cranes in Alaska, Canada, and two Texas sites, and found only one ingested lead shot (0.8%) in a crane collected in northwestern Texas. Less than 10 cranes diagnosed at the National Health Center at Madison, Wisconsin had lead contamination; two of these had ingested lead sinkers. Wallace et al. (1983) suggested that the insignificance of lead shot ingestion by cranes resulted from relatively low hunting pressure, as generally birds fed over widely dispersed areas, covering numerous separate grain fields, not concentrating at a few localized feeding sites.

Cranes in Florida have been found with a variety of foreign objects on their bills, such as a plastic wad from a shotgun shell, a toy tractor wheel, the core of a golf ball, a rubber o-ring, a rubber ball, and more commonly, shreds of plastic-mulch used on long rows of vegetable crops for conserving moisture and reducing weed growth; for firmly affixed objects, cranes can die without human intervention (Folk et al. 2001). Observed foreign objects in the western United States have been benign, generally consisting of dried cattle excretion accumulating on *G. c. tabida* bills as birds fed on invertebrates beneath the excretions. One crane died of starvation at Monte Vista National Wildlife Refuge in Colorado because an impaled shotgun wad on its mandibles prevented feeding (Drewien et al. 2000).

1.12.12. Stress. Corticosterone is the major adrenal steroid in the blood plasma of avian species. Corticosterone is often used as an indicator of stress in birds, and is suspected to affect overall health (Hadley 1996). *G. c. canadensis* of the Mid-Continent Population wintering in Mexico have higher corticosterone levels when occupying small and ephemeral wetlands compared to cranes occupying larger and more permanent water bodies (Llanes 2012).

1.12.13. Management.

1.12.13.1. *Conservation Status.* Sandhill cranes are the most abundant crane species on earth (Meine and Archibald 1996a). However, of the 6 subspecies, *G. c. pulla* in Mississippi and *G. c. nesiotes* in Cuba are classified as endangered, and protected under the U.S. Endangered Species Act.

The non-migratory Cuban Population is low but likely stable (Aguilera and Chavex-Ramierz 2010; Table 1.1), despite no national management plan. Until recently, limited information was available for the *G. c. nesiotes.* In 1997 a nesting ecology and productivity study was initiated on the Isle de la Juventud (Aguilera et al. 2005) to direct conservation actions where needed.

The non-migratory Florida Population appears to be declining (Nesbitt and Hatchitt 2008) and is of concern. The Florida Fish and Wildlife Conservation Commission recently creating an action plan intended to improve the conservation status of the Florida sandhill crane so the species is secure within its historical range (Dwyer 2013). To meet this goal, the state of Florida aims to maintain or increase habitat at or above 31, 200 km^2.

The non-migratory Mississippi Population is stable due to population augmentation from captive individuals and is managed according to a recovery plan under the Endangered Species Act. However, high allelic relatedness among wild and captive individuals (Henkel et al. 2012) likely limits *G. c. pulla* reproduction and thus the populations ability to increase without ongoing assistance. Maintenance of the *G. c. pulla* population has required regular infusions of captive-reared birds in normal years (Ellis et al. 1996), with additional management necessary after hurricane Katrina further impacted the wild population in September 2005.

The Eastern Flyway Population is increasing in numbers and distribution (Kruse et al. 2013); this population is managed according to a 2010 plan (Ad Hoc Eastern Population Sandhill Crane Committee 2010).

The Mid-Continent Population is generally stable (Kruse et al 2013) and is managed according to a 2006 plan (Central Flyway Webless Migratory Game Bird Technical Committee 2006).

The Rocky Mountain Population is also generally stable and is managed following a 2007 plan (The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007).

The Lower Colorado River Valley Population is small but stable (Kruse et al. 2013), although there is currently no management plan for this population.

The Central Valley Population and the Pacific Flyway Population have unknown population trends and are managed according to old plans (Pacific Flyway Council 1983, Pacific Flyway Study Committee 1997).

1.12.14. Measures proposed and taken.

1.12.14.1. *Habitat Loss.* Maintenance of essential habitats should be the primary conservation and management focus for all populations of sandhill cranes. Wetland conservation is particularly important in the ranges of non-migratory subspecies, and in staging and wintering areas of migratory subspecies. For example, fewer than 20 salt lakes in west Texas have historically provided roost areas for a large percentage of the Mid-Continent Population in winter; 12 of these lakes are now dry much of the time because nearby underground water mining for agriculture has dried associated freshwater springs. Lakes and wet-meadow areas associated with the North Platte and Platte River Valleys in Nebraska, where 80% of the Mid-Continent Population of cranes stage in spring, are essential for habitat conservation efforts in the Great Plains states. In the far west and southwestern states, several federal and state agencies and The Nature Conservancy have management programs specifically for sandhill cranes (e.g., Conboy National Wildlife Refuge (NWR), Washington; Malheur

NWR, Oregon; Modoc NWR, California: Grays Lake NWR and Bear Lake NWR, Idaho; Monte Vista NWR, Colorado; Bosque del Apache NWR, New Mexico; Cokeville Meadows NWR, Wyoming; Woodbridge Ecological Preserve, California; Sycan Marsh, Oregon; and Cosumnes River Preserve, California). Mississippi Sandhill Crane NWR, Mississippi, was established for the protection and welfare of the non-migratory *G. c. pulla*, and the Whooping Crane Maintenance Trust and the National Audubon Society manage for cranes in the Platte River Valley of central Nebraska.

Management areas for sandhill cranes in Canada and Mexico are not as widespread as in the U.S. Increased planting of corn for use as biofuel (to make ethanol) will benefit cranes, at least in the short-term, if traditional harvesting methods are used. However, because with current technologies, corn kernels require 29% more energy to produce than the ethanol produced from them (Pimentel and Patzek 2005), unless greatly subsidized it is likely this increased food source will be of short duration. Developing technologies that use corn cellulose instead of corn kernels to produce ethanol may allow a better return on investment. With this approach, planted hectares will remain above historical levels, particularly in areas were ethanol refineries exist (G. Krapu, pers. comm.), but because the entire corn plant is removed during harvest, waste corn availability will be reduced, as will any potential increase in food resources for cranes.

1.12.15. Collisions with Stationary or Moving Objects.

1.12.15.1. *Power lines.* Many avian species collide with power lines and other human structures (Sporer et al. 2013). Sandhill cranes are more likely to collide with power lines between feeding and roosting habitats because birds traverse these areas daily, typically at dawn and dusk when visibility is minimal (Bevanger 1994, Faanes 1987, Savereno et al. 1996, Wright et al. 2009). Mortality and injury are unlikely to affect large populations with good reproduction, but collision mortality can be biologically significant to local aggregations of birds. Despite ongoing debate, sandhill cranes are also used as a model species for Whooping Cranes (Morkill and Anderson 1991, Murphy et al. 2009, Navarrete and Griffis-Kyle 2013), where power line collision mortality is a more pressing concern (Lewis 1995).

Sandhill cranes have been documented colliding with power lines throughout North America during migratory movements and in their summer and winter ranges (Morkill and Anderson 1991, Stehn and Wassenich 2008). A combination of factors likely lead to collisions, including the visibility of power lines, particularly overhead shield wires (APLIC 2006), age of the bird, nocturnal flying, numbers of birds present, power line height, weather (e.g., wind speed and direction, precipitation), and disturbance (Faanes and Johnson 1992, Brown 1987, Ward and Anderson 1992, Brown and Drewien 1995). Juvenile birds have a higher probability of collisions than adults (Ward and Anderson 1992, Brown and Drewien 1995), perhaps due to lack of flying experience and familiarity with specific areas.

Most power line collisions occur with high-voltage transmission lines (Morkill and Anderson 1991, Tacha et al. 1979, Brown and Drewien 1995). Mitigation measures to reduce power line collisions include habitat management to reduce bird flights across power line corridors, management of human disturbance to reduce escape flights across power line corridors, placement of lines near tall trees or landscape features to encourage birds to fly above lines, and increasing the visibility of power lines with power line markers (Brown and Drewien 1995).

Power line markers have been used successfully in many areas. To reduce power line collisions, orange aviation balls were placed on problem lines at National Wildlife Refuges in Oregon and California where *G. c. tabida* breed. In Nebraska, yellow aviation balls reduced collisions by 54% (Morkill and Anderson 1991). This approach can pose of variety of challenges, however. First, one of the most important challenges is that because aviation balls are designed to alert pilots to overhead power lines near airports, over major roads, and at very long spans crossing deep valleys, installation of marker balls in other areas can lead to potential pilot errors (JFD). Second, the public sometimes objects to the increased visual profile of marked lines (JFD). Third, on California wintering areas local utility companies were reluctant to mark lines because the added weight of markers might result in the collapse of a line (R. Schlorff, pers. comm.).

An alternative strategy to marking lines with marker balls is to install avian flight diverters specifically designed to be noticeable by birds, but not distracting to pilots or the public. Early approaches to this strategy involved using spiral vibration dampers to increase the diameter, and thus the visibility of distribution lines and overhead shield wires on transmission lines. In Colorado, collision mortality was reduced 61-63% with this approach (Brown and Drewien 1995), but dampers caused wear on distribution wires and were removed after the study. Numerous products are now available that appear to minimize engineering concerns (wire wear, wind loading, ice loading), including materials which glow in the dark. Unfortunately, installation often must be conducted by a team in a helicopter, an expensive and high-risk task. Because of this, the relative durability and effectiveness of competing markers has rarely been evaluated (Sporer et al. 2013).

To alleviate future collisions and conflicts, federal and state agencies should provide input into the planning and placement of utility corridors (CDL). In southeastern Oregon, for example, a new 500 kV transmission line was proposed to cross the Silvies River Floodplain where approximately 70 *G. c. tabida* pairs nested. Consultation and subsequent discussion with the Oregon Public Utilities Commission resulted in the line being constructed 6 km north, likely preventing serious losses at one of the most important migratory and breeding bird use areas of the Pacific Flyway Population (CDL). Substantial increases in power lines associated with "green energy" technologies (e.g. wind turbine and solar farms) throughout the primary migration routes of the Mid-Continent Population and whooping crane migratory corridor could increase mortality for both species (CDL). Given the potential for both solar and wind renewable energy development across the United States, this represents a critical piece of missing information that should be resolved quickly.

1.12.16. Hunting. All migratory populations are currently subject to hunting, with rules and regulations specific to each population. A cohesive continent-wide approach may be most successful in the long term.

1.12.17. Pesticides. Pesticide management has not been specifically described for sandhill cranes. Presumably, measures designed to protect ecological systems in general will be sufficient to protect cranes.

1.12.18. Oil and Biotoxins. Threats to sandhill cranes and other birds from open pits and tanks containing crude oil and oil field waste have been reduced or eliminated in the southwestern United States (especially in Texas) since the mid-1990s. Consultation between the U. S. Fish and Wildlife Service and the Texas Railroad Commission resulted in major regulation changes, requiring oil companies to cover small pits and tanks, and place netting over mid-sized pits. Larger pits were required to have scare-devices to keep birds from landing; most oil companies elected to use netting because netting is consistently effective, while fright devices are not. Fines if tanks and pits were not protected were set by the railroad commission at $10,000 per bird (R. Sweeney, pers. comm.). For protection against biotoxins, fields contaminated with high quantities of the mycotoxin producing fungi Fusarium, should be deeply plowed. Plowing makes contaminated waste peanuts or grain unavailable for cranes and other wildlife; if a field cannot be plowed, hazing has been proposed.

1.12.19. INGESTION OR CONTACT WITH LEAD, PLASTIC, OR OTHER OBJECTS. Sandhill crane mortalities from ingestion or contact with foreign objects are not frequently documented. Items firmly affixed to cranes mostly have been reported from Florida where affected individuals were captured and the objects removed (Folk et al. 2001). Lead ingestion (and subsequent poisoning) was noted as insignificant for sandhill cranes in the early 1980's (Wallace et al. 1983); however lead (and boron) contaminants still were being reported from cranes in Nebraska in the early 1990's (Fannin 1992). Natural resource agencies should periodically analyze salvaged crane carcasses to determine if metals, pesticides, and other contaminants are present (SAN).

1.12.19.1. *Nuisance Behavior.* To address the problem of nuisance behavior caused by feeding (and thereby taming) Florida sandhill cranes, the Florida Fish and Wildlife Conservation Commission in 2002 passed a rule prohibiting the intentional feeding of sandhill cranes. This rule was a result of citizen complaints that intentional feeding altered the natural feeding behavior of cranes, posing a threat to human safety.

1.12.19.2. *Capture and marking.* Capture and marking can change behavior and cause mortality. Trapping and marking caused mortality of 3.9% of captured individuals in Florida where oral tranquilizers were used (SAN), and 4% of captured individuals in Wisconsin where the oral tranquilizer Alpha-chloralose was used (Hayes et al. 2005, Hartup et al. 2014). When canon nets were used, 6.9% mortality occurred in Nebraska (Wheeler and Lewis 1972), and 15% mortality occurred in Texas (Tacha et al. 1982). By contrast, low mortality (0.26%)

occurred capturing mainly flightless young by hand on breeding areas in Rocky Mountain states (Drewien et al. 2000). Mortality associated with oral tranquilizers can be reduced if capture attempts are not made when temperatures are below 0° C.

From 1969 through 1994, greater than 1,900 *G. c. tabida* were captured in Colorado, Idaho, Montana, Utah, and Wyoming, by running after flightless young and the occasional adult on the ground (60.3%), from a helicopter (25.1%), using night-lighting (13.1%), and by rocket-netting (Drewien and Clegg 1992). With the exception of rocket-netting, cranes did not vacate capture areas. Mortality associated with rocket netting can be reduced by placing rockets and launching platforms 60-75 cm off the ground. Placement of angle-iron launchers can also affect mortality. Generally, to reduce injury and mortality, the central rocket should be perpendicular to the net, with the outside two rockets about 2.5 m from center and angled toward corners of the net; launchers should be aimed 5° above horizontal. Higher rocket netting mortality results when two sets of nets are set up in close proximity facing each other and fired simultaneously.

Cranes are often marked with legs bands, and sometimes with patagial tags and neck collars. Colored plastic leg bands have been used extensively with no apparent adverse affects on behavior or survival (Hoffman 1985, RCD, CDL). Patagial tags can influence post-release behavior by delaying migration (Tacha 1979). However, given that few individuals appear to be affected, patagial tags appear mostly reliable; affected cranes should be re-caught and their tags removed. Neck collars can cause mortality when the collar length is short enough for a cranes bill to be lodged inside (Bennett 1992), but do not otherwise adversely affect behavior (Drewien 1973). As such, marking with neck collars generally seems safe, but care should be taken to ensure the collar cannot slip up and down the neck. All tags used on cranes are known to fail and detach and thus do not persist for the life of the animal.

1.12.19.3. *Crop Damage.* Sandhill cranes are managed at the population level to minimize crop damage (Central Flyway Webless Migratory Game Bird Technical Committee 2006, The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007). Localized damage to crops, however, can be a substantial concern. Fall migrants readily feed in agricultural fields where small grains and waste corn occur. During a wet fall when farmers are unable to harvest prior to September, cranes can consume economically critical proportions of crops. Spring damage to crops can also occur. In the first 2-3 weeks of growth, cranes will consume the gymnosperm of sprouting corn if the gymnosperm is available in the seed. While predicting specifically where and when crop damage may occur is difficult because cranes are highly mobile, crop damage will generally be higher where preferred foods occur in close proximity to roosting areas. In Wisconsin, the average loss of corn in areas of sandhill crane habitat is approximately 20%, but can be as high as 50 to 60% in localized areas (Schramm et al. 2010). Measures to reduce crop damage have commonly used a combination of scare and harassment techniques (e.g., explosive devices, aircrafts, scarecrows, dogs, and nets; The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007) along with lure crops. Such measures are likely to provide only temporary relief as cranes habituate quickly to hazing or simply move to an adjacent location (Sudgen et al 1988). Measures to reduce crane damage to grain crops, such as corn, also include treating seeds with anthraquinone, a non-lethal bird repellent. In one experiment comparing untreated and treated whole-kernel corn, crane pairs consumed approximately 9 times more untreated corn (Blackwell et al.

2001). As crane populations continue to expand, prevalence and severity of crop damage, increased public demand for a hunting seasons, and increased demand for depredation control measures are likely.

Actions taken to reduce crop damage are likely a function of cultural and economic values. Because sandhill cranes range over a large geographic expanse encompassing a large diversity of local cultures and societies, attitudes towards sandhill cranes are likely to vary considerably. In one major migratory stopover, the San Luis Valley, farmers attitudes toward viewing cranes on their own property was related to the perceived crop depredation caused by the cranes (Laubhan and Gammonley 2001). The value of viewing sandhill cranes was higher when considering seeing them somewhere in the San Luis Valley. Because sandhill cranes are so conspicuous, realized depredation can be much lower than perceived depredation. For example, cranes in Utah and Wyoming were perceived to have caused severe damage where realized damage was less than 3% of the total crop (McIvor and Conover 1994b). In c and n Mexico, farmers do not consider wintering *G. c. canadensis* of the Mid-Continent Population to be a problem despite depredation on crops (Llanes 2012). However, direct competition between farmers and cranes for water resources, coupled with tension over perceived crop damage, may lead to increased conflict in the future.

1.12.19.4. *Human Health.* With sandhill cranes often using farm fields, there is some risk of crop contamination leading to food-borne illnesses. For example, in sc Alaska, a community-wide outbreak of campylobacteriosis (an infection producing painful cramps, fever, and diarrhea) was caused by contamination of peas by feces from large aggregations of sandhill cranes (Gardner et al. 2011).

1.13. APPEARANCE

1.13.1. MOLTS AND PLUMAGES. Plumage descriptions and colors follow Ridgway and Friedmann (1941), and Smithe (1975, 1981).

1.13.1.1. *Hatchlings.* Sandhill crane chicks are ptilopaedic at hatching (almost entirely covered with down). Their downy plumage is golden brown, darker on the rump and mid-back, fading to a pale dull buffy to pale tawny underneath. This soft counter shading camouflages young birds among the dry grasses commonly found around their nests.

1.13.1.2. *Juvenal plumage.* Overall, juvenal plumage has a mottled brown and gray appearance through the first fall and into the winter. As hatchlings develop into juveniles, the upper wing coverts, back feathers, and feathers on the upper hind neck remain edged with a rusty cinnamon-rufous, retaining some of the camouflaging shades of hatchlings. The crown is covered with a downy orange-brown to salmon feathering. Some juvenal feathers, especially the outer greater primary coverts and nape feathers, persist through the first year, mixing with the first definitive basic plumage in individually unique patterns of rust and grey.

By November-January, when in mixed juvenal and definitive basic plumage, juvenile characteristics can be difficult to distinguish. *G. c. tabida* retain their unique crown, nape and secondary covert characteristics into January when individuals are 6-8 months of age (Drewien et al. 1995). *G. c. canadensis* juveniles of the Mid-Continent Population retain crown and nape characteristics into January and February (Tacha and Vohs 1984), and *G. c. rowani* juveniles are difficult to distinguish as early as November (Lewis 1979a). A close examination of feathers when a bird is in hand may allow one to distinguish older juveniles from adults, but this is not 100% accurate (Nesbitt 1985). Beyond the first year, wing feather replacement pattern can sometimes distinguish immatures from adults (Nesbitt and Schwikert 2005). The inability to distinguish age classes makes it logistically infeasible to ascertain the age structure of sandhill cranes by more than age ratios of juveniles (<1 year old) to adults.

1.13.1.3. *Definitive Basic Plumage.* Overall plumage is generally pale mouse gray to ashy slate gray, the occiput (back of the head) and nape is pale mouse gray, though the occiput tends to be darker in *G. c. pratensis* than most other subspecies. Cheeks are paler than the occiput, blending from a pale gull-gray to white on the chin and upper throat. The extent and consistency of the coloring of the cheek, chin, and upper neck varies among individuals. Flight feathers are dark neutral gray with paler shafts; in *G. c. canadensis*, shafts tend to be as dark as the vane. Breast, abdomen, back feathers, and upper wing coverts are margined with a pale gull-gray. Plumage becomes colored adventitiously for camouflage from predators when located in areas of water, vegetation, and mud. Sandhill cranes also intentionally rub their plumage with soil (Taverner 1929, Drewien 1973, Nesbitt 1975b), which causes variation in plumage color ranging from drab-clay to cinnamon-rufous (ferric oxide). Stained feathers occur anywhere below the mid-neck but are particularly apparent among the primary and secondary wing coverts and upper breast feathers. Extent of light feathering on the cheek varies among individuals after definitive basic plumage is achieved; 43% of individuals have scattered white feathers in the occiput and in some (7%) form a solid line of white feathers (Nesbitt and Schwikert 1998).

1.13.2. BARE PARTS.

1.13.2.1. *Bill, Forehead, Lores and Anterior Crown.* At hatching the bill is flesh colored but darker toward the tip. The egg tooth is lost within two weeks, though a light tip persists into week 4 or 5. The adult bill is dark drab gray fading to an olive gray in the mid-mandibular area.

At hatching, the forehead, lores and anterior crown are covered with an ochraceous-salmon colored down. Young maintain a feathered crown until they acquire definitive basic plumage. The unfeathered crown is covered with dull reddish to begonia rose pappillose skin of adults. The pappilli are scattered, dark, short, hairlike bristles. This bare crown area can be extended and the color intensified during episodes of aggressive or sexual behavior.

1.13.2.2. *Iris.* At hatching, eyes are dark raw amber. By 18 months, the eye color of individual adults differs from buff-yellow and orange-yellow to spectrum orange, chrome orange and flame scarlet. Most are chrome orange or flame scarlet (Nesbitt and Schwikert 1998).

1.13.2.3. *Legs and feet.* At hatching, legs and feet are yellowish. In adults, legs and feet are very dark olive to dull greenish black. Toe nails are consistently black.

1.13.3. SCHEDULE AND ORDER OF MOLT. Juvenal plumage begins to replace natal plumage 4 to 5 wk after hatching, starting with the remiges, then the upper wing coverts and dorsal feathers in the inter-scapular region. At 8 wk, juvenile contour plumage is almost completely erupted though some down remains on the head, neck, thighs, belly, and at the base of the tail. By wk 10, remiges are completely developed, and by wk 13 or 14 juvenile contour feathering is complete, though some feathers are still downy-tipped. The last of the natal down to be lost is from the head and upper neck.

Acquisition of the definitive basic plumage follows the first prebasic molt which begins after the attainment of the juvenile remiges and continues throughout the first year. In migratory subspecies, the prebasic molt is suspended during migration but resumes once the birds arrive on wintering grounds. The last non-flight feathers to be replaced (after the first full year of life) are on the nape and wings (e.g., the upper greater primary coverts; Lewis 1979b, Tacha and Vohs 1984, Nesbitt and Schwikert 2005). In breeding birds, the prebasic molt begins with the remiges after the first clutch hatches (Fig. 5). If the birds begin nesting late or renest following the loss of the first clutch, molting of the flight feathers may commence before the eggs hatch, and cast-off remiges may be found at the nest site. Non-breeders typically begin the prebasic molt of remiges before breeding birds. Replacement of remiges requires 3 or 4 yr to complete and proceeds from several foci (Lewis 1979b, Layne 1981, Nesbitt and Schwikert 2005). In *G. c pratensis*, median date for ecdysis of flight feathers was 2 June and median date for endysis of flight feathers was 29 July, continuing through early November. Growth of individual wing feathers requires 45 to 70 days to complete (Nesbitt and Schwikert 2008). Some individual *G. c. tabida* of the Central Valley Population become annually flightless during wing molt (Littlefield 1970), which may result from a latitudinal or altitudinal compression of molt period with concomitant acceleration in remigial ecdysis.

1.13.4. Geographic Variation. Appearance among regional populations is generally similar. The non-migratory population of *G. c. pulla* appears “much darker” than other populations (Aldrich 1972) and other non-migratory populations appear darker than birds of the Eastern Flyway Population (Peters 1925). There is a general increase in body size from northern to southern latitudes (see Measurements); arctic nesting cranes are the smallest, Rocky Mountain and other western/northern U.S. nesting birds are the largest. Cranes from central Canada and the non-migratory populations are of intermediate size.

1.14. Measurements

Measurements of mass and length generally increase from north to south (Table 3.4). One exception to this is that the legs of *G. c. pratensis* are longer than eastern nesting *G. c. tabida* (Nesbitt et al. 1992). Wing chord measurements have often been reported but once basic plumage is acquired, each primary is replaced only every third or fourth year. Therefore, wing length is more a function of feather age than subspecies or sex (Nesbitt and Schwikert 2005). Additional published information on sandhill crane measurements would certainly lead to a better understand geographic and subspecies related variability.

1.15. Priorities for Future Research

1.15.1. Terminology. Literature describing sandhill cranes can be confusing partly because identifying population membership and subspecies can be difficult depending on the location and timing of a study, and partly because apparently inconsistent definitions of populations make the scope of inference difficult to identify for some studies. Future research may help minimize confusion by clearly defining the population(s) and subspecies under study, ideally based on genetic analyses (e.g., Rhymer et al. 2001, Petersen et al. 2001, Glenn et al. 2002, Petersen et al. 2003, Jones et al. 2005a, 2005b, 2005c, Henkel 2009), each time results are published.

1.15.2. Populations. Despite sometimes confusing definitions, managing cranes at the population level has been a consistently successful approach for resource managers. This strategy worked particularly well when sandhill cranes were poorly understood, numbers were low, and conservation and management focused on breeding areas. As numbers and knowledge increased, breeding populations began to overlap, and wintering areas were identified where populations apparently always overlapped. These advances suggest that expansion from population level foci to a continent-wide focus may be the next important step in managing sandhill cranes. Particularly as hunting at stopover and wintering areas becomes more common, the implications of hunting mortality need to be correctly applied to all affected groups regardless of historical definitions of populations. A useful resolution of group membership (population, sub-population, regional population, local area population) will ultimately depend on the priority and scope of individual management agencies.

Perhaps the most important avenue for future research on sandhill cranes is the continued application of modern genetic tools (e.g., Rhymer et al. 2001, Petersen et al. 2001, Glenn et al. 2002, Petersen et al. 2003, Jones et al. 2005a, 2005b, 2005c, Henkel 2009) to investigate questions regarding relationships between populations and subspecies. In concert with implementation of genetic tools, future research should continue to investigate the movements of sandhill cranes where the population they belong to is unresolved, as in Krapu et al (2011). Arbitrary distinctions between populations and subpopulations should be identified and addressed, and practical advantages of additional divisions (i.e., subpopulations), should be made clear by recognizing spatial and temporal separation of individuals in the breeding, staging, and wintering areas. Gaps in knowledge are particularly apparent for cranes breeding and migrating along the western edge of North America, and for cranes wintering in Mexico where very little is known regarding the separation or overlap of different breeding populations.

A major gap in our understanding of populations and subspecies of sandhill cranes is in the Pacific Flyway. Birds wintering in Californias Central Valley appear to migrate to breeding areas included in the Mid-Continent Population, the Central Valley Population, and the Pacific Flyway Population. There is very little evidence to support identifying birds which breed in Alaska and British Columbia as a separate population from those breeding in Washington, Oregon, and California. Rather, if one considers *G. c. rowani* as a clinal gradient of body size between the small *G. c. canadensis* and the large *G. c. tabida*, then these birds appear to be all from a single population, in a genetic sense. Future research should investigate relatedness of cranes breeding from north to south along the west coast of North America to help identify true differences in populations. Results of more detailed information on movement among groups of birds will help to support, explain, or provide background to the results of genetic analyses. The two approaches together will likely facilitate movement toward a unified continent-wide conservation and management strategy.

The Mid-Continent Population is currently managed as a whole, but Tacha et al. (1984) proposed the Mid-Continent be divided into a Gulf Coast subpopulation and a Western subpopulation for management. This proposal was based on observations of distinctly different migration routes and wintering grounds for the two groups (Tacha et al. 1984), and is supported by the finding that there is known genetic exchange among the two groups (Krapu et al. 2011). A competing proposal, based on breeding-ground affiliations, winter use areas, disproportional harvest, and use of fall staging areas, Krapu et al. (2011) recommended managing the Mid-Continent population in four subpopulations: 1) east-central Canada-Minnesota, 2) west-central Canada-Alaska, 3) western Alaska-Siberia, and 4) northern Canada-Nunavut. Future research should continue to be used to inform our understanding of the relative merits of these two proposals.

1.15.3. HABITAT. Perhaps the single greatest threat to sandhill cranes appears to be loss of non-breeding habitat, i.e., migratory stopover sites and wintering areas. Cranes depend on very few widely scattered critical migratory stopover and wintering areas. If major habitat changes occur in those areas, progress that has enabled the success of current conservation and management strategies, and allowed populations to increase to safely hunted levels, may be reversed. For all but the Eastern Flyway Population, changing practices on private agricultural lands, including shifts from grains to other crops and shifts in harvesting strategies, threaten to substantially reduce the forage that cranes have come to rely on since food resources in their historical habitats was lost when North American prairies and grasslands were converted to agriculture. The impacts of changing human activities on the landscape present immediate challenges to cranes. Study of the effects of these changes in light of ongoing climate change and wind energy development, and the expense of creating new habitat will be particularly important in creating long-term conservation and management strategies.

1.15.4. GENERAL ECOLOGY. Surprisingly, given the level of effort invested in sandhill crane conservation and management, some basic biology has not been published outside the Mid-Continent Population. Specifically, very little quantitative information is available to describe courtship behavior and mate selection criteria, dancing outside of the breeding season, or even time budgets. Difficult questions, such as investigations of potential costs and benefits of flocking (as in Krause and Ruxton 2002, Dwyer 2010), survival of non-breeding cranes or survival of cranes of any breeding status during non-breeding seasons (as in Dwyer et al. 2012b), and detailed ecological study of non-breeding birds (as in Dwyer et al. 2013) are completely unexplored. General ecological studies do not always have clear conservation or management implications initially, but provide critical foundations and insights to sound long-term management plans. Incorporating general ecological research into ongoing studies should be a priority during future efforts. The Eastern Flyway Population has recently expanded eastward from New Jersey to Maine. No data other than observations of occurrences are available from those areas. Future research should explore whether the annual cycles and other ecological aspects of those birds is consistent with the rest of the Eastern Flyway Population.

1.15.5. COLLISIONS WITH ANTHROPOGENIC STRUCTURES. Sandhill crane collisions with anthropogenic structures, particularly transmission power lines, have been a substantial concern since at least 1987 when 62 cranes were reported to have collided with power lines in North Dakota (Faanes 1987). Concerns are likely to persist, particularly because a first record of two sandhill crane collision mortalities involving wind turbines was recently published (Navarrete and Griffis-Kyle 2013). Interactions between cranes and transmission power lines near wind resource areas will be important because new transmission lines are often constructed to link wind resource areas to the national power grid. Collision management also will continue to be important partly for sandhill cranes themselves, and partly because sandhill cranes serve as models of collision risk for whooping cranes (Morkill and Anderson 1991, Murphy et al. 2009, Navarrete and Griffis-Kyle 2013).

Numerous devices are available to help increase the visibility of power lines for birds, but studies of their relative effectiveness for cranes and of the durability of line markers have largely been precluded by cost. Resource managers should collaborate with utilities to share the financial burden of testing these devices for the benefit of all stakeholders. Collision is typically associated with crepuscular movements (Faanes 1987, APLIC 2006). This has lead manufacturers to develop collision mitigation devices which glow-in-the-dark. Evaluation of the costs and benefits of installing glow-in-the-dark line markers should be a priority in areas where collision risks are known.

High rates of collision are not unique to sandhill cranes. In the U.S., whooping cranes also are impacted by power lines (Miller et al. 2010, Folk et al. 2013), as are sarus cranes (*Grus antigone*) in Asia (Sundar and Choudhury 2005), blue cranes (*Anthropoides paradiseus*) in South Africa (Shaw et al. 2010), ecologically similar white storks in Europe (Garrido and Fernndez-Cruz 2003), and bustards in Africa (Jenkins et al. 2011). Future research should compare studies of collision mortality among these species to identify whether solutions implemented to protect some might be adopted elsewhere to protect others.

1.15.6. SURVIVAL. Collision is not the only source of mortality for sandhill cranes, but other than hunting, little is known of agents of mortality. Survival from post-hatching to fledgling is poorly understood because cranes often breed in remote areas. Mortality is primarily attributed to predation, but how predation pressure varies across populations, subspecies, habitats, and seasons is unknown. Survival of non-breeding individuals is poorly understood because these individuals appear to wander widely, making them difficult to track.

1.15.7. POPULATION MODELING INFORMING CONSERVATION AND MANAGEMENT ACTIONS.

There have been few attempts at empirical or theoretical modeling of sandhill crane population dynamics. There is a need to integrate the currently available data to 1) better understand crane population dynamics by population, and 2) understand the information gaps that could motivate future studies and will aid in future population modeling. A project is underway to do just that for the Rocky Mountain Population of sandhill cranes (pers. comm, Gerber, B.). However, there is also the need to do the same for all other sandhill crane populations, especially the migratory and hunted populations. General information gaps for the Rocky Mountain population, includes estimates of true population size, current annual survival (post 1992), spatial and age-specific variation in fecundity, movement phenology from the breeding to staging grounds, and age structure. Population level information on migratory species is often logically and financially challenging. However, new technologies, including unmanned aerial vehicles (UAV) and satellite-transmitters could significantly help in reducing information gaps, once these technologies become financially viable.

1.16. Tables and Figures

Table 1.1. Non-migratory sandhill crane populations and defining characteristics

Population	**Cuban**	**Florida**	**Mississippi**
Abbreviation	CP	FP	MP
Sub-Populations	none	none	none
Subspecies[1]	*G. c. nesiotes*	*G. c. pratensis*	*G. c. pulla*
Primary Breeding Area	Cuba	FL	Jackson County, MS
Secondary Breeding Area	none	none	none
Primary Wintering Area	Cuba	FL	Jackson County, MS
Secondary Wintering Area	Cuba	GA	Jackson County, MS
Overlapping Breeding Pop.	none	none	none
Overlapping Wintering Pop.	none	EFP	none
Current Pop. Trend	stable[2]	declining[3]	stable/increasing due to augmentation [4]
Recent Pop. Estimates	526 (2002)[2]	4594 (2003)[3]	105 (2012)[4]
Status[5]	E	P	E

[1] Colloquial nomenclature: Cuban Sandhill Crane (*G. c. nesiotes*), Florida Sandhill Crane (*G. c. pratensis*), Mississippi Sandhill Crane (*G. c pulla*).

[2] Aguilera and Chavex-Ramierz 2010

[3] Nesbitt and Hatchitt (2008)

[4] Henkel et al. 2012 and see Demography section

[5] E = protected under the federal Endangered Species Act, P = not subject to recreational hunting.

Table 1.2. Migratory Sandhill Crane Populations and Defining Characteristics

Population	**Eastern Flyway**	**Mid-Continent**[2]	**Rocky Mountain**	**Lower Colorado River Valley**	**Central Valley**[3]	**Pacific Flyway**[3]
Abbreviation	EFP	MCP	RMP	LCRVP	CVP	PFP
Sub-Populations	none	Gulf Coast, Western	none	none	Northern, Southern	none
Subspecies[1]	*G. c. tabida*	*G. c. tabida* *G. c. canadensis* *G. c rowani*	*G. c. tabida*	*G. c. tabida*	*G. c. tabida* *G. c. rowani?*	*G. c. canadensis* *G. c. rowani?*
Primary BA	Great Lakes area	Arctic & Subarctic	Rocky Mtns	ne.	BC, CA, NV, OR, and WA	Coastal AK
Secondary BA	Atlantic Coast	none	sw. Alberta	ID, OR, UT	none	AK and BC
Primary WA	FL to IN and TE	TX & n. Mexico	NM	AZ and CA	CA- Central Valley	CA- Central Valley
Secondary WA	s. Ontario	AZ, KS, NM, OK	N. Mexico, AZ, and CO	none	sw. WA	CA- Central Valley
Major Stopover Area	IN, TN	NE, CO	CO	NV	WA, OR	BC, WA
Overlapping Breeding Pop.	MCP	EFP	LCRVP likely	RMP and CVP likely	PFP, LCRVP likely	MCP, CVP
Overlapping Wintering Pop.	FP	RMP	MCP	none	PFP	CVP
Current Pop. Trend	increasing[4]	stable[4]	stable[4]	stable[4]	unknown	unknown
Recent Pop. Estimates	87,796 (2012)[4]	356,742 (2012)[4]	15,417 (2012)[5]	3,079 (2013)[4]	13,940 (2000)[6]	25,000[7]
Status[8]	H	H	H	H	H	H

[1] Colloquial nomenclature: Greater Sandhill Crane (*G. c. tabida*), Lesser Sandhill Crane (*G. c. canadensis*), Canadian Sandhill Crane (*G. c rowani*).

[2] This population is sometimes referred to as the Mid-Continent population "complex" in the literature.

[3] It is unclear whether the coastal nesting *G. c. rowani* belong to their own population, or to either the Pacific Flyway of Central Valley Population.

[4] Recognized as an index and not a total population estimate, Kruse et al., 2013.

[5] Recognized as an index and not a total population estimate, Central Flyway Council.

[6] West Coast Crane Working Group, 2000.

[7] Littlefield and Thompson 1982.

[8] H = subject to recreational hunting.

Table 1.3. Grain consumption by Sandhill Cranes

Location	Season	Item	% Volume or dry weight	Source
Saskatchewan	Fall	Wheat	93	Stephen (1967)
		Wheat	95	Tacha et al. (1985a)
KS, OK, TX	Fall	Sorghum	48	Lewis (1974)
		Wheat	40	
ND	Fall	Wheat	52	Madsen (1967)(a)
		Barley	36	
		Oats	15	
		Corn	12	
KS, OK	Spring	Sorghum	95	Lewis (1974)
NE	Spring	Corn	97	Reinecke and Krapu (1986)
		Corn	98	Iverson et al. (1982)
		Corn	89	Lewis (1979b)
Saskatchewan	Spring	Wheat	99	Iverson et al. (1982)
AK	Spring	Barley	99	Iverson et al. (1982)
NM	Winter	Corn	87	Walker and Shemnitz (1987)
OK	Winter	Sorghum	94	Lewis (1974)
AZ	Winter	Corn	99	Perkins and Brown (1981)
TX (West)	Winter	Sorghum	97	Iverson et al. (1982)
TX (South)	Winter	*Cyperus*	50	Guthery (1975)
		Nymphara	9	
		Sorghum	7	
		Sorghum	42	Lewis (1974)
		Rice	21	

TABLE 1.4. Mass (kg) and linear dimensions (mm) of Sandhill Cranes by subspecies and sex (sample size): Mean ± SD.

	G. c. canadensis[2]		***G. c. rowani***[2]		***G. c. pratensis***[3]		***G. c. tabida***[2]	
	Females (17)	**Males (31)**	**Females (33)**	**Males (51)**	**Females (34)**	**Males (34)**	**Females (10)**	**Males (11)**
Mass (kg)[1]	3.5 ± 0.3	4.0 ± 0.3	4.1 ± 0.3	4.8 ± 0.4	4.1 ± 0.3	4.7 ± 34.0	4.5 ± 0.4	4.9 0.4
Exposed culmen (mm)	92.0 ± 5.2	97.3 ± 3.9	114.1 ± 3.9	119.7 ± 5.9	98.8 ± 4.23	103.9 ± 4.2	120.4 ± 2.9	131.8 ± 5.0
Tarsus (mm)	179.2 ± 10.8	187.5 ± 14.4	217.0 ± 7.6	230.6 ± 9.5	247.1 ± 12.0[4]	265.9 ± 10.1[4]	228.3 ± 6.3	236.5 ± 8.3
Longest toe (third) (mm)	73.4 ± 4.8	75.4 ± 3.2	83.3 ± 3.7	86.4 ± 3.2	N/A	N/A	84.5 ± 2.6	87.2 ± 2.5
Tail length (mm)	159 ± 6.7	168.0 ± 6.5	179.8 ± 6.0	190.2 ± 7.4	N/A	N/A	184.1 ± 6.2	196.6 ± 4.5

[1] Measurement of G. c. pulla and nesiotes of equivalent sample size not available.

[2] Johnson and Stewart 1973.

[3] Nesbitt et al. 1992.

[4] Nesbitt and Moore unpubl. data.

FIGURE 1.1. Sandhill Sonata, by Linda Hunter. Used with permission of the artist.

Figure 1.2. Adult sandhill crane flying at Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico in January 2011. Photo credit: Terry Cacek.

FIGURE 1.3. Adult sandhill cranes in a shallow marsh. Photo credit: William L. Newton.

FIGURE 1.4. A family unit of the subspecies *Grus canadensis tabida* (adults on both ends with two juveniles in the middle) flying to a foraging site in the San Luis Valley, Alamosa County, Colorado in October 2011. Photo credit: Brian D. Gerber.

FIGURE 1.5. Greater Sandhill Cranes (*Grus canadensis tabida*) flying to an evening roosting site during a migration stopover in the San Luis Valley, Alamosa County, Colorado in October 2011. Photo credit: Brian D. Gerber.

FIGURE 1.6. Adult Florida sandhill crane (*G. c. pratensis*) from Venice, Florida in April. The large bill of this species is well-suited to an omnivorous diet - insects, reptile and amphibians, nestling birds, small mammals, seeds of various plants, and berries. Photo credit: D. McNicholas.

Figure 1.7. Greater sandhill crane (*G. c. tabida*) at Bosque Del Apache, Socorro County, NM, January 2011. Photo credit: Norm Smith.

FIGURE 1.8. Sandhill cranes of the Mid-Continent Population flying over the Platte River during spring migration, Buffalo County, Nebraska in March 2013. Photo credit: Brian D. Gerber.

Figure 1.9. Sandhill cranes of the Rocky Mountain Population loafing in a field while stopped in the San Luis Valley, Alamosa County, Colorado in October 2011. Photo credit: Brian D. Gerber.

Figure 1.10. Sandhill cranes foraging near wind turbines in High Plains of Texas, winter 2010. Photo credit: Laura Navarrete.

FIGURE 1.11. Sandhill cranes foraging while stopped-over in the San Luis Valley, Alamosa County, Colorado in October 2011. Photo credit: Brian D. Gerber.

Figure 1.12. Hatchling sandhill cranes with parents in a pasture in Highlands County, Florida in January 2008. Photo credit: James F. Dwyer.

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CHAPTER 2

OPTIMAL POPULATION PREDICTION OF SANDHILL CRANE RECRUITMENT BASED ON CLIMATE-MEDIATED HABITAT LIMITATIONS

2.1. SUMMARY

1. Prediction is fundamental to scientific inquiry and application; however, ecologists tend to favor explanatory modeling. We discuss a predictive modeling framework to evaluate ecological hypotheses and to explore novel/unobserved environmental scenarios to assist conservation and management decision makers. We apply this framework to develop an optimal predictive model for juvenile (<1 year old) sandhill crane (*Grus canadensis*) recruitment of the Rocky Mountain Population (RMP). We consider spatial climate predictors motivated by hypotheses of how drought across multiple time-scales and spring/summer weather affect recruitment.
2. Our predictive modeling framework focuses on developing a single model that includes all relevant predictor variables, regardless of collinearity. This model is then optimized for prediction by controlling model complexity using a data-driven approach that marginalizes or removes irrelevant predictors from the model. Specifically, we highlight two approaches of statistical regularization, Bayesian LASSO and ridge regression.
3. Our optimal predictive Bayesian LASSO and ridge regression models were similar and on average 37% superior in predictive accuracy to an explanatory modeling approach. Our predictive models confirmed *a priori* hypotheses that drought and cold summers negatively affect juvenile recruitment in the RMP. The effects of long-term drought can be alleviated

by short-term wet spring-summer months; however, the alleviation of long-term drought has a much greater positive effect on juvenile recruitment. The number of freezing days and snowpack during the summer months can also negatively affect recruitment, while spring snowpack has a positive effect.

4. Breeding habitat, mediated through climate, is a limiting factor on population growth of sandhill cranes in the RMP, which could become more limiting with a changing climate (i.e., increased drought). These effects are likely not unique to cranes. The alteration of hydrological patterns and water levels by drought may impact many migratory, wetland nesting birds in the Rocky Mountains and beyond.
5. Generalizable predictive models (trained by out-of-sample fit and based on ecological hypotheses) are needed by conservation and management decision makers. Statistical regularization improves predictions and provides a general framework for fitting models with a large number of predictors, even those with collinearity, to simultaneously identify an optimal predictive model while conducting rigorous Bayesian model selection. Our framework is important for understanding population dynamics under a changing climate and has direct applications for making harvest and habitat management decisions.

Key-words: *Grus canadensis*, LASSO, modeling; multicollinearity; palmer drought index; PDSI; predictive, ridge regression; SPEI, standardized precipitation-evapotranspiration index

2.2. Introduction

"*It remains true that if we can predict successfully on the basis of a certain explanation, we have good reason, and perhaps the best sort of reason, for accepting the explanation*" (Kaplan 1964, Pg. 350).

Prediction is a fundamental part of science and paramount in science based decision-making. There is both a need and a demand for predictive models to assist decision-makers (Kendall, 2001; Sutherland, 2006). Generalizable predictive models are needed to explore how novel conditions, such as future environmental changes and anthropogenic disturbances, will affect ecosystems, species distributions, and populations of managed species (e.g., harvested or endangered). These models are also crucial to evaluating alternative conservation and management actions (e.g., hunting, habitat-manipulation, or reintroduction scenarios; Nichols et al. 2007). As such, predictive modeling has practical importance to conservation decision-making and is an important approach to provide insights about ecological processes (Sutherland, 2006).

Ecologists tend to use explanatory modeling to understand ecological processes, rather than predictive modeling, perhaps even when prediction is the goal (Shmueli, 2008; Evans, Norris & Benton, 2012; Hooten & Hobbs, 2014). An explanatory modeling approach often focuses on a small set of discrete models to evaluate competing hypotheses about mechanistic processes motivated from theory and past observations to infer processes from data (Burnham and Anderson, 2002). In contrast, a predictive modeling approach emphasizes the forecasting of new or future observations, possibly under novel scenarios. A continuous model set may be evaluated, which can lead to better predictive performance than from a discrete set (Hastie et al., 2009). From a statistical perspective, predictive modeling is concerned with the generalizability of the model to predict beyond the sample-space and thus it is preferred to measure model fit based on out-of-sample performance, rather than within-sample as often used for explanatory modeling (Shmueli, 2008; Hooten & Hobbs, 2014). Predictive and explanatory approaches are not mutually exclusive and thus not inconsistent or incompatible

(Kaplan, 1964; Bickel & Li, 2006); however, there can be advantages in model performance when the intended application of the model is consistent with the modeling approach (Hastie et al., 2009).

Ecologists may not be readily applying predictive modeling (i.e., out-of-sample model fitting) for a number of reasons. Firstly, statistical tools may not be known and accessible (Mac Nally 2000; Hooten & Hobbs 2014). Alternatively, ecologists may consider prediction to be hopeless; species, population, and ecosystem responses to environmental change is often highly complex, non-linear, and perhaps computationally irreducible (Beckage, Gross & Kauffman, 2011). A more insidious reason may be that ecologists conflate prediction and explanation (Shmueli, 2008); it is often assumed that a highly explanatory model will also be a good predictive model. This is not strictly the case. Even when the causal mechanisms of a process are identified and estimated well enough by an approximating model ($\mathcal{M}$), a model other than $\mathcal{M}$ might be preferable for prediction (Shmueli, 2008; Gelman, Hwang & Vehtari, 2014). Lastly, ecologists may be concerned that predictive modeling lacks the ability to provide explanation of underlying processes. This is also not strictly true. While predictive modeling can be done without predictors based on clear motivating hypotheses (due to Simpson's Paradox, Simpson 2008; Pearl 2014), doing so will likely lead to a more robust generalizable model, as well as provide explanatory power (Ashley, 1980). Comparing models by their out-of-sample predictive performance is often considered the very best way for investigating support of hypotheses (Kaplan, 1964; Ashley, 1980; Hooten & Hobbs, 2014).

We are interested in developing a predictive modeling framework that links correlated climate variables to migratory animal population vital rates. Specifically, we focus on developing a generalizable model that links drought across multiple temporal scales to measures of juvenile (< 1 year old) sandhill crane (*Grus canadensis*) recruitment in the Rocky Mountains. Exploring how climate affects crane recruitment is important in understanding future crane population dynamics, especially when considering climate change. Secondly, by taking a predictive approach, novel climate scenarios can easily be explored to help inform managers about habitat or harvest decisions or be integrated into a formal decision framework. Lastly, knowledge of how climate affects crane breeding productivity in the Rocky Mountains could also be informative to other migratory, ground-nesting birds that breed in similar wetland habitats, including shorebirds, wading birds, and waterfowl (Austin & Pyle, 2004).

Sandhill cranes are a long-lived North American bird and have the lowest annual recruitment of any harvested game bird in North America (Drewien et al., 1995). Typically, cranes do not breed until several years of age, after which they produce two eggs in a single clutch per year, but generally only one chick survives to fledging (see Gerber et al. 2014). Re-nesting can occur if the first nesting attempt fails early in the incubation period, but multiple successful clutches per year have not been observed. We are specifically focused on the Rocky Mountain Population (RMP), consisting of a single subspecies (*G. c. tabida*), which migrate annually (Fig. 2.1). Cranes breed during the summer within palustrine and riparian wetlands throughout the central Rocky Mountains, along with other species, including the Canada Goose (*Branta canadensis*), Eared Grebe (*Podiceps nigricollis*), Mallard (*Anas platyrhynchos*), American Avocet (*Recurvirostra americana*), Long-billed Curlew (*Numenius americanus*), and Virginia Rail (*Rallus limicola*; Austin & Pyle 2004). In the fall and spring during migration, birds stop over in the San Luis Valley (SLV) in central southern Colorado, while wintering takes place primarily in the Rio Grande Valley of New Mexico (Drewien and Bizeau 1974). A survival analysis of RMP cranes has revealed low temporal variation in adult survival (Drewien, R.C., et al., unpublished data), suggesting recruitment may be a driver of RMP dynamics (Sæther & Bakke, 2000).

Following previous findings of a negative trend in recruitment during a period of drought (Drewien et al., 1995), we hypothesize that drought within the RMP breeding range limits the availability of suitable wetlands for nesting, which negatively affects annual recruitment. We define drought as a combination of meteorological and hydrological processes that lead to a "period of abnormally dry weather sufficiently prolonged for the lack of precipitation to cause a serious hydrological imbalance" (Heim, 2002). As with many species of waterfowl, sandhill cranes almost exclusively nest in wetlands, and have high site fidelity that may limit the availability of potential wetlands for nesting (see Gerber et al. 2014). Regional drying of wetlands due to drought is likely to affect recruitment in two ways: 1) reduce the proportion of the population that attempts nesting, and 2) reduce nest success for those that do nest. Water depth around nests has been shown to be an important factor in nesting success, where deeper water is thought to inhibit terrestrial predators from accessing nests (Austin, Henry & Ball, 2007; McWethy & Austin, 2009).

We also hypothesize that cold temperatures and snowpack during the post-hatching and colt stage (June-Aug) will reduce survival between hatching and arrival at the SLV. Sandhill cranes are nidifugous, begin feeding within 24 h of hatching, and are brooded for up to three weeks (see Gerber et al. 2014). Cold weather during the post-brooding stage could be fatal or may limit developmental growth due to increased thermoregulatory demands. Secondly, cold weather is likely to limit the availability of insect prey, which are an important resource for chicks/colts in obtaining necessary protein and to increase weight. Cranes that grow slowly during the colt stage are known to have a lower probability of surviving until 6 months of age (Drewien, R.C., et al., unpublished data). Lastly, a deeper snowpack in summer may inhibit nesting or indicate a mismatch in timing of runoff and recharging of wetlands during the crane nesting season.

To consider our hypotheses in a modeling framework, we need predictor variables, which commonly in ecological and climate studies are collinear. This creates certain challenges in fitting many types of models and can prevent accurate measures of parameters and their uncertainty. We take an approach that can accommodate these challenges. We highlight a predictive modeling approach using statistical regularization to achieve a generalizable model using a relatively large set of possibly collinear predictors, motivated from ecological hypotheses. Statistical regularization is a broad concept that includes model selection and the idea of parsimony in model performance (Bickel & Li, 2006; Hooten & Hobbs, 2014). We specifically are interested in Bayesian ridge regression (Hoerl & Kennard, 1970) and LASSO (least absolute shrinkage and selection operator; Tibshirani 1996). Ridge regression and LASSO provide a rigorous approach to Bayesian model selection and prediction (Hooten & Hobbs, 2014). Each approach regularizes parameters based on out-of-sample performance, but they penalize model complexity differently. Most importantly, LASSO has variable selection properties and can remove effects of predictors by allowing them to be zero, which gives the optimal model an additional amount of interpretability (Hastie et al., 2009). Our objectives are to 1) develop a predictive modeling framework for linking climate effects to migratory animal populations using the Bayesian LASSO and ridge regression techniques, 2) identify an optimal out-of-sample (via cross-validation) predictive model of RMP juvenile recruitment (i.e., proportion of total population) and compare it to an explanatory model,

3) formally evaluate ecological hypotheses concerning climate effects on RMP juvenile recruitment, and 4) provide predictions of recruitment across a range of climate scenarios to inform future management decisions.

2.3. MATERIALS AND METHODS

2.3.1. RECRUITMENT MONITORING. Starting in 1972, an annual survey of juvenile recruitment has been conducted in the RMP during the fall stopover at the SLV (Brown 2013); the survey has been conducted consistently by the same crane biologists (RCD or W. Brown) in mid-late October when most of the population is present (Drewien et al., 1995). The survey covers the entire distribution of cranes within the SLV where birds are assessed to subspecies and age group based on morphological characteristics. During this time, juvenile cranes can be distinguished from adults, but these differences typically disappear by the following summer and thus only allow two age classes to be identified (Drewien et al., 1995).

Biologists sampled cranes by observing flocks at roost, diurnal feeding and midday loafing sites. Sites were only visited once during the 3-6 day survey. A flock was defined as an aggregate of cranes separated from others by >50 m. Flocks of all sizes were sampled to minimize bias associated with the disproportional number of juveniles that occur in smaller-sized flocks (Drewien et al., 1995). Smaller flocks are generally not difficult to observe in the SLV and thus under-detection is not a concern (see Supporing Information). Large flocks (>300 individuals) were spot-sampled (10-25 birds) at intervals along random zig-zag lines in both the perimeter and interior of the group to avoid bias due to family groups concentrating on the edges of large flocks. Between 1972 and 2013, an average of 5518 cranes were sampled each year (range, 1997-8318, Table 2.1). The recruitment estimate is a function of several biological and ecological processes, including the proportion of the population that attempts breeding, clutch size, nesting success, and survival from chick to the fall migration stopover at the SLV.

2.3.2. Predictors for hypotheses.

2.3.2.1. *Drought.* Measuring drought is difficult. No consensus exists on operational definitions and the complexity of the spatial and temporal climate mechanisms that make up a drought are challenging to capture. This lack of consensus led to the development of a multitude of drought indices (Heim, 2002). Two popular indices that are consistent with our interpretation of drought are included in separate models: the Palmer drought indices ($\mathcal{M}_P$, Mishra & Singh 2010) and the standardized precipitation-evapotranspiration indices (SPEI; $\mathcal{M}_{SP}$; Vicente et al. 2010a). The Palmer indices are the most widely used and readily available indices of drought (Mishra & Singh, 2010). They account for precipitation, evapotranspiration, and capacity for soils to hold moisture. The SPEI is a difference equation of precipitation and potential evapotranspiration that is measured at sequential temporal scales, making it applicable to multiple hydrological processes that influence drought (i.e., river discharge from headwaters, reservoir storage, and groundwater storage; Vicente et al. 2010a).

We include three types of Palmer drought index for $\mathcal{M}_P$: 1) the Palmer drought severity index (PDSI), 2) the Palmer hydrological drought index (PHDI), and 3) the Palmer drought Z-index (PDZI). All indices are unitless, estimated monthly, and generally range from -6 to 6, where positive values indicate wet conditions and negative values dry conditions (0.00-0.49 are near normal events, 0.50-0.99 are incipient, 1.00-1.99 are mild, 2.00-2.99 are moderate, 3.00-3.99 are severe, and 4.00-6.00 are extreme). PDSI measures meteorological drought over a 12-18 month time period (Vicente-Serrano, Beguera & López-Moreno, 2010b); PHDI is a hydrological measure of water-supply that operates on time scales longer than PDSI. PDSI and PHDI are insensitive to temporary drought relief and are thus slow to change. Therefore, for both PDSI and PHDI we include only a single annual value in $\mathcal{M}_P$ (April). PDZI is a short-time scale measure of monthly drought with no influence from previous months. Thus, PDZI can capture temporary drought relief from precipitation, that may recharge wetlands, that is not captured in the longer time-scale drought indices. We include monthly PDZI from pre-nesting through nesting and into the colt stage (April-July).

A number of criticisms have been made of the Palmer indices (Heim 2002; Mishra & Singh 2010), which led to also investigating the SPEI. Because we are interested in drought at multiple temporal scales, we include several indices in $\mathcal{M}_{SP}$, with measures of SPEI on short- (1 month, April-July), medium- (12 months, April), and long-term scales (24, 36, and 48 months, April). SPEI is unitless and generally ranges from -3 to 3, where positive values indicate wet conditions and negative values dry conditions (0.00-0.39 are near normal events, 0.50-0.70 are abnormal, 0.80-1.20 are moderate, 1.30-1.50 are severe, 1.60-1.90 are extreme, and 2.00-3.00 are exceptional).

A shortcoming of all drought indices is that they ignore snowpack and subsequent spring/summer runoff, which is likely to influence wetland water levels used by RMP cranes. As such, we explicitly incorporate snowpack using measurements of maximum snow depth (MXSD) from 30 Cooperative Observer Network stations (COOP) chosen throughout the breeding range that 1) are located in areas representative of where cranes nest (e.g., elevation between 1500 and 3500 m), and 2) continuous data are available from 1972-2013. We include MXSD for March and April in both models, where higher values are hypothesized to be beneficial in recharging wetlands during spring runoff.

2.3.2.2. *Cold weather.* To incorporate our summer cold weather hypotheses into both models, predictors of the number of days below freezing in a given month (DT32; measurements from COOP) in May, June, July, and August are included. MXSD is included for months with snow (May and June).

2.3.2.3. *Spatially explicit predictors.* Since the recruitment survey is conducted during migration, spatially explicit knowledge of recruitment by state or region within the breeding area is unavailable; thus, inference is for the entire RMP. However, regional variation in weather/drought could affect local breeding aggregations disproportionately. In addition, the RMP is not evenly distributed within its breeding range (Fig. 2.2) and thus regional climate effects will have disproportional impact on the total recruitment depending on the proportion of the breeding population exposed to the regional climate. We investigated the within-year spatial variability in drought indices across the RMP breeding range using the climate divisions defined by NOAA and found considerable variation (see Supporting Information in Chapter 4.1, Fig. 2.3), which we attempt to accommodate.

Four weighting strategies ($\mathbf{w}_{t,}$, see Statistical Model) are applied to the predictors of both models ($\mathcal{M}_P, \mathcal{M}_{SP}$), which are compared by their predictive performance. First, $\mathcal{M}_{\cdot 1}$ predictors are weighted uniformly across all years by the long-run average proportion of the annual RMP pre-migratory fall survey count within each climate region; this count covers the known staging grounds (Thorpe, Donnelly & Collins, 2013) and has been in operation since 1995 (Kruse et al., 2014). Second, $\mathcal{M}_{\cdot 2}$ predictors are weighted by the proportional size of each climate region within the breeding area and thus assumes larger areas have more breeding cranes than smaller areas. Third, $\mathcal{M}_{\cdot 3}$ predictors are weighted equally across all climate divisions in each year. Fourth, $\mathcal{M}_{\cdot 4}$ predictors are weighted by the RMP fall count by year; for years prior to 1995, we calculate a climate region weight by the average proportion of cranes over the first five years of the survey.

In total, 14 ($\mathcal{M}_P$) and 16 ($\mathcal{M}_{SP}$) predictor variables are considered that we hypothesize are related to the realized climate mechanisms that affect sandhill crane recruitment (Table 2.2). However, the climate and weather variables are at least partially and potentially strongly correlated. Rather than remove collinear variables, which is often done in explanatory modeling (a form of variable selection prior to formal model selection), we see potential value in each for predicting recruitment and take a modeling approach that can accommodate the mathematical difficulties of collinear variables. Palmer indices and weather variables (MXSD, DT32) are available from NOAA (http://www.ncdc.noaa.gov/) and SPEI is available from CSIC (http://sac.csic.es/spei/index.html).

2.3.3. Statistical regularization and model fitting.

2.3.3.1. *Statistical regularization.* Statistical regularization seeks to optimize the generalizability of a model by trading off bias and variance by constraining model complexity, such that there is a decrease in variance for a smaller gain in bias. First, a criterion to optimize needs to be chosen that combines model fit (e.g., model deviance) or conversely, lack of fit (e.g., squared prediction error), with a weighted measure of model complexity (criterion = model fit + λ × model complexity; Reineking & Schröder 2006); the parameter λ provides the weighting or regularization that controls the relative importance (i.e., exchange rate) of model fit and complexity. Model fit can be any loss function, which measures the discrepancy between observations and within- or out-of-sample model predictions. Preferably, this function has the necessary characteristics (local and proper) that guarantees an honest evaluation for the chosen model and data (Gelman, Hwang & Vehtari 2014). For linear models, model complexity is often measured by the number of estimated parameters (P; i.e., degrees of freedom) and can be generalized to include the magnitude of parameter estimates (β) as $\sum_{p=1}^{P} |\beta_i|^q$, when $q > 0$ (Reineking & Schröder 2006; Fig. 2.4). The value of q has a large effect on the measure of model complexity and the behavior it imposes on estimates and model performance for different values of λ (see Discussion; Hastie et al. 2009). Two special cases that have been studied extensively are $q = 1$ and $q = 2$, which correspond to LASSO and ridge regression, respectively. Both LASSO and ridge have likelihood and Bayesian interpretations. In a Bayesian context, choosing how model complexity is controlled can equivalently be defined via the type of prior distribution (prior) that is chosen for each β_i, where LASSO ($q = 1$) is achieved using the Laplace distribution and ridge ($q = 2$) is achieved using the normal distribution (Hastie et al., 2009). The magnitude of the prior 'regulating' the parameter estimates is controlled by λ as part of the prior variance (see 'Statistical Model' for how λ is used in the prior). For an explicit link between constrained optimization in the likelihood paradigm (q=1, LASSO and q=2, ridge) and prior specification in the Bayesian paradigm (Laplace Prior, LASSO and Normal Prior, ridge) see Hoerl & Kennard (1970) and Tibshirani (1996).

Choosing a loss function and measure of model complexity will depend on a study's objectives and assumptions of the structure of the data and predictors (Reineking & Schröder, 2006). Because we are interested in developing a generalizable model that is appropriate for predicting outside of the sample-space, we chose to find an optimal value of λ based on an out-of-sample log predictive score (Gelman, Hwang & Vehtari 2014, equation presented in

'Statistical model'). In doing so, a continuous model selection is effectively performed via regularization to optimize predictive accuracy.

2.3.3.2. *Statistical model.* A Bayesian binary regression model was developed to provide inference (Fig. 2.5). The observation process is the number of juveniles observed (y_t) from the total number of cranes assessed by age (N_t) from year $t = 1, 2, ..., T$. The proportion of juveniles (p_t) is linked to scaled and centered predictor variables (P in total for Q climate regions) from the breeding area for each year t. Predictors are defined in a P×Q matrix ($\mathbf{X}_t$) that is weighted by a Q×1 vector ($\mathbf{w}_t$, which is different for models $\mathcal{M}_{\cdot 1-4}$), to estimate a P×1 vector of coefficients ($\boldsymbol{\beta}$). We evaluate alternative regulators (λ) by out-of-sample cross-validation, in which coefficients are shrunk toward zero using the prior as a constraint; the intercept (α_0) is not regularized and given a relatively uninformative prior (Fig. 2.5). For ridge regression, the exchangeable prior for each parameter is defined as the normal distribution ($\beta_p \sim N(0, \tau^2)$, where the variance $\tau^2 = \frac{1}{\lambda}$), while a Laplace or double-exponential distribution ($\beta_p \sim L(0, \tau^2)$) is used to specify the LASSO. The Laplace distribution is more pointed at the mean than the normal distribution and has heavier tails (Fig. 2.6). A random effect ($\boldsymbol{\eta}$) is also included to accommodate additional process uncertainty for annual variation that is not explained by our predictors.

For each model and regularization method, a search is performed for the optimal value of λ using out-of-sample cross-validation, in which a portion of the data is left out from the model (y_{hold}) while the rest (y_{train}) is used for estimation of unknown parameters. This portion of the data that is not observed by the model (y_{hold}) and thus does not belong to the sample being used to estimate parameters is applied to evaluate the predictive accuracy of the model. We use a y_{hold} of length n = 1, 2, 3, and 6 (CV1, CV2, CV3, CV6, respectively) to evaluate the stability of small sample cross-validation in selecting λ. The data left out as a group are chosen randomly. We consider 100 evenly spaced regulators (ridge: $\lambda \in [exp(-5)\ ,\ exp(15)]$; LASSO: $\lambda \in [exp(0)\ ,\ exp(20)]$). For leave-one-out cross validation (CV1), the out-of-sample predictive fit is calculated as the log pointwise predictive density (*lppd*) for a given λ across all Markov chain Monte Carlo (MCMC) samples (post burn-in) from $s = 1, 2, ..., S$ and all hold outs of data from $i = 1, 2, ..., n$, where $\boldsymbol{\theta} = [\alpha_0, \boldsymbol{\beta}, \sigma^2]$:

$$\text{lppd}_{\text{CV1}} = \sum_{i=1}^{n} log_e \int [y_{i,hold}|\boldsymbol{\theta}][\boldsymbol{\theta}|y_{train}]d\boldsymbol{\theta}, \tag{1}$$

and computed as,

$$\sum_{i=1}^{n} log_e \left(\frac{1}{S} \sum_{s=1}^{S} p\left(y_{i,hold}|\boldsymbol{\theta}_{is}\right) \right). \tag{2}$$

We consider the λ value with the highest E[*lppd*] as the regularization parameter that achieves the best prediction and we consider the model ($\mathcal{M}_{SP\text{1-4}}, \mathcal{M}_{P\text{1-4}}$) with the highest E[*lppd*] as our best predictive model. We fit all models using MCMC methods by sampling from full-conditional distributions using the R Programming Language (R Core Team, 2014); 500,000 MCMC samples were used with a burn-in of 100,000 samples. Posterior convergence was primarily assessed graphically. Additional information on applying statistical regularization and CV with the *lppd* in Bayesian modeling can be found in the Appendix.

2.3.4. PREDICTION FROM AN EXPLANATORY MODEL. We compare the E[*lppd*] of our best model chosen using cross-validation for LASSO and ridge regression ($\mathcal{M}_{SP\text{1-4}}, \mathcal{M}_{P\text{1-4}}$) with a model developed following an explanatory modeling approach. The explanatory model includes only a subset of predictors; collinear predictors are removed when pairwise correlation coefficients between predictors ($|r|$) are > 0.28 (Graham, 2003) and no regularization is performed. This is the most common approach to remove collinear variables (Graham, 2003). We also use the full correlation matrix ($\boldsymbol{R}$) to investigate collinearity by taking its determinant ($|\boldsymbol{R}|$) as well as calculate the condition number (CN). The $|\boldsymbol{R}|$ is a summary of all r, such that if no correlation exists, this value will be 1.0, and otherwise it will be less than 1.0, with worse collinearity being present as the value approaches zero. The CN is the ratio of the largest to smallest non-zero singular value of the predictor matrix ($(\boldsymbol{X}_t\boldsymbol{w}_t)^T$), where the predictors all have a mean of zero and a standard deviation of one. Multicollinearity becomes an issue in estimating parameters when the CN > 5.4 (Lazaridis, 2007).

2.3.5. Ecological effects and prediction. We evaluate our ecological hypotheses by summarizing the posterior distribution of our coefficients of the optimal predictive model as either $\mathrm{P}(\beta_p > 0|\mathbf{y})$ for those effects we consider to have a positive effect on recruitment and $\mathrm{P}(\beta_p < 0|\mathbf{y})$ for those predictors that have a negative effect (Table 2.2); predictors that have little effect on recruitment will have probabilities near 0.5. We also investigate variability in juvenile recruitment by predicting recruitment from our best model under a variety of climate scenarios.

2.4. Results

The best out-of-sample predictive model for $\mathcal{M}_{\cdot 1\text{-}4}$ was found to be similar for ridge and LASSO, but with ridge consistently performing slightly better. Overall, there was little difference in predictive accuracy between $\mathcal{M}_{P2\text{-}4}$ and $\mathcal{M}_{SP1\text{-}4}$, while $\mathcal{M}_{P1}$ was clearly superior (Fig. 2.7). Across all models and both regularization methods, CV1-CV3 were mostly consistent in selecting the same optimal λ, while CV6 tended to select a slightly larger regulator value (e.g., Fig. 2.8). The differences in selected regulators have a small effect on the expected predictive accuracy (E[*lppd*]), but are clearly not different when considering the complete posterior distribution of *lppd* (Fig. 2.9). Across all weighting strategies, the *lppd* was found to be optimal at different values of λ for ridge regression and LASSO due to their different forms of regularization. However, functionally λ occurred at similar values of the regularized coefficients (e.g., Fig. 2.10), which led to similar conclusions about our ecological hypotheses (Table 2.3). For $\mathcal{M}_{P1}$, the optimal λ using ridge regression improved the predictive accuracy by 21.3% compared to a non-regularized model (diffuse prior), while LASSO improved by 20.8%.

Predictors of all our models were found to be considerably collinear, including the best performing model, ($\mathcal{M}_{P1}$: mean, sd, and range of r was 0.26, 0.27, -0.31-0.96, respectively). Additionally, the $|\boldsymbol{R}|$ was 0.00004 and the CN was 33.06. After removing collinear predictors, the explanatory model $\mathcal{M}_{P1-Explanatory}$ had a total of five predictors (PDZI-May, DT32-May-July-Aug, and MXSD-June) that were considerably less collinear ($\mathcal{M}_{P1-Explanatory}$: mean, sd, and range of r was -0.01, 0.16, -0.21-0.22, respectively). The $|\boldsymbol{R}|$ was 0.77 and the CN was 2.16. However, there was also a loss of predictive accuracy from the explanatory model, with $\mathcal{M}_{P1}$ fit using ridge and LASSO being $\approx$ 37% more accurate than $\mathcal{M}_{P1-Explanatory}$.

For more than four decades, the annual juvenile recruitment varied considerably while remaining consistently low (0.034-0.120 [range, Brown 2013], Fig. 2.11). We found the majority of our ecological hypotheses regarding the effect of drought and weather on juvenile recruitment to be supported using either LASSO and ridge for the best predictive model, $\mathcal{M}_{P1}$ (Table 2.3). Contrary to our hypotheses, there was strong support for a negative influence of PDZI-April and positive support of DT32-May on recruitment. There was also no significant effect of PDZI-July. Two of the drought indices (PDZI-May-July) were highly sensitive to the weighting strategy used with at least a 0.1 change in probability of the hypothesis (Table 2.4); we are therefore less confident about inferring the importance of these predictors. We found similar general support of our hypotheses using the SPEI drought indices $\mathcal{M}_{SP1-4}$, but more variability in support across weighting strategies (Table 2.5).

Using our best model ($\mathcal{M}_{P1}$), we predicted juvenile recruitment under a range of climate scenarios. We found short-term (PDZI) and long-term drought (PDSI, PHDI) to affect juvenile sandhill crane recruitment differently. Our model suggests that the alleviation of drought by the increasing of short-term drought indices can positively affect juvenile recruitment, but not as much compared to alleviation of long-term drought (Fig. 2.12). We also found that the number of freezing days in the summer months (June, July, and August) have a less pronounced effect on juvenile recruitment than drought, but one that is consistently negative (Fig. 2.13). Investigating the timing of maximum snowpack across spring and summer revealed strong effects on sandhill crane recruitment, with the best scenario for crane production being high snowpack in the spring that is drastically reduced by the summer months (Fig. 2.14).

2.5. Discussion

2.5.1. Predictions, vital rates, and harvest decisions. We demonstrated a predictive modeling framework that links ecological hypotheses of correlated climate mechanisms to a migratory population's vital rates, while overcoming common data and modeling issues. Most importantly, we did not limit our investigation of climate effects to a single value of drought, but instead allowed the model to evaluate a set of numerous temporally-scaled measures of drought that were considered *a priori* to be candidate predictors of recruitment. Understanding whether climate drives variation in vital rates will often depend on evaluating temporally correlated mechanisms. By doing so, we were able to improve predictions and better understand how short- and long-term drought proportionally impact cranes.

In the RMP, juvenile recruitment may be especially important in understanding crane population dynamics. While adult survival is known to have the greatest potential to affect population change (i.e., more elastic and sensitive), observed temporal variation is often low in long-lived birds (Sæther & Bakke, 2000). In contrast, juvenile recruitment and survival may have a lower potential to affect population change, but greater observed influence on long-lived birds due to high temporal variation (Sæther & Bakke, 2000). For the RMP, adult survival has been found to be stable over a 23 year period (Drewien, R.C., et al., unpublished data), while recruitment has high temporal variation (Fig. 2.11, Brown 2013). Our best predictive model suggests that this variation is at least partly due to drought (short and long-term) as well as spring/summer weather in the Rocky Mountains. Climate can be said to exert a population limiting effect on the RMP, mediated through breeding habitat constraints. Specifically, in periods of drought, breeding cranes are limited in the quality of nesting habitat and choose not to nest and/or are less successful at producing young that make it to their main migratory stopover when they do nest. These findings are likely not unique to sandhill cranes, but apply more generally to migratory, ground nesting birds that also rely on palustrine and riparian wetlands for breeding.

Exploring variation in predictors (e.g., Figs. 4, 5, 6) can lead to important general findings of how future climate scenarios may impact RMP sandhill crane recruitment, which decision makers may find useful. Most important is that the drought in the central Rocky

Mountains is generally expected to increase in severity (Dai, 2011), likely due to increased temperatures and decreased spring snow cover (McKelvey et al., 2011). The timing of flows in the Rocky Mountains are also expected to occur earlier in the spring (Rood et al., 2008) with higher flows in the winter and substantially reduced flows in the summer. These changes may eventually cause a mismatch in timing of wetland recharge and water needs of nesting cranes, unless their migration chronology is sufficiently plastic to adapt. Our predictions suggest that future annual recruitment is likely to be lower than currently observed, thus limiting population growth more than in the past, unless survival rates could compensate. Limited population growth could be detrimental to the long-term stability of the RMP, as adult cranes have a natural mortality of $\approx 6\%$, which could be exceeded by harvest mortality under an increasing harvest rate (Drewien, R.C., et al., unpublished data). Even relatively low harvest rates coupled with low recruitment could have an effect on the population's trajectory. If the population began to decline, the low expected recruitment coupled with delayed breeding would make for a very slow recovery.

2.5.2. MODELING AND DATA LIMITATIONS AND CONCERNS. Some caution in using our model directly in harvest decisions is warranted. First, the juveniles we survey are those that survived through fledging and early sport hunting mortality and successfully migrated to the SLV. Thus, the recruitment we observe is likely lower than would be at the breeding area. Annual variation in the differential survival of juvenile and adults from the breeding grounds to the SLV may mask true variation in our estimates of recruitment to the population at the fall staging area in any given year. Juvenile and adult survival appear not to be highly temporally variable (Drewien, R.C., et al., unpublished data), however, juvenile survival during this period is dependent on their body condition prior to migration (Drewien, R.C., et al., unpublished data). Such variation across cohorts could occur as a result of changes in food availability, which could be exacerbated by environmental changes resulting from a changing climate. Climate predictors should capture the variation in survival effects on recruitment due to climate effects, but not so for other temporally varying factors. Thus, this may not be a systemic issue but affect only a few years.

Secondly, the scale of monitoring recruitment has important implications of how we incorporate climate variables for the breeding area. Monitoring recruitment at the SLV has clear benefits in increasing the likelihood of obtaining a representative sample from the entire RMP and is less financially burdensome than a survey conducted over the entire breeding area. However, more informative measures of recruitment would result from monitoring at a finer grain than that of the entire RMP breeding area, because drought and local weather conditions vary considerably at a finer scale. Such tradeoffs between sampling efficiency, scale, and grain are likely common in studies of widely dispersed populations. Because fine-scale estimates of recruitment were not available, we used a modeling framework to spatially weight climate variation at the breeding area, based on relative abundance in migration staging areas, and then apply it to the population-level measure of recruitment. This is challenging because the distribution of the nesting cranes is unknown and has likely shifted over time due to habitat change, changing land practices, loss of wetlands, and increasing exurban development. It gives us hope that we have generally captured the spatial variation of climate on recruitment in the population as our best predictive model used the annual pre-migratory counts ($\mathcal{M}_{P1}$), but we did expect the time-varying weighted model ($\mathcal{M}_{P4}$) to have more support. Perhaps this was because we have no information on the distribution of cranes from 1972 to 1994.

Lastly, we have attempted to link drought with crane recruitment, where we assume one effect of drought is the reduction of wetland water levels, which increases a predator's ability to locate nests. Predation risk to crane nests is likely driven by predator abundance, activity, and alternative prey availability (Austin, Henry & Ball, 2007). These are in turn influenced by a number of factors, including land-use change and human activity, which have varied spatially and temporally within the Rocky Mountains over the last four decades. In the future, it may be possible to incorporate land-use change into this modeling framework. Work is currently underway by the Intermountain West Joint Venture to quantify the magnitude and distribution of landscape change (Donnelly and Vest, 2006). However, this will not necessarily solve the issue of spatio-temporal variation in predation risk, which may remain imprecise over such a large area. A major benefit of the land-use data could be the ability to weight climate predictors by the availability of wetland habitats. This may allow crane recruitment to be used as a general index of overall wetland breeding productivity of certain waterfowl, shorebirds, and wading birds in the Rocky Mountain region. However, this application would require testing.

2.5.3. PREDICTION AND MODEL SELECTION. We suggest the field of ecology could benefit from increased application of formal predictive modeling. By formal, we mean models trained by out-of-sample data and measured by a truly predictive criterion that does not depend on asymptotic properties (e.g., *lppd*), which will help identify generalizable predictive models. This is often considered the gold-standard in discriminating among hypotheses (Kaplan, 1964; Ashley, 1980). In addition, this approach is ideal for predicting system response over a range of realistic scenarios that includes unobserved or even novel conditions, to help decision makers visualize possible outcomes of environmental change. Lastly, hypotheses of ecological or climate processes will often lead to a set of correlated variables, which a predictive modeling approach can easily accommodate.

We contend that viewing model selection within the domain of regularization is advantageous, because it opens up the wide array of interesting statistical approaches to fitting and comparing models (Hastie et al., 2009; Hooten & Hobbs, 2014). Regularization helps one to think about measures of model complexity and whether within-sample explanation or out-of-sample prediction is preferred. There is no one-size-fits-all regularization method; choosing an approach should be based on the research or management issue of interest, the assumptions of the structure of the data, and the operating characteristics of the method (Reineking & Schröder, 2006). If predicting beyond the current sample space is a priority, as it was here, it is preferable to use an out-of-sample measure of model fit, as it generalizes the model and helps guard against overfitting (Gelman, Hwang & Vehtari, 2014). This is not to suggest prediction is inappropriate when optimizing a model based on within-sample fit, but if prediction is the goal, out-of-sample predictive performance is known to be worse (i.e., less accurate and/or precise) when fitting a model optimized using within-sample fitting (Hastie et al., 2009). When there is sufficient data, the best practice is to use true out-of-sample predictive fit where a subset of the total data is completely left out and is never used to fit the model, only to evaluate predictive accuracy; otherwise, cross-validation as used here, which randomly leaves out a portion of the data to evaluate predictive accuracy is a valid option (Hastie et al., 2009).

Regularization is commonly discussed and applied in ecological research, but mostly narrowly and focused in the likelihood framework using variable subset selection via information theoretics (IT, Burnham and Anderson 2002). The more general notion of statistical regularization being used for model selection is more rarely discussed in the ecological literature (Hooten & Hobbs, 2014). One of the widely applied IT criterion, Akaike's Information Criterion (AIC), can easily be understood in the context of regularization, as AIC = -2×Log-Likelihood + $\lambda \times \sum_{p=1}^{P} |\beta_i|^q$, where $q = 0$ and $\lambda = 2$. AIC is based on minimizing within-sample expected prediction error (Hastie et al., 2009; Burnham and Anderson, 2002). Recommendations of using AIC include comparing a small set of ecologically motivated models (Burnham and Anderson, 2002), which is ideal for an explanatory modeling approach. However, because variable selection is a discrete process ($q = 0$, predictor is either in or out) it can be unstable and exhibit high variance when it comes to prediction, and thus often leads to considerable predictive loss compared to continuous regularization methods where the amount of regularization (λ) is data-driven (e.g., by cross validation) rather than fixed (Breiman, 1996; Hastie et al., 2009).

In this study, we applied the Bayesian LASSO and ridge, as they are known to perform well under a wide range of conditions, including, binary data, and especially at small sample size, such as ours (Reineking & Schröder, 2006). A key issue in modeling binary data is the known overestimation of coefficients for small sample size, which is compounded when the event of interest is rare (small p_t, low recruitment) and when interested in many predictors (Makalic & Schmidt, 2010); these issues commonly lead to poor prediction, which regularization can ameliorate. For our crane data, LASSO and ridge performed equally well in predictive accuracy and led to the same ecological findings. The differences between the two in their model specification are slight, but they have different operating characteristics that were not clearly illustrative in our study. Ridge is best when there are many non-zero coefficients and when there is strong collinearity among predictors, while LASSO operates best when there are many coefficients close to or at zero with a few larger coefficients and only some predictor collinearity (Friedman, Hastie & Tibshirani, 2010; Tibshirani, 1996; Reineking & Schröder, 2006). For our analysis, if we had considered additional variables that were less motivated by clear ecological hypotheses and thus were more likely to be unrelated to recruitment, LASSO would have likely outperformed ridge by removing these variables from the optimal model; instead, the stronger collinearity among are important predictors lead to ridge outperforming LASSO.

Ecologists should consider their study goals and examine the wide range of regularization methods and their performance for their specific situation. We took a Bayesian approach to regularization, which can easily accommodate various sources of uncertainty, including parametric uncertainty, directly in our measure of predictive accuracy. We see a high utility in regularization specifically for meeting the increasing demands from decision-makers for increased predictive modeling in ecology. Further details on applying Bayesian model fitting can be found in the Appendix; for those interested in likelihood statistical regularization, see the R package 'glmnet' (Friedman, Hastie & Tibshirani, 2010).

2.6. Tables and Figures

Table 2.1. Annual survey data used to develop an optimal out-of-sample predictive model of juvenile sandhill crane recruitment.

Year	Juvenile Count	Total Count
1973	240	1997
1974	296	3151
1975	262	2730
1976	206	2191
1977	198	2749
1978	236	2267
1979	204	2018
1980	224	2362
1981	195	2564
1982	342	3881
1983	782	6744
1984	433	5347
1985	515	5722
1986	482	8318
1987	282	5226
1988	222	6516
1989	294	7164
1990	491	7556
1991	310	5849
1992	217	4168
1993	456	7510
1994	271	6894
1995	461	7185
1996	693	7366
1997	639	6586
1998	877	7853
1999	577	6891
2000	441	6622
2001	478	8211
2002	361	6883
2003	587	7650
2004	726	7735
2005	836	7734
2006	739	7440
2007	592	7095
2008	462	5056
2009	728	6342
2010	547	6554
2011	383	5848
2012	263	3375
2013	307	4359

TABLE 2.2. Ecological hypotheses about the direction of effect of climate predictors on sandhill crane recruitment. Models included either Palmer drought indices ($\mathcal{M}_P$) or standardized precipitation-evapotranspiration indices (SPEI, $\mathcal{M}_{SP}$.)

Time Scale (months)	**$\mathcal{M}_{SP}$ Predictors***	**$\mathcal{M}_{P}$ Predictors**	**Hypothesized Effect on Recruitment**
Short(1)	SPEI1 (April-July)	PDZI (April-July)	Positive*∗
Short(1)	MXSD (March, April)	MXSD (March, April)	Positive
Short(1)	DT32 & MXSD (May)	DT32 & MXSD (May)	Negative
Short(1)	DT32 (June-Aug) & MXSD (June)	DT32 (June-Aug) & MXSD (June)	Negative
Medium(12)	SPEI12 (April)	-	Positive
Long(>12)	-	PHDI (April)	Positive
Long(12-18)	-	PDSI (April)	Positive
Long(24)	SPEI24 (April)	-	Positive
Long(36)	SPEI36 (April)	-	Positive
Long(48)	SPEI48 (April)	-	Positive

*MXSD = maximum snow depth, DT32 = number of freezing days, PDSI= Palmer drought severity index, PDZI = Palmer drougth Z-index, PHDI = Palmer hydrological drought index. The number following SPEI indicates the time scale and the parentheses following a predictor variable indicate the month(s) it pertains to.

** Positive values of drought indicate wetter years, thus a positive effect on recruitment means that increasing values of a drought index leads to higher recruitment.

Table 2.3. Ecological hypotheses, predictor variables, and evidence of the relationship from the optimal out-of-sample predictive model, $\mathcal{M}_{P1}$.

Predictor		**Hypothesized Effect on Recruitment**	**Ridge Regression P(Hypothesis|Data)**	**LASSO P(Hypothesis|Data)**
PDSI	- April	Positive	1.00	1.00
PHDI	- April	Positive	1.00	1.00
PDZI	- April	Positive	0.01	0.01
	- May	Positive	0.98	0.97
	- June	Positive	1.00	1.00
	- July	Positive	0.31	0.40
DT32	- May	Negative	0.00	0.00
	- June	Negative	1.00	1.00
	- July	Negative	1.00	1.00
	- August	Negative	1.00	1.00
MXSD	- March	Positive	1.00	1.00
	- April	Positive	1.00	1.00
	- May	Negative	1.00	1.00
	- June	Negative	1.00	1.00

Table 2.4. Ecological hypotheses, predictor variables, and evidence of the relationship (P(Hypothesis|Data)) of how drought (Palmer indices) and weather predictors influence sandhill crane juvenile recruitment.

Predictor		**Hypothesis**	**Ridge Regression**				**LASSO**			
			$\mathcal{M}_{P1}$	$\mathcal{M}_{P2}$	$\mathcal{M}_{P3}$	$\mathcal{M}_{P4}$	$\mathcal{M}_{P1}$	$\mathcal{M}_{P2}$	$\mathcal{M}_{P3}$	$\mathcal{M}_{P4}$
PDSI	- April	Positive	1.00	0.98	1.00	0.90	1.00	0.95	1.00	0.90
PHDI	- April	Positive	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PDZI	- April	Positive	0.01	0.00	0.10	0.00	0.01	0.00	0.05	0.00
	- May	Positive	0.98	0.63	0.42	1.00	0.97	0.66	0.39	1.00
	- June	Positive	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- July	Positive	0.31	0.10	0.39	0.42	0.40	0.11	0.63	0.43
DT32	- May	Negative	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	- June	Negative	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00
	- July	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- August	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
MXSD	- March	Positive	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00
	- April	Positive	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- May	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- June	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 2.5. Ecological hypotheses, predictor variables, and evidence of the relationship (P(Hypothesis|Data)) of how drought (SPEI) and weather predictors influence sandhill crane juvenile recruitment.

Predictor		**Hypothesis**	**Ridge Regression**				**LASSO**			
			$\mathcal{M}_{SP1}$	$\mathcal{M}_{SP2}$	$\mathcal{M}_{SP3}$	$\mathcal{M}_{SP4}$	$\mathcal{M}_{SP1}$	$\mathcal{M}_{SP2}$	$\mathcal{M}_{SP3}$	$\mathcal{M}_{SP4}$
SPEI1	- April	Positive	0.37	0.00	0.04	0.19	0.35	0.01	0.09	0.10
	- May	Positive	0.12	0.08	0.01	0.14	0.12	0.09	0.01	0.13
	- June	Positive	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- July	Positive	0.12	0.18	0.45	0.32	0.14	0.18	0.45	0.32
SPEI12	- April	Positive	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
SPEI24	- April	Positive	0.90	0.15	0.69	0.85	0.88	0.24	0.81	0.72
SPEI36	- April	Positive	0.99	1.00	0.99	0.99	0.98	1.00	0.99	0.99
SPEI48	- April	Positive	0.88	0.94	0.46	0.86	0.88	0.95	0.5	0.83
DT32	- May	Negative	0.99	1.00	0.99	0.99	0.98	1.00	0.98	1.00
	- June	Negative	0.99	1.00	1.00	1.00	0.99	0.99	1.00	1.00
	- July	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- August	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
MXSD	- March	Positive	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00
	- April	Positive	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	- May	Negative	0.14	0.90	0.82	0.83	0.15	0.91	0.84	0.82
	- June	Negative	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

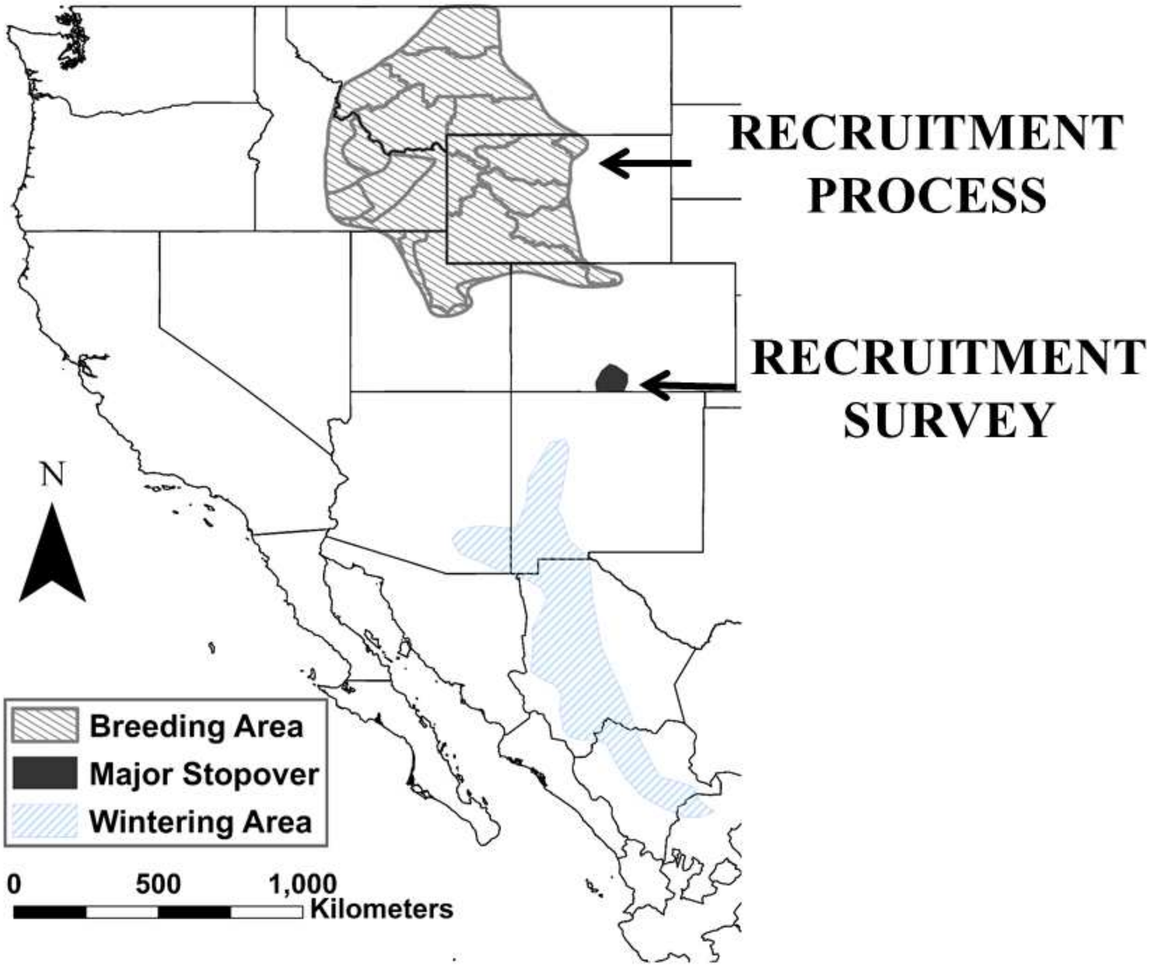

FIGURE 2.1. Seasonal distribution of the sandhill crane Rocky Mountain population. The major stopover for spring and fall migrants is the San Luis Valley of southern Colorado, where crane biologists have conducted juvenile recruitment surveys since 1972 (Recruitment Survey). Juveniles are reared in the central Rocky Mountains (Recruitment Process). The regions within the breeding area indicate NOAA climate divisions.

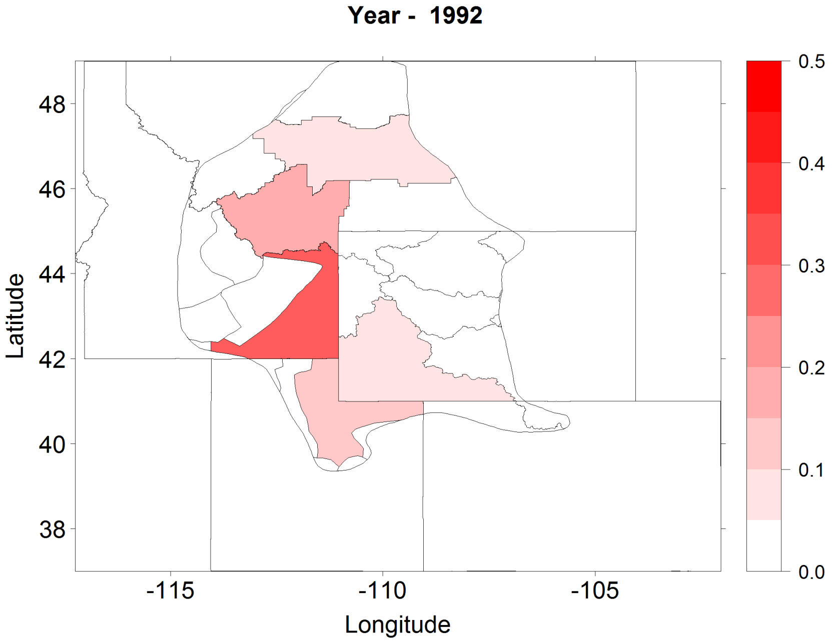

Figure 2.2. Animation of the proportion of the annual pre-migration count of the Rocky Mountain population of sandhill cranes on their staging areas (1992, 1995 to 2013); spatial units are NOAA climate regions.

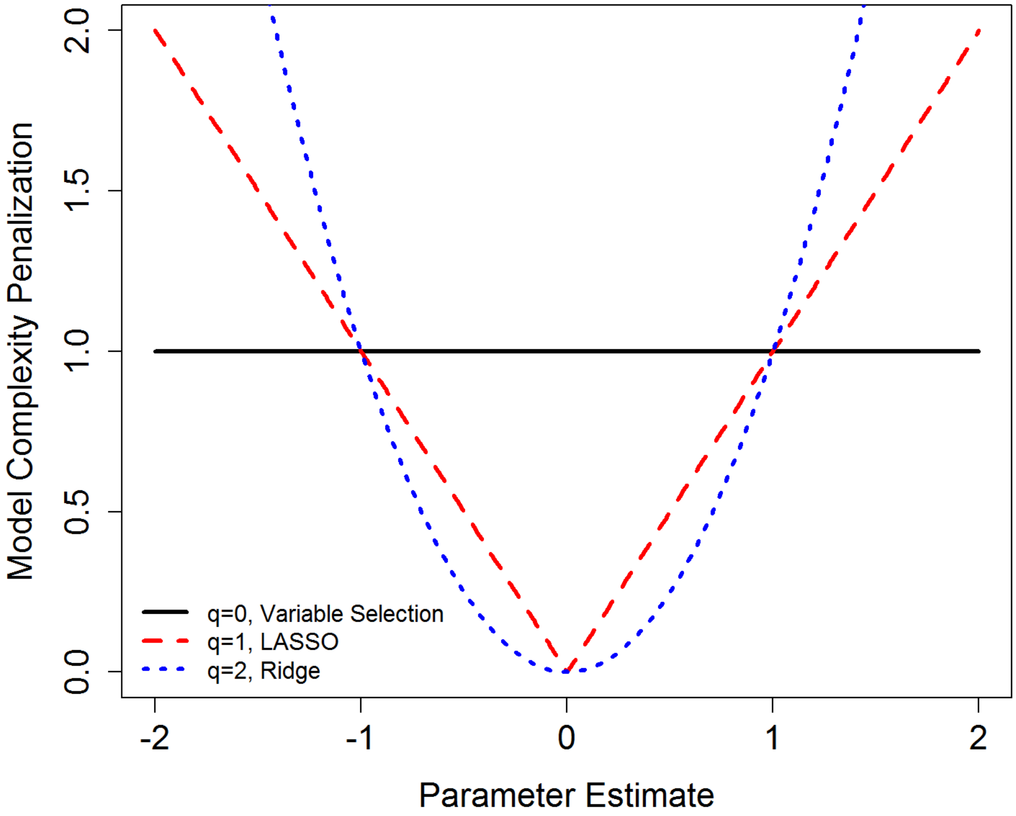

FIGURE 2.3. Illustration of the continuous effect of model complexity under different forms.

$$
\begin{aligned}
\text{Observation Process:} \quad & y_t \sim \text{Binomial}\left(N_t, p_t\right) \\
\text{Ecological Process:} \quad & \text{logit}\left(p_t\right) = \alpha_0 + \left(\boldsymbol{X}_t \boldsymbol{w}_t\right)^T \boldsymbol{\beta} + \eta_t \\
\text{Process Uncertainty:} \quad & \eta_t \sim \text{Normal}(0, \sigma^2) \\
\text{Intercept Prior Information:} \quad & \alpha_0 \sim \text{Normal}(0, 1000) \\
\text{Uncertainty Prior Information:} \quad & log\left(\sigma^2\right) \sim \text{Normal}(0, 2) \\
\text{Ridge Regularization (prior):} \quad & \boldsymbol{\beta} \sim \text{MVN}\left(\mathbf{0}, \tau^2 \boldsymbol{I}_p\right) \\
\text{LASSO Regularization (prior):} \quad & \boldsymbol{\beta} \sim \text{Laplace}\left(\mathbf{0}, \tau^2 \boldsymbol{I}_p\right) \\
\text{Joint Posterior Distribution:} \quad & [\alpha_0, \boldsymbol{\beta}, \sigma^2 | \boldsymbol{y}, \boldsymbol{X}, \boldsymbol{w}] \propto [\boldsymbol{y} | \boldsymbol{X}, \boldsymbol{w}, \boldsymbol{\beta}, \alpha_0, \sigma^2][\boldsymbol{\beta}][\alpha_0][\sigma^2]
\end{aligned}
$$

Figure 2.4. Regularized Bayesian binary regression model used to identify a generalizable predictive model of sandhill crane recruitment based on climate effects; shown with the prior specification for ridge regression and LASSO, which act to control model complexity. Note, we are specifying variances, rather than precisions.

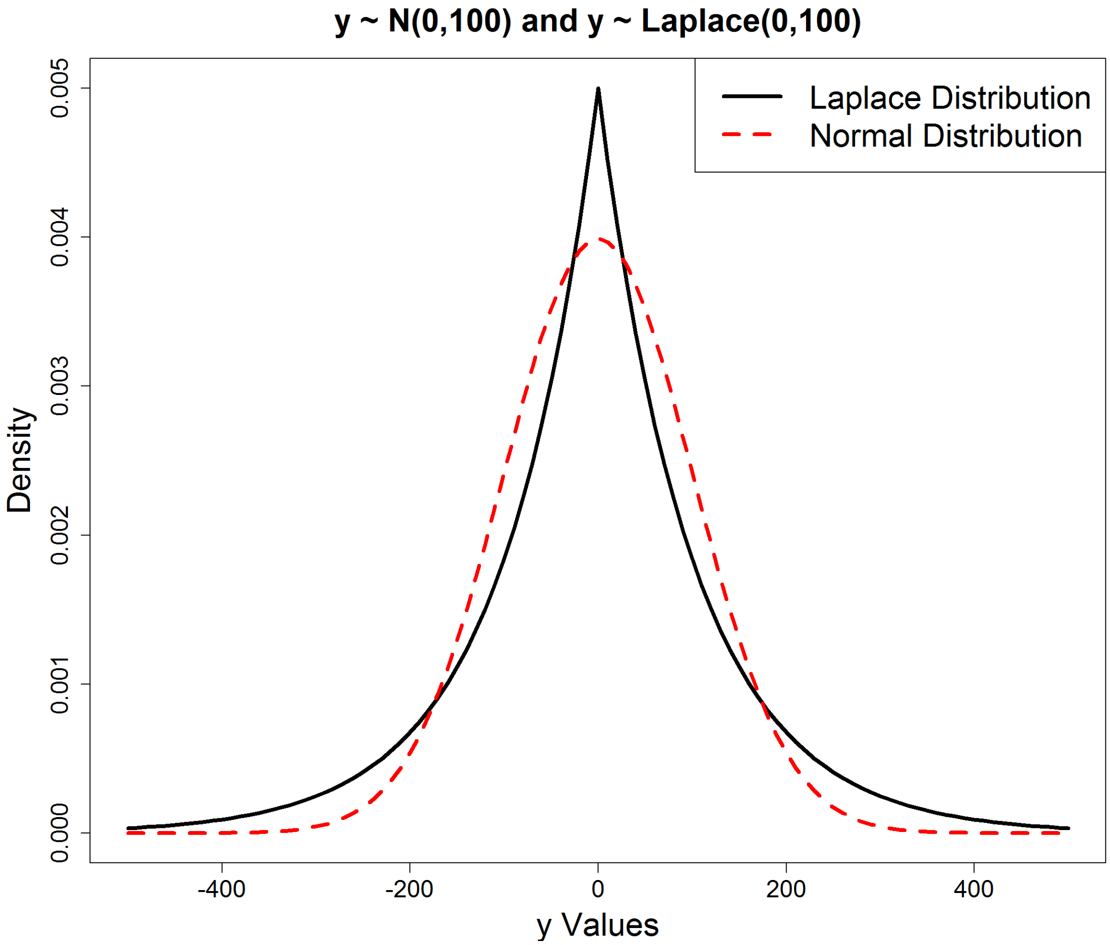

Figure 2.5. Comparison of the Laplace and Normal distribution, used to constrain model complexity in Bayesian regularization, where prior specification of coefficients are equivalent to LASSO and ridge regression, respectively.

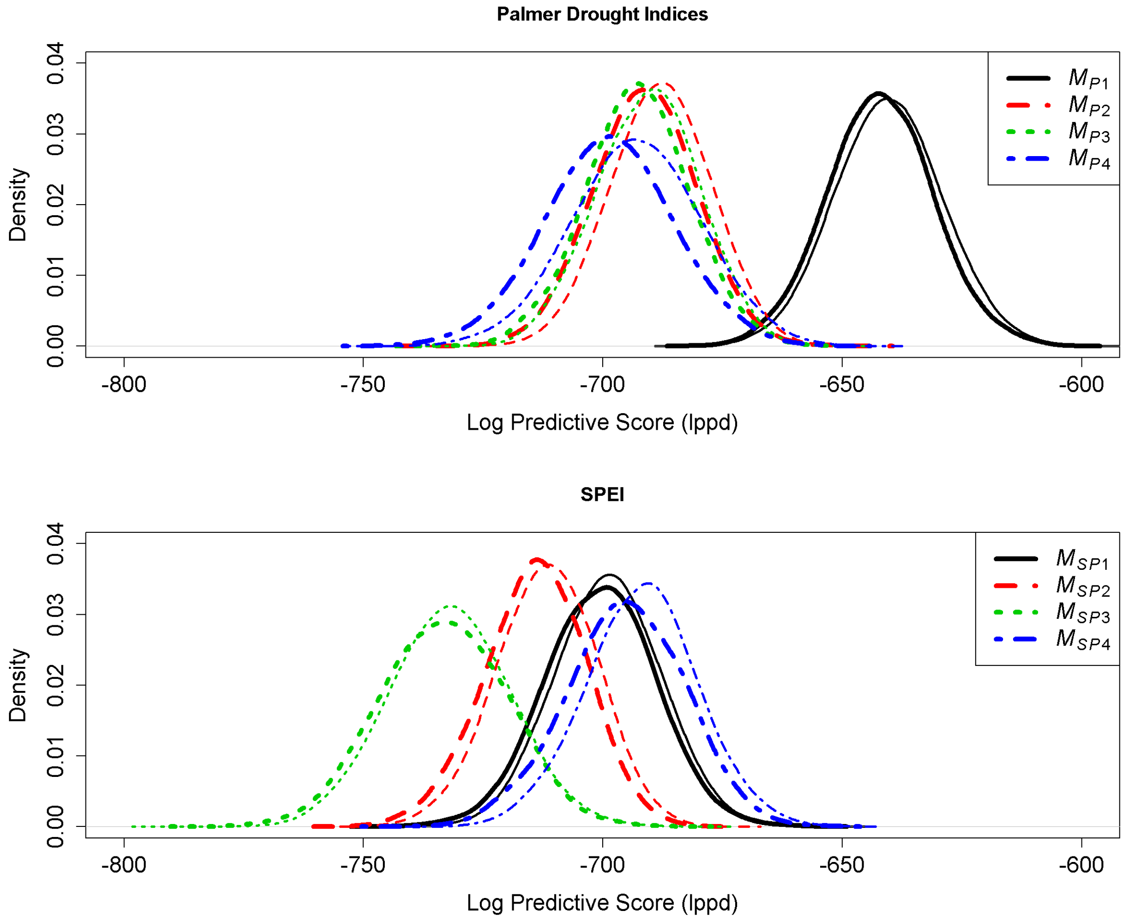

FIGURE 2.6. Posterior distributions of the optimal log pointwise predictive density from models using Palmer drought indices and SPEI (standardized precipitation-evapotranspiration indices), spatially weighted by different strategies ($\mathcal{M}_{P1-4}, \mathcal{M}_{SP1-4}$, respectively); thick lines indicate the model was fit using LASSO and narrow lines indicate ridge.

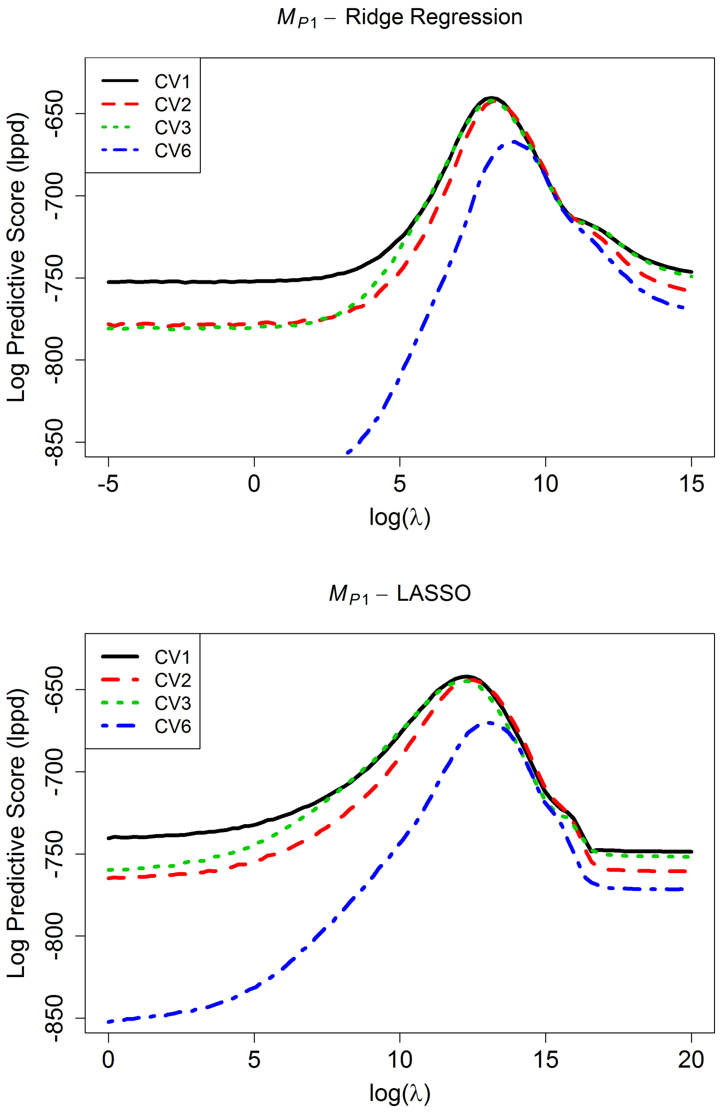

Figure 2.7. Out-of-sample cross validation (CV) log-predictive scores (E[lppd]) under different amounts of training data (CV1, CV2, CV3, CV6) for identifying an optimal regulator (λ).

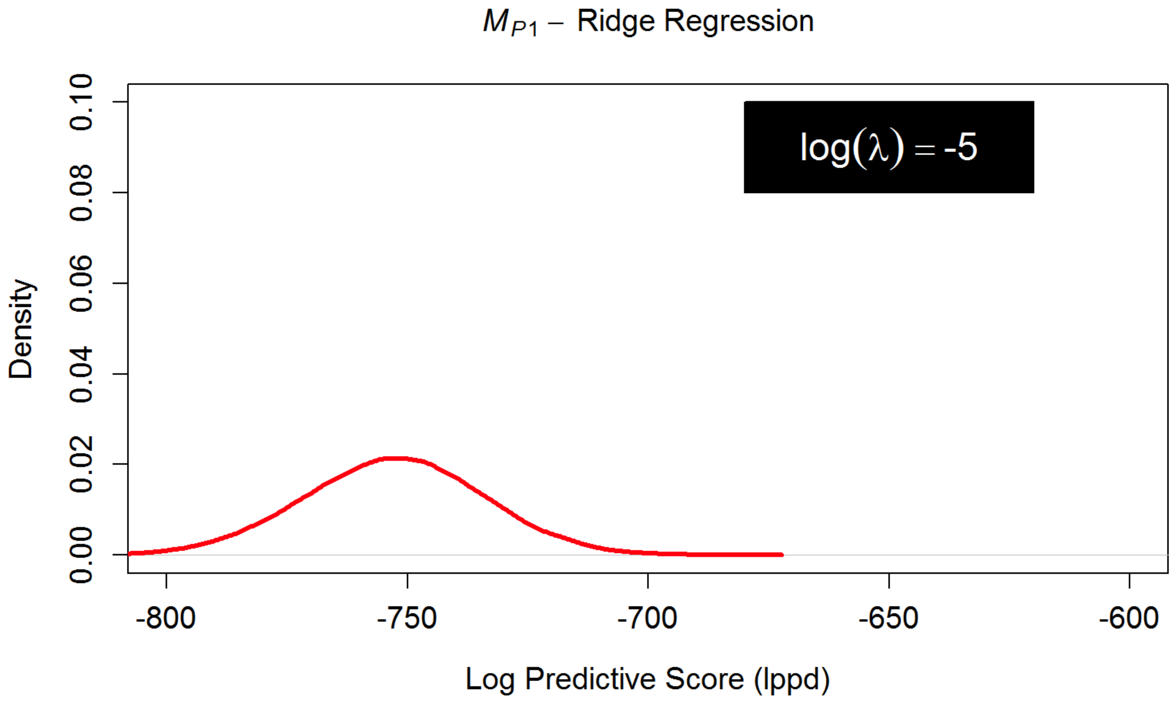

FIGURE 2.8. Animation of the posterior distribution of the log predictive score across a range of regulators (λ); the thick black line indicates the optimal or highest expected value.

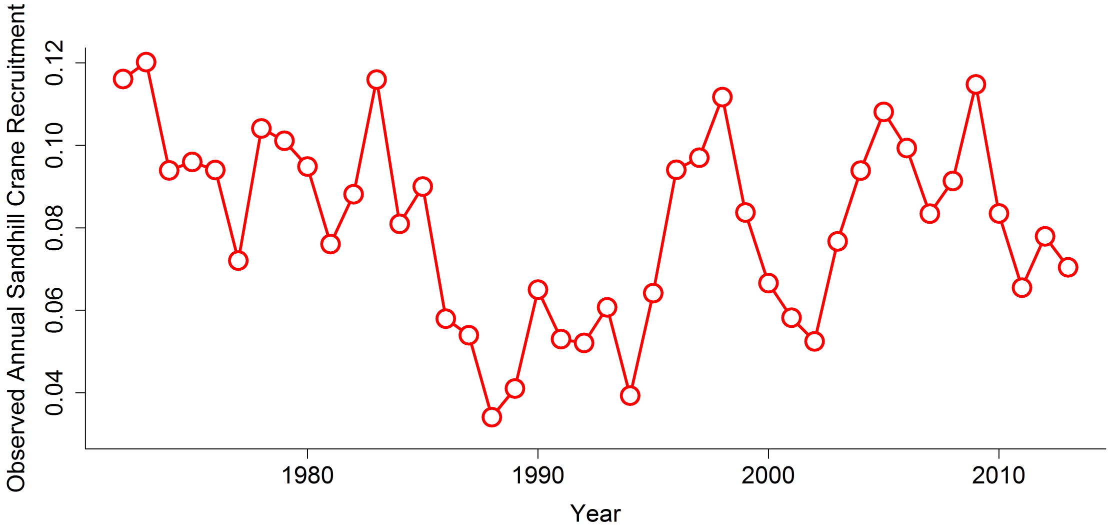

FIGURE 2.9. Observed variation in juvenile recruitment of the Rocky Mountain Population of sandhill cranes from 1972 to 2013 during migration at the San Luis Valley in southern Colorado.

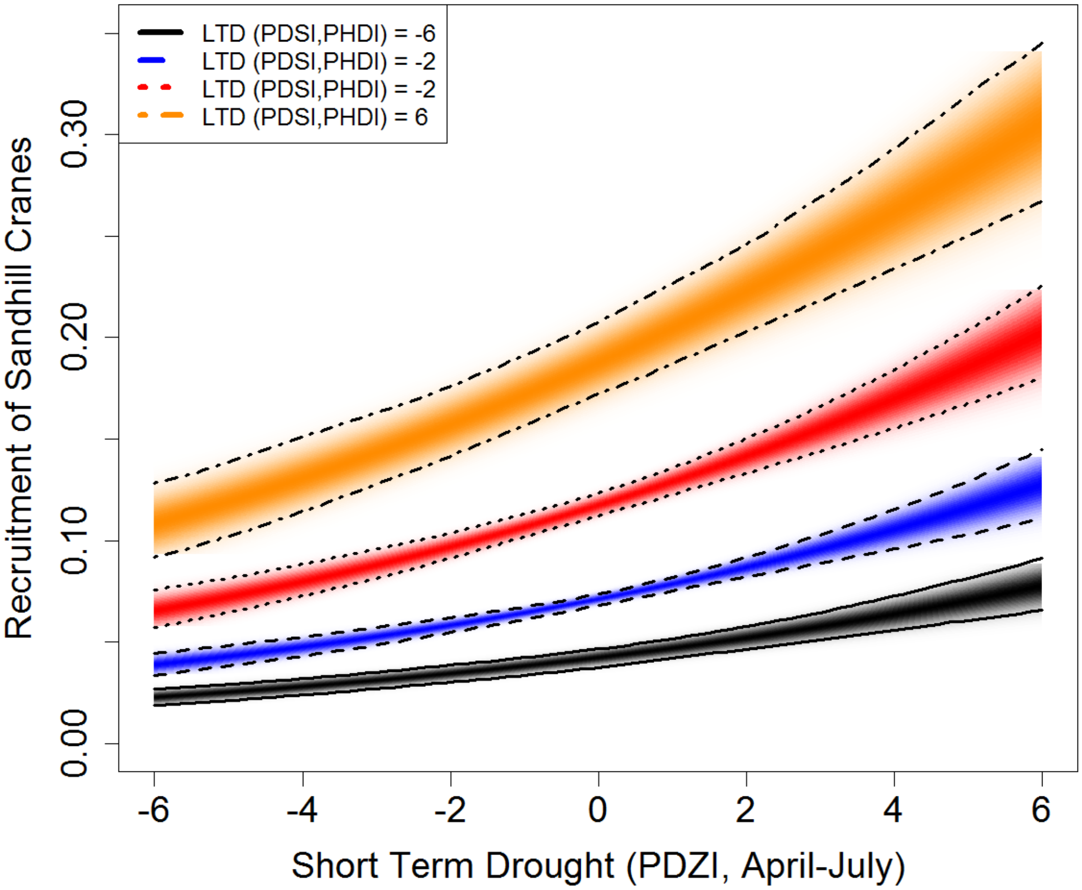

FIGURE 2.10. Variation in predicted juvenile sandhill crane recruitment across values of long-term (LTD) and short-term drought from an optimal out-of-sample predictive model, fit by LASSO ($\mathcal{M}_{P1}$). Weather predictors (maximum snow depth and the number of freezing days within a month) are held constant at their mean. The uncertainty is shaded in proportion to the posterior distribution and the lines are 95% credible intervals.

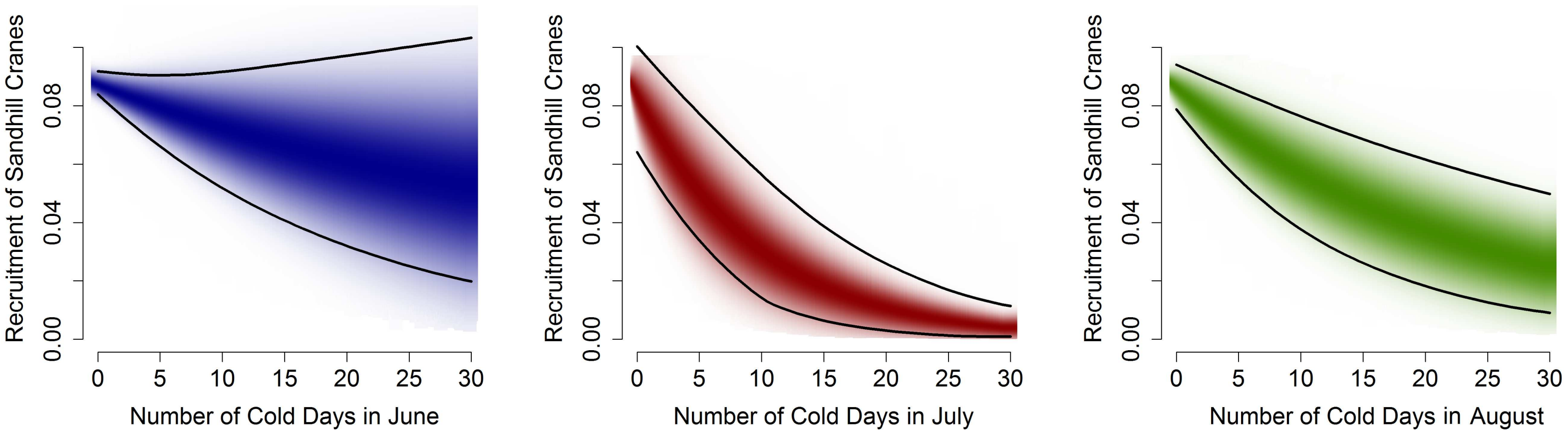

FIGURE 2.11. Variation in predicted juvenile sandhill crane recruitment across the number of freezing days during the breeding season from an optimal out-of-sample predictive model, fit by LASSO ($\mathcal{M}_{P1}$). Drought indices are held constant at their mean. The uncertainty is shaded in proportion to the posterior predictive distribution and the lines are 95% credible intervals.

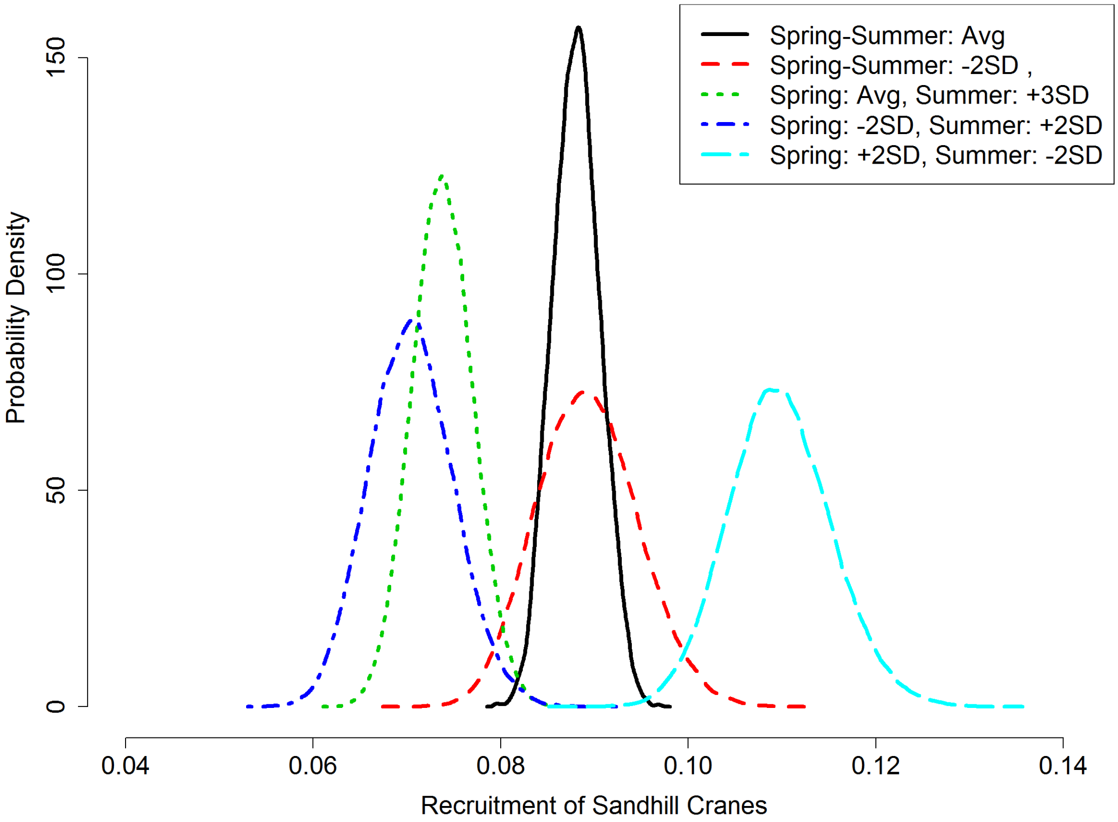

FIGURE 2.12. Variation in predicted juvenile sandhill crane recruitment across alternative scenarios of maximum snow depth during the spring (March-April) and summer months (May-Aug) from an optimal out-of-sample predictive model, fit by LASSO ($\mathcal{M}_{P1}$). The number of freezing days within a month and drought predictors are held constant at their mean. SD indicates standard deviation, such that -2SD is 2 SD below the mean predictor value.

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CHAPTER 3

Transient dynamics of a slow life-history species exposed to anthropogenic removal

3.1. Summary

The importance of transient dynamics of structured populations (non-equilibrium population change due to the stage structure) is increasingly recognized in ecology. Populations with high potential for transient dynamics are those that are frequently perturbed and/or of species that are long-lived and slowly reproduce (i.e., slow life-history). Despite calls for investigating transient dynamics of these most sensitive species and populations, applications are uncommon in animal ecology. We use the sandhill crane (*Grus canadensis*) as a model species to investigate short- and long-term population dynamics to better understand potential and realized transient effects of slow life-history species that may be subject to anthropogenic removal of individuals (e.g., harvest, poaching, translocation, incidental take). We specifically investigate, transient potential, population growth under non-equilibrium dynamics, transient and asymptotic sensitivity to vital rate perturbations, and whether observed harvest could impact crane stage structure and lead to population inertia. 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 significant 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. Highly oscillating short-term dynamics are not expected, unless behaviorally mediated. We found sandhill cranes, and likely other long-lived species, are robust to the effects of population inertia due to vital rate perturbations. We also found transient population growth can be very sensitive to vital rates that are relatively insensitive under equilibrium; for sandhill cranes, adult fecundity and survival can equally be important to short-term growth when the majority of the population is in the most productive stage. Practitioners often have to manage wild animal populations without current or historical knowledge about the stage structure. For populations of slow life-history species that are not prone to relatively large perturbations to their most productive individuals (e.g., disease die-offs, large-scale over-harvest, major transformation of key habitats), assuming the population is near the stable stage distribution may be reasonable.

Key-words: hunting, long-lived, non-equilibrium, poaching, population dynamics, sandhill crane, short-term, slow reproducing, transient bounds

3.2. Introduction

Understanding the driving influences (endogenous and exogenous) on wild animal populations is a primary concern in ecology and wildlife conservation and management. For both ecological and conservation studies, prospective analyses using population projection matrices (PPM) 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). However, because limited available data often leads to PPM with stringent assumptions, including time-invariant vital rates and density-independence, these models may often have poor predictive capability (Stott et al., 2011). Despite these limitations, their intuitive structure, analytical tractability (in contrast to high dimensional stochastic models), ability to use projections to better understand the consequences of present conditions (Keyfitz, 1972) and considerable literature on application and interpretation solidifies the importance of PPM in enabling researchers to garner a deep understanding of essential elements of the dynamics of structured populations.

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, 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 management recommendations because a population is unlikely to remain stable for long-term dynamics to shape populations (Koons et al., 2005, 2006). Instead, focusing on short-term dynamics may lead to developing more accurate predictive models (Stott et al., 2010) and a better understanding of perturbation affects 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) = right eigenvector of PPM) and producing dynamics that are different than long-term population trajectories (Stott et al., 2011). Transient dynamics are population change due to 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). Transient effects can contribute to greater variation in population growth than demographic variation alone (Ellis and Crone, 2013). Modeling of structured populations that assume SSD should provide empirical evidence of the appropriateness of this assumption, or otherwise evaluating non-equilibrium dynamics is critical (Koons et al., 2005).

Populations with the highest potential for transient dynamics are of those species with a slow life-history (sensu Sæther and Bakke 2000; long-lived and slow reproducing) and exposed to frequent disturbance (Koons et al., 2005, 2006; Gamelon et al., 2014). Investigating transient dynamics is often encouraged when a population is being harvested (Koons et al., 2006; 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 direct and intentional removal by hunting or fishing, poaching, translocation, or incidental take (e.g., bycatch, collisions with man-made structures). Conversely, transient dynamics may be manipulated to assist in the removal of invasive species (Kidd and Amarasekare , 2012). 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). Population inertia could move a population past management objectives or influence the time it takes for a population to reach a population objective (Koons et al., 2006).

Despite the recent advancements and recommendations for evaluating transient dynamics in wild animal populations, their application remains largely in plant ecology (Stott et al., 2010; Ellis, 2013). Few have investigated animal species and populations that are potentially most sensitive to learn about short-term dynamics that could inform ecologists and wildlife practitioners (Buhnerkempe et al., 2011). We are interested in exploring both short- and long-term population change using a potentially sensitive and harvested species, while considering a range of common uncertainties, 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 annual harvest (see Gerber et al. 2014). Crane researchers and managers have identified a high priority for information regarding how harvest may affect population inertia (Case and Sanders, 2009).

We hypothesize stage-structured population models for the sandhill crane to, 1) evaluate characteristics of maximum potential transient dynamics of slow life-history species, 2) examine how stage structure effects population growth and the time it takes for population recovery, 3) examine transient and asymptotic sensitivity to 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 insights into short- and long-term dynamics of species that are long-lived, slow reproducing, and with delayed reproduction that may be subjected to anthropogenic removal of individuals (e.g., harvest, poaching, translocation, incidental take). We also provide specific recommendations informing sandhill crane population management.

3.3. Materials and methods

3.3.1. Study species and population.

Sandhill cranes are large birds that primarily nest in shallow freshwater wetlands (Gerber et al., 2014). 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). 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 (Gerber et al., 2014). Typically, a pair of sandhill cranes produce a single clutch of two eggs per nesting season.

We focus on the Rocky Mountain Population (RMP) of sandhill cranes because it has been harvested for a number of years and detailed information on vital rates exists. The RMP is migratory, nesting in low densities throughout Wyoming, Montana, Idaho, Utah, and Colorado, stopover during spring and fall migration in the San Luis Valley (SLV) of Colorado, and winter primarily in the Rio Grande Valley of New Mexico (Drewien & Bizeau, 1974). Historical abundances have been estimated to be as low as 400-600 in the mid-1940's (Walkinshaw, 1949) and 10,000-15,000 in 1971-1972 (Drewien & Bizeau, 1974). More recently, the population has been estimated (using a 3-year mean of pre-migratory fall counts) to average 19,560 between 2000-2013 (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.

3.3.2. POPULATION MODELS. We hypothesized four population models that integrate available empirical population-level vital rates and capture uncertainties about age-specific reproduction. Survival parameters come from a long-term mark-resight study (1972-1992, Kendall, W.L. and R.C. Drewien, unpublished data), which indicate differential survival without harvest by ages 0-0.5, 0.5-1.5, and $\geq$1.5 years of age. We consider four PPM: 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, Figure 3.1), 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, , Figure 3.1), and 4) 9 stages with non-zero fecundity increasing starting at stage 3 (PPM4, , Figure 3.1).

We parameterized all PPM 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 is the survival between ages i and $i+1$, and F is the per capita fecundity in the SLV. The terminal column represents the dynamics of all individuals that live beyond the finite number of stages represented by each PPM. For all PPM, S_1 and S_2 are unique values, while survival remains constant after 2 years of age ($S_1 = 0.848$, $S_2 = 0.947$, $S_{\geq 3} = 0.955$). 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 scale fecundity by partial year terminal survival. The fecundity per individual is thus calculated as, $F = PropBreeders \times \frac{brood}{2} \times S_5^{8/12}$. Analyses were performed in the R (R Core Team, 2015) using the package "popdemo" (Stott et al., 2012b).

3.3.3. Transient potential. 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-case 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 3.1 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).

3.3.4. 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 each population model using initial stage distributions from the complete set of permutations of each stage at increments of 0.05 (e.g., PPM1: [1 0 0 0 0] = only juveniles, [0.95 0.05 0 0 0], etc.). We initialize each population 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.

3.3.5. Transient and asymptotic sensitivity analysis. 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). 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 affect 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) and apply them to PPM1.

3.3.6. Transient dynamics under 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 α_i for each i^{th} stage. We considered two scenarios, 1) where harvest of juveniles averages 20% and the rest of the harvest is evenly distributed, on average, among the remaining stages (e.g., PPM1, $\alpha_i = 1$ 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 indicates 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 and then ceased 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 2000-2013 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.

3.4. RESULTS

3.4.1. TRANSIENT POTENTIAL. Population models indicate the RMP would be growing slowly without harvest (Table 3.2); 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. Our population models reveal, relative to a population at the SSD and over the same time frame, a greater potential to reach lower abundances than higher abundances (Table 3.2). Thus, there is a high potential for non-SSD to reduce population growth. 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 (Figure 3.2). However, the potential for the population growth to exceed one growing according to the SSD in the long-run is not tied necessarily to a population initialized with only individuals in the first stage with non-zero fecundity. 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 (Figure 3.2). Lastly, an increase in delayed reproduction (PPM1 vs. PPM2) has a minor affect on reactivity and first-time step attenuation, but has a relatively large affect on long-term outcomes of population size (Table 3.2).

3.4.2. 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 (Figures 3.3-3.6). 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 eventually 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 (Figure 3.3). Among population models, 6-81% of initial stage structures translate into immediate population growth (GR>1) in the first year and 3 to 7 years before ≥95% were positively growing (Figure 3.7). 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 (≥95%) in 4-12 years and the lower RMP objective in 5-18 years.

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 (Figure 3.8). The *Tacha* stage structure 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 3.3). 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.

3.4.3. TRANSIENT AND ASYMPTOTIC SENSITIVITY ANALYSIS. Traditional sensitivity analyses generally approximated the non-linear relationship between vital rate perturbation and its affect on λ_∞, except for relatively large magnitude perturbations (Figures 3.9-3.12; e.g., PPM1 perturbation on survival > 0.2); large perturbations to terminal-stage fecundity and non-terminal-staged survival were underestimated, while terminal staged survival was overestimated. Survival parameters that are not of the terminal stage are robust to perturbations; a decrease of survival by 0.4 would not cause λ_∞ to decline below one (Figure S5-8). Across all models, we found λ_∞ most sensitive to terminal-stage 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 3.4). However, a direct drop in terminal stage fecundity by 0.06 or 0.07 would cease growth for PPM1-2, and 4. 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 (Figure 3.13-3.16). The most sensitive vital rates to population 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 (Figure 3.13-3.16). 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 affect 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 affects of perturbations are mostly similar to the SSD for all models.

Transient sensitivity of population growth to vital rates of PPM1 were highly variable depending on the stage structure (Figure 3.17). There was strong temporal variation until sensitivities converged to asymptotic results (i.e., unscaled derivative of the population growth rate with respect to a vital rate), which occurred in 10 to 15 years, depending on the vital rate. 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 affect 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. 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 (Figure 3.17). In addition, while asymptotically population growth is more sensitive to terminal-stage survival than fecundity, under non-equilibrium dynamics with even the majority of the population in the terminal stage, transient growth is fairly equivalently sensitive to both vital rates.

3.4.4. TRANSIENT DYNAMICS UNDER 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 population model or whether harvest was on average evenly distributed or in proportion to the stage structure (Figure 3.18 and 3.19). 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 affects 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 - 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 stricture (1.000, 1.000), and an even distribution (1.000, 1.001) were not considerable.

3.5. Discussion

3.5.1. Transient dynamics and life-history. For a slow life-history species, such as the sandhill crane, there is 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). Every 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 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 these species have evolved behavioral 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 Bakke 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 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 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).

Slow life-history species may be robust to transient dynamics because of 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 amplified inertia and transient growth above λ_∞ is limited by the slow reproductive potential (i.e., low fecundity) of even the most productive individuals. In contrast, attenuated inertia and transient growth is unlikely because of evolutionary strategies that have minimized natural variability of adult survival (Sæther and Bakke, 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 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 ±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).

The affect 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 effects 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 effect population demography, 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, can not be sexed or aged (beyond a short immature stage), thus harvest programs are neither sex- or 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 be harvested.

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 be harvested. 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). However, this additional impact on juveniles may have little affect 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 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 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., 2014). 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.

The affect of removal of individuals on social dynamics can not be overlooked. Selective removal of certain 'keystone' individuals from the population can have an overwhelming disproportional affect 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.

3.5.2. RMP TRANSIENT DYNAMICS. Based on the increasing conservation of wetland habitats in the 20^{th} century, a long duration during which the RMP was not exposed to sport harvest, substantial population growth between the 1940's and the beginning of harvest in 1981, and low variability in adult survival (Drewien, R.C., unpublished data), it is reasonable to suspect 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. We found our crane population models to be robust to current levels of harvest and relatively large perturbations to vital rates in causing transient dynamics. 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., 2006), effects may have to be relatively large and skewed toward the productive stages to actually cause considerable population inertia (this study; Koons et al. 2006). 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 less than 10 years.

Assuming the RMP is 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. 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. 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 2-4 years before the population will be harvestable and 6-9 years (without harvest) before the population exceeds the lower population objective. 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, B., unpublished data), thus obscuring true abundance and the time it would take to detect a population decline and adjust harvest.

This lack of reliable annual population estimates also inhibits us in validating whether any of 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 (*Grus americana*; only other North American crane), which was estimated over a 73 year time period to average near 4% growth (Butler et al., 2013). Golden eagles, which also have a similar life-history history to cranes (delayed reproduction to 5 years of age and a typical clutch of two eggs per nest) are also estimated to have a similar growth rate ($\approx$ 2% annual growth; Tack, J. unpublished data).

3.5.3. Conclusion. Recently developed tools to investigate transient dynamics enable ecologists and wildlife practitioners to better understand animal population dynamics. These tools are most powerful when the stage structure is known and transient growth, and its sensitivity to changes in vital rates for the current reality, can be explicitly examined. Even when the stage structure is not known, 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 can't 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 likely disturbances and their affect 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, particular the extremes, which would cause the largest potential differences between stage structures.

Populations may be buffered from perturbations inducing transient effects because of density-dependent processes. 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 the sandhill crane RMP, 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).

Wildlife 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; assuming population growth is most sensitive based on asymptotic findings may lead to sub-optimal and even ineffectual strategies. 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 returns.

Having direct information on the stage or age structure can be beneficial in predicting short-term dynamics (Ellis and Crone, 2013) that can help guide management decisions (Hauser et al., 2006). However, for many animals this information is not easily obtained. For long-lived species, it may be reasonable to assume 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 affects 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 potential.

3.6. Tables and Figures

Table 3.1. Biological interpretations of transient metrics, adapted from Stott et al. (2011, Table 1).

Index	Interpretation
Reactivity	Maximum population size of a structured population not at equilibrium in a single time step, relative to a population size at equilibrium.
First Time Step Attenuation	Minimum population size of a structured population not at equilibrium in a single time step, relative to a population at equilibrium.
Max. Amplification	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.
Max. Attenuation	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.
Amplified Inertia	The maximum asymptotic (long-term) population size of a population initialized not at equilibrium, relative to a population of the same size and initialized at equilibrium.
Attenuated Inertia	The minimum asymptotic (long-term) population size of a population initialized not at equilibrium, relative to a population of the same size and initialized at equilibrium.

TABLE 3.2. 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 Rocky Mountain Population.

	Years to Population >15,000				Years to Population >17,000			
Model	Adult[b]	Stable[c]	Tacha[d]	Even[e]	Adult	Stable	Tacha	Even
PPM1[a]	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] Population projection matrix (PPM).

[b] Initial population of only the terminal stage.

[c] Initial population following the stable stage distribution.

[d] Initial population at the stage distribution according to Tacha et al. 1989.

[e] Initial population evenly distributed among all stages.

Table 3.3. Single vital rate perturbations to sandhill crane population projection matrices (PPM) that stabilize long-term growth ($\lambda_\infty = 1$). The most sensitive survival by stage (S_{stage}) and per capita fecundity (F_{stage}) for each PPM are highlighted in grey.

Vital Rate	PPM1	PPM2	PPM3	PPM4
F or F9[a]	-0.06	-0.05	-0.27	-0.05
F8	NA[b]	NA	NA	NF[c]
F7	NA	NA	NA	NF
F6	NA	NA	NA	NF
F5	NA	NA	NA	NF
F4	NA	NA	NA	NF
S_1	-0.42	-0.34	-0.67	-0.36
S_2	-0.47	-0.38	-0.75	-0.41
S_3	-0.47	-0.38	-0.75	-0.41
S_4	-0.47	-0.38	-0.75	-0.41
S_5	-0.04	-0.38	-0.75	-0.41
S_6	NA	-0.38	-0.76	-0.42
S_7	NA	-0.38	-0.79	-0.42
S_8	NA	-0.38	-0.83	-0.44
S_9	NA	-0.03	-0.29	-0.04

[a] Stage structured vital rates of survival by stage (S_{stage}) and per capita fecundity (F_{stage}).

[a] F applies only to PPM1 and F9 applies to PPM2-4.

[b] NA = Not Applicable.

[c] NF = Not Feasible.

Table 3.4. Transient metrics for four hypothesized sandhill crane population models for the Rocky Mountain Population.

Indices	PPM1	PPM2	PPM3	PPM4
Asymptotic Growth (λ_∞)	1.03	1.02	1.09	1.02
Reactivity ($\bar{P}_1$)	1.04	1.06	1.22	1.05
First Time Step Attenuation ($\underline{P}_1$)	0.82	0.83	0.78	0.83
Max. Amplification ($\bar{P}_{max}$)	1.07	1.14	1.34	1.12
Max. Attenuation ($\underline{P}_{max}$)	0.65	0.52	0.45	0.59
Amplified Inertia ($\bar{P}_\infty$)	0.69	0.59	0.53	0.62
Attenuated Inertia ($\underline{P}_\infty$)	1.06	1.12	1.29	1.11

$$PPM2 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & F \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_7 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_8 & S_9 \end{pmatrix}$$

$$PPM3 = \begin{pmatrix} \alpha_1 & \alpha_2 & \alpha_3 & \alpha_4 & \alpha_5 & \alpha_6 & \alpha_7 & \alpha_8 & \alpha_9 \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_7 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_8 & S_9 \end{pmatrix}$$

$$PPM4 = \begin{pmatrix} \alpha_1 & \alpha_2 & \alpha_3 & \alpha_4 & \alpha_5 & \alpha_6 & \alpha_7 & \alpha_8 & \alpha_9 \\ 0 & 0 & 0 & 0.05 \times F & 0.1 \times F & 0.2 \times F & 0.4 \times F & 0.5 \times F & F \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_7 & 0 & \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_8 & S_9 \end{pmatrix}$$

FIGURE 3.1. For PPM2 and PPM3, F = $PropBreeders \times \frac{brood}{2} \times S_9^{8/12}$, *PropBreeders* = 0.20 from Drewien, R.C., pers. comm. and Case and Sanders (2009). For PPM3 and PPM4, $\alpha_i = PropBreeding_i \times \frac{brood}{2} \times S_i$, where *PropBreeding* = [0 0 0 0 0 0.154 0.333 0.600 0.500] from Tacha (1989) for PPM3 and *PropBreeding* = [0 0 0 0.05 0 0.10 0.20 0.40 0.50 1] from Tacha (1989) for PPM4. For all PPM, *brood* = 1.23 from Drewien (2011).

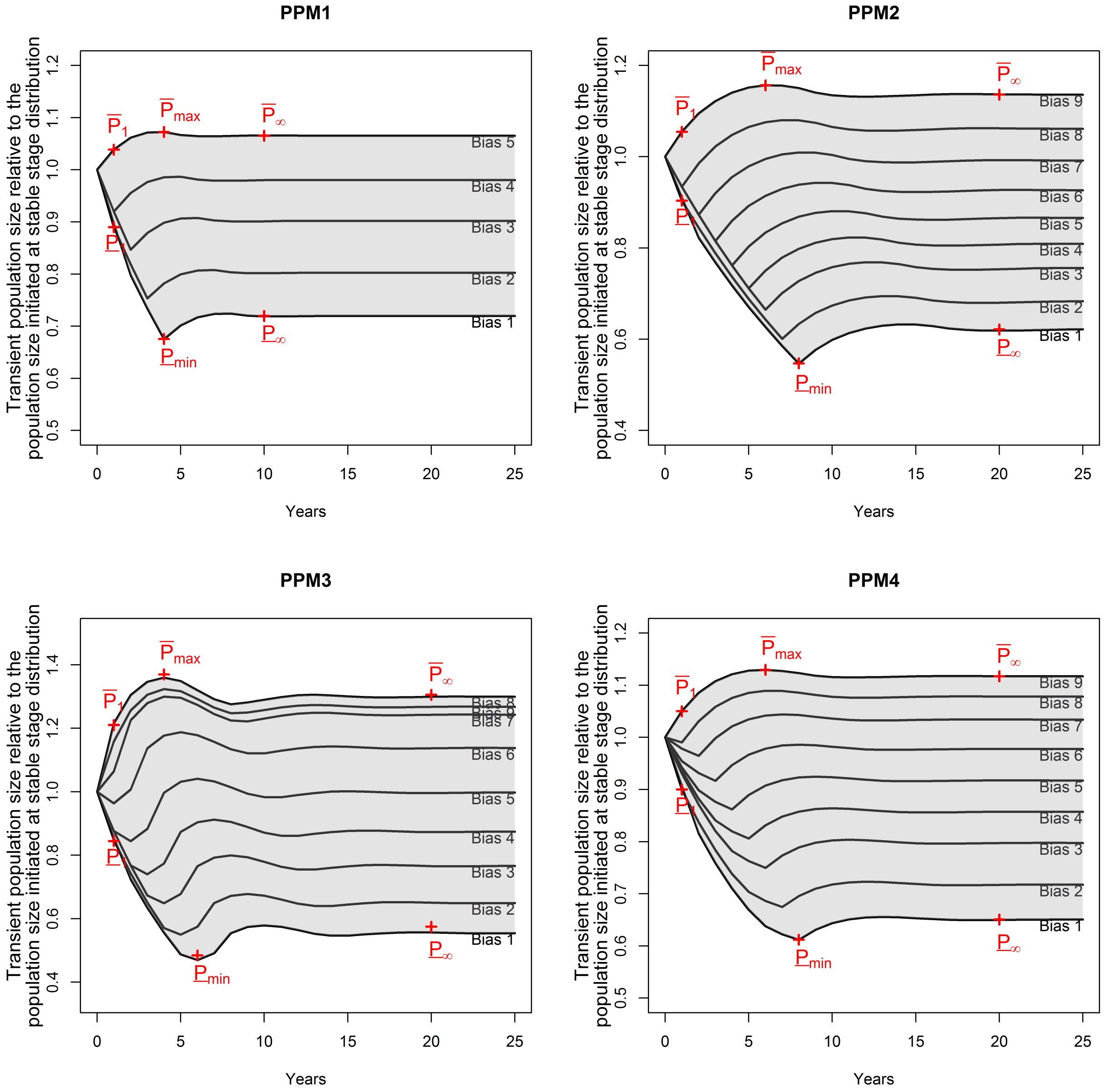

FIGURE 3.2. Stage-biased transient potential for sandhill cranes of the Rocky Mountain Population. Each line is a population initialized with individuals only belonging to a single stage, relative to a population initialized at the stable stage distribution. $\bar{P}_1$ =Reactivity. $\underline{P}_1$ =First time step Attenuation. $\bar{P}_{max}$ = Maximum amplification. $\underline{P}_{min}$ = Maximum Attenuation. $\bar{P}_\infty$ = Amplified Inertia. $\underline{P}_\infty$ = Attenuated Inertia.

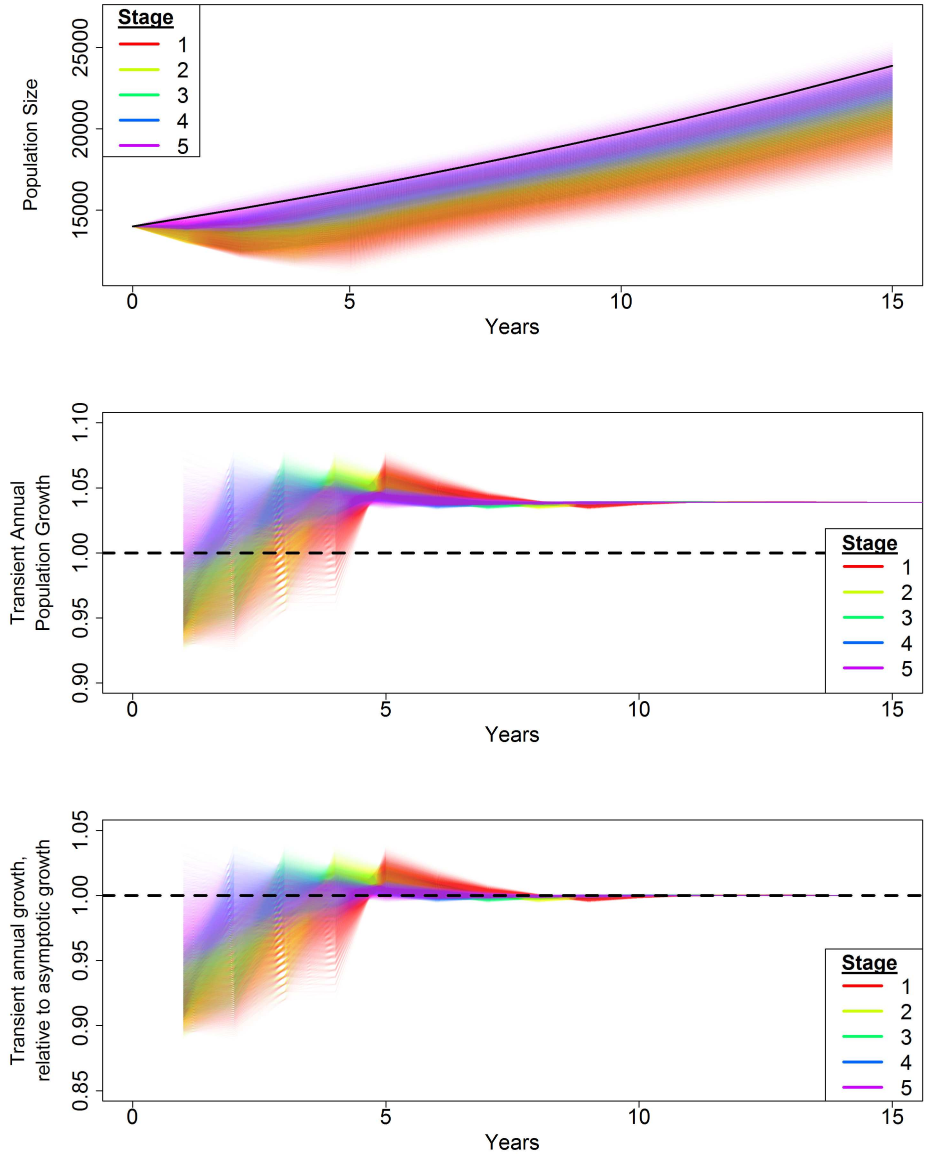

FIGURE 3.3. Projected population size over time (top), transient population growth (middle), and transient population growth relative to λ_∞ (bottom) across all permutations of initial population structures for PPM1. The legend indicates the initial stage (1= juvenile, 5= oldest stage) with the majority of individuals ($\geq$50%). The solid black line in the top figure is population growth according to the stable stage distribution.

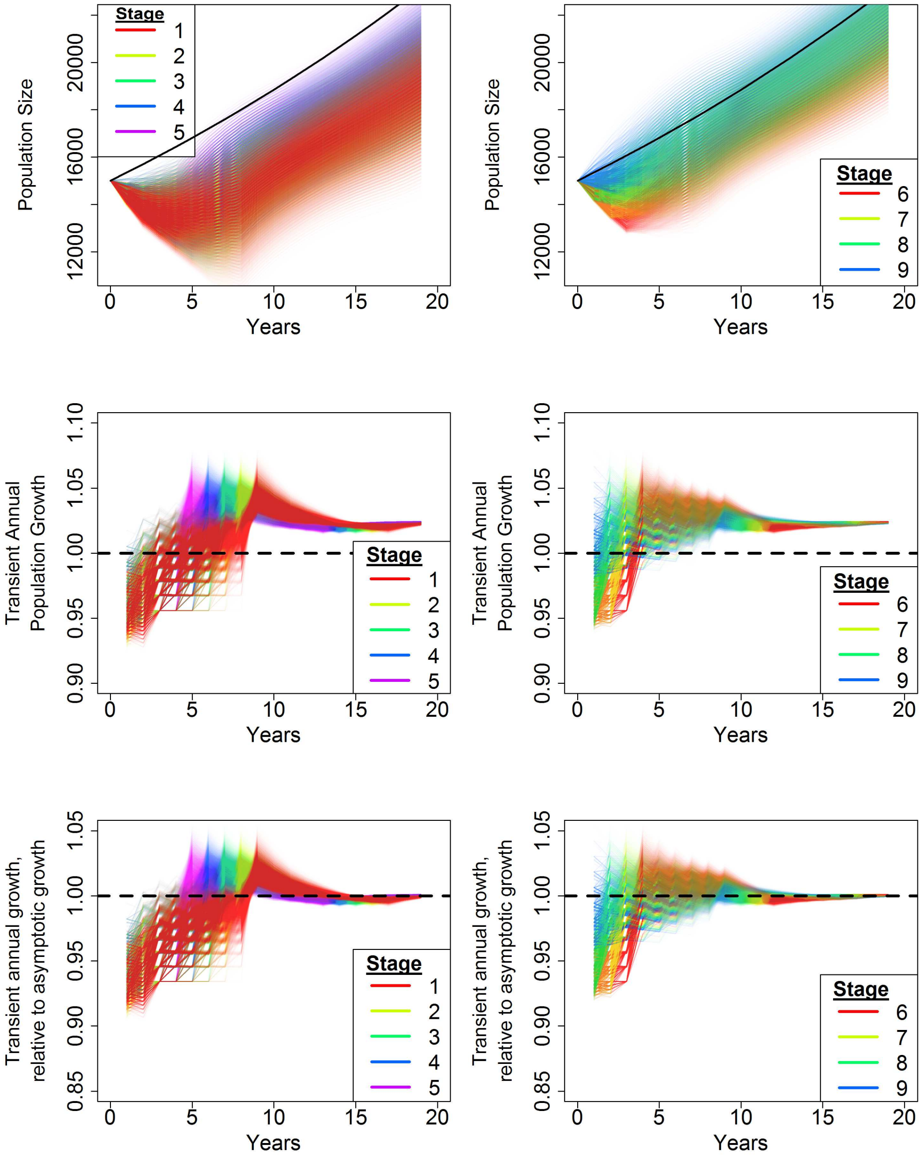

FIGURE 3.4. Projected population size over time, transient population growth, and transient population growth relative to λ_∞ across the complete set of initial population structures at intervals of 0.05 for PPM2. The numbers in the legend indicate the initial stage (1= juvenile, 9= oldest stage) with the majority of individuals. The solid black line in the top figure is population growth according to the stable stage distribution.

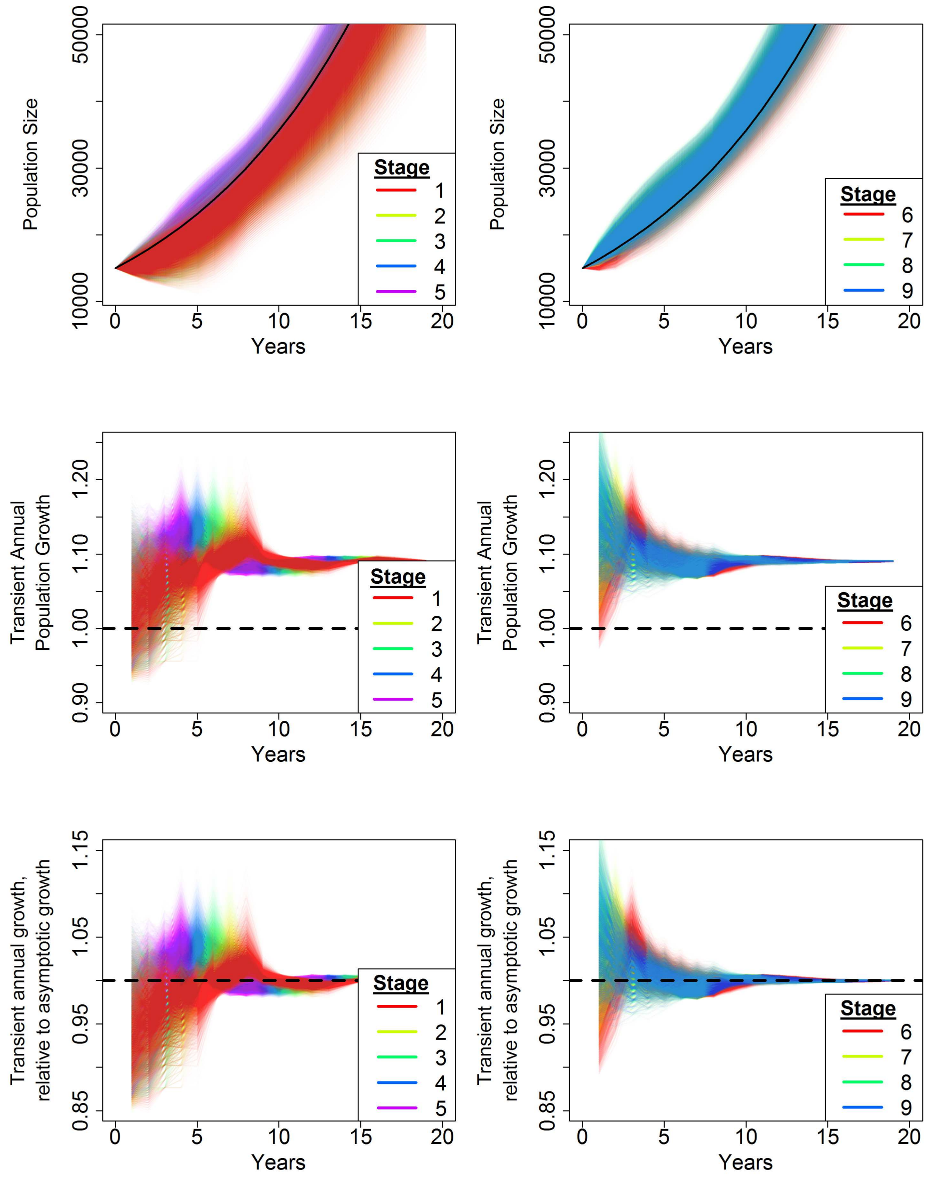

FIGURE 3.5. Projected population size over time, transient population growth, and transient population growth relative to λ_∞ across the complete set of initial population structures at intervals of 0.05 for PPM3. The numbers in the legend indicate the initial stage (1= juvenile, 9= oldest stage) with the majority of individuals. The solid black line in the top figure is population growth according to the stable stage distribution.

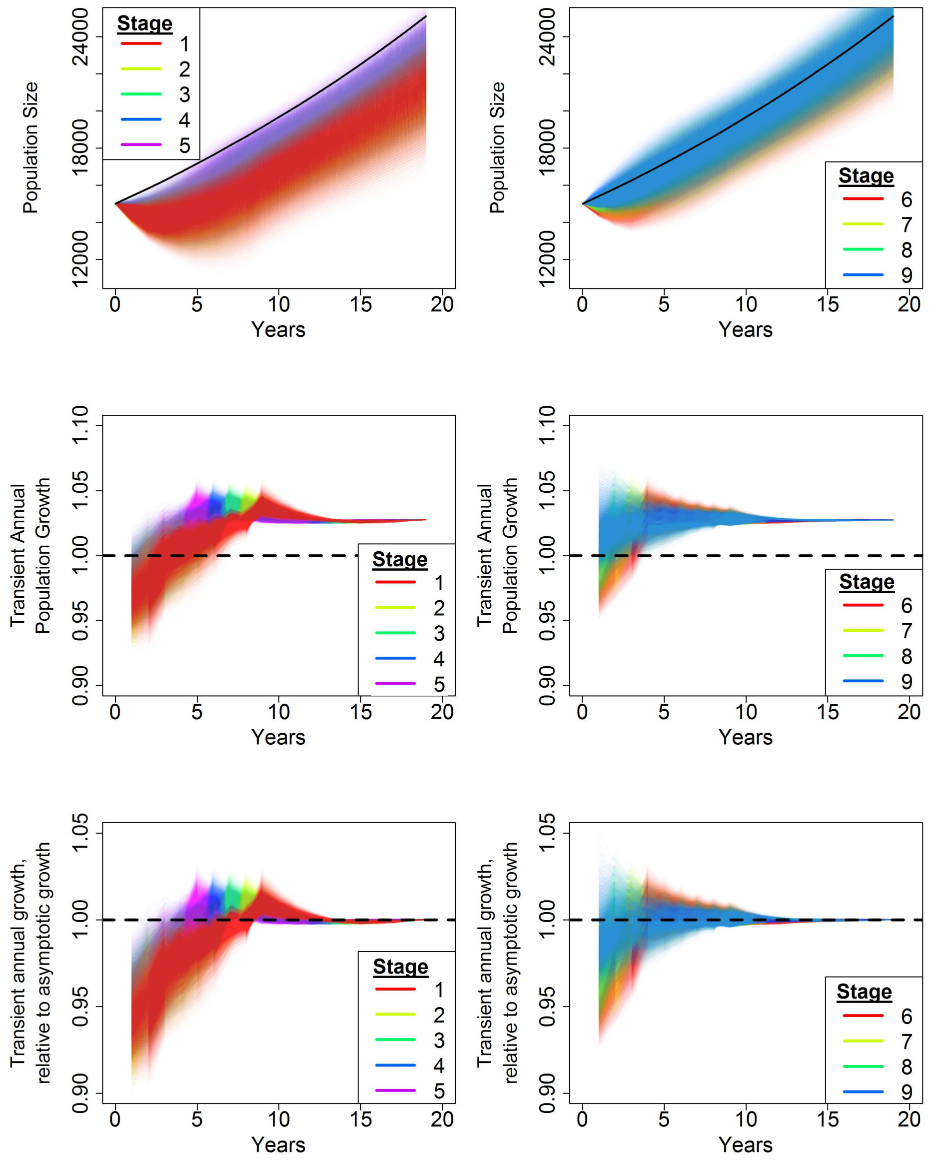

FIGURE 3.6. Projected population size over time, transient population growth, and transient population growth relative to λ_∞ across the complete set of initial population structures at intervals of 0.05 for PPM4. The numbers in the legend indicate the initial stage (1= juvenile, 9= oldest stage) with the majority of individuals. The solid black line in the top figure is population growth according to the stable stage distribution.

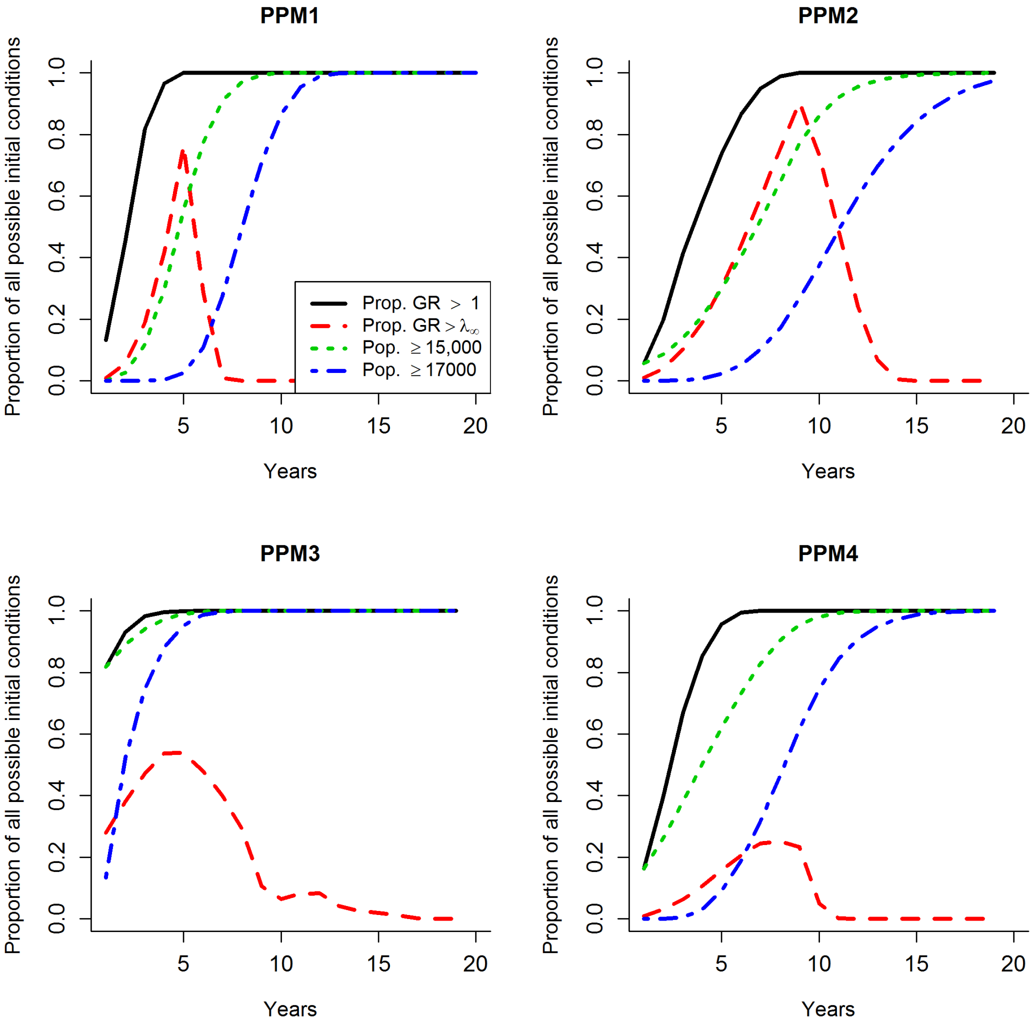

FIGURE 3.7. Proportion of projected populations initialized at all permutations of stage structures that: have a positive growth rate (GR), are growing equal to or larger than the asymptotic growth rate, are harvestable (Pop. ≥ 15,000), and are above the lowest population objective (Pop. ≥ 17,000), for each year from initiation 1-20.

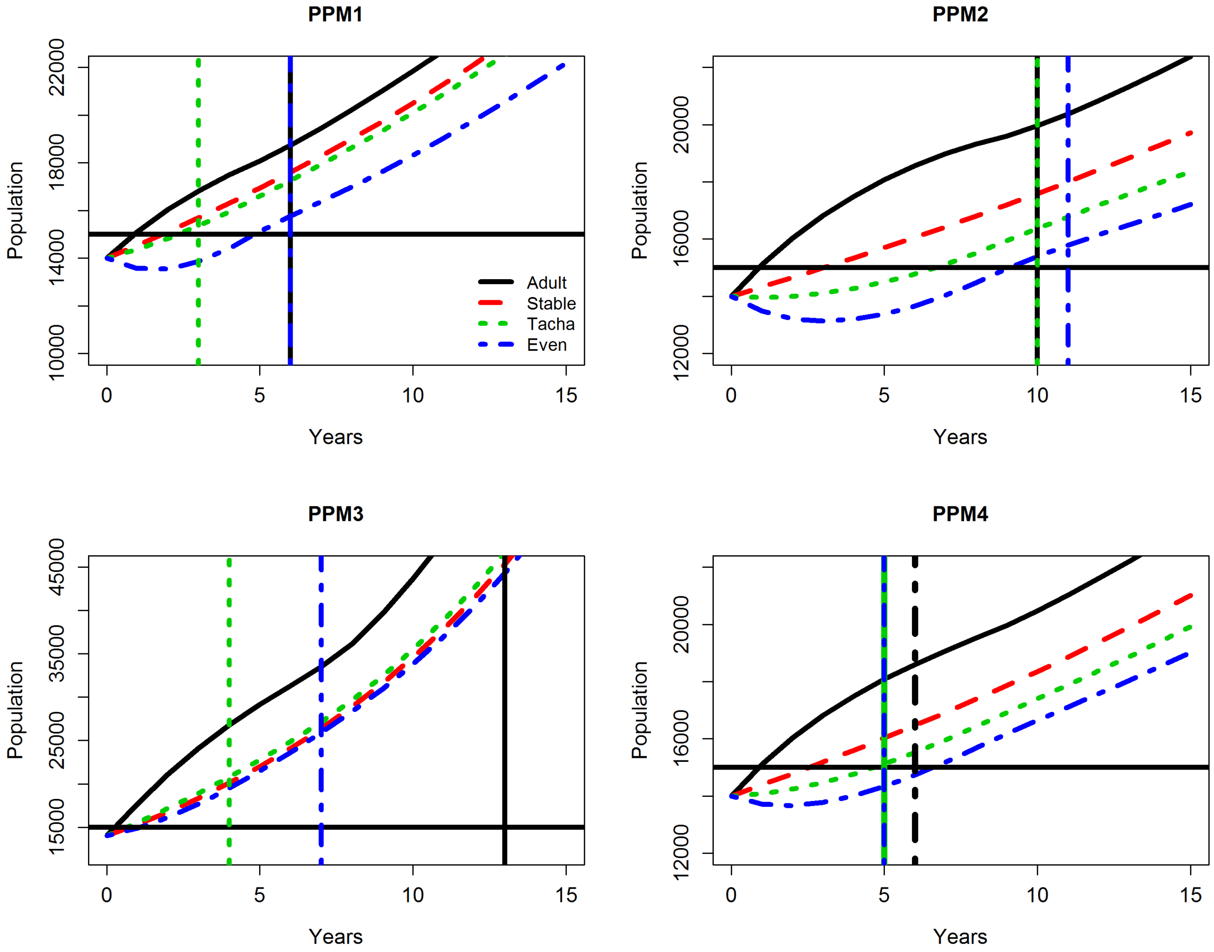

Figure 3.8. Projected populations under four population projection matrices (PPM) for sandhill cranes of the Rocky Mountain Population (RMP). Each is initialized at 14,000 birds with four alternative initial stage distributions. The vertical lines indicate convergence to asymptotic dynamics and the horizontal line indicates when RMP cranes can begin to be harvested. Notice the y-axes are not equivalent.

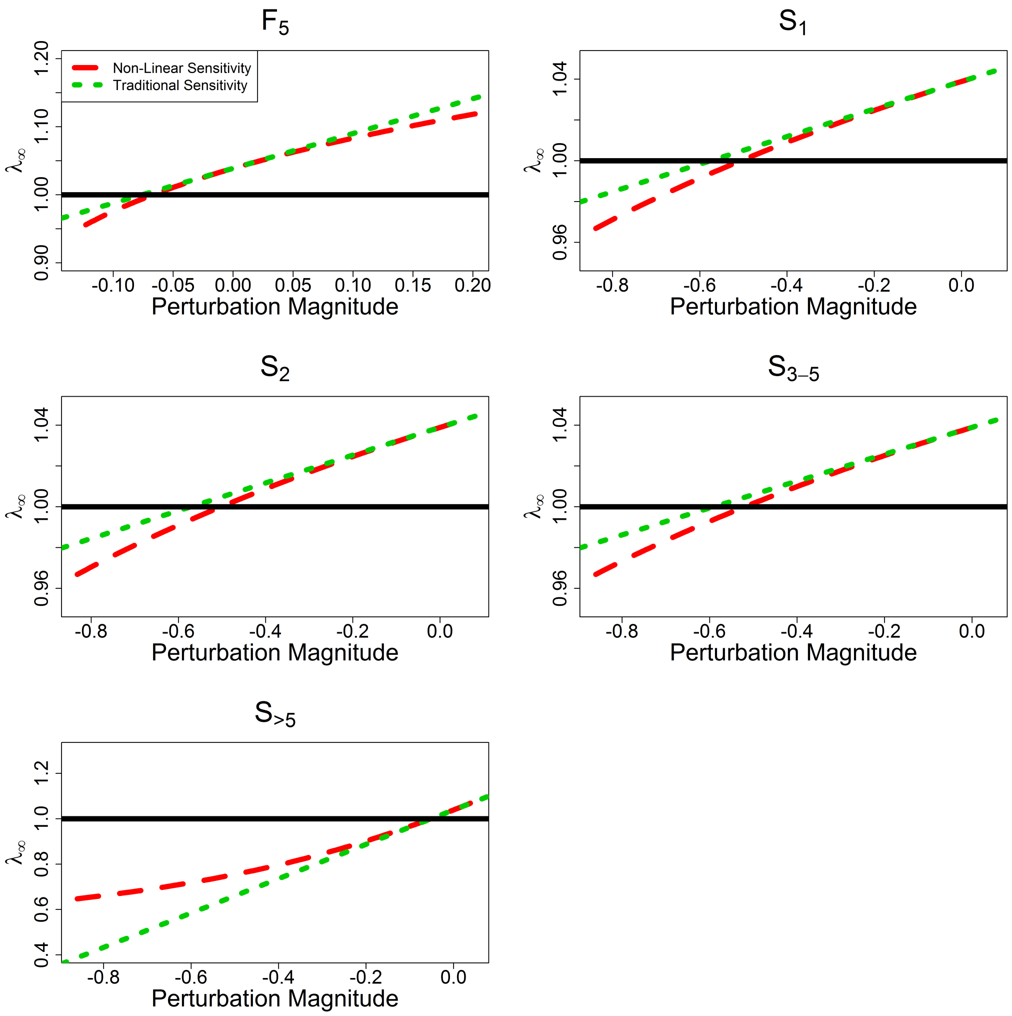

FIGURE 3.9. Traditional linear and non-linear (transfer function analysis) sensitivity analyses of vital rates of PPM1 and their affect on the asymptotic growth rate (λ_∞). Notice the y-axes are not the same.

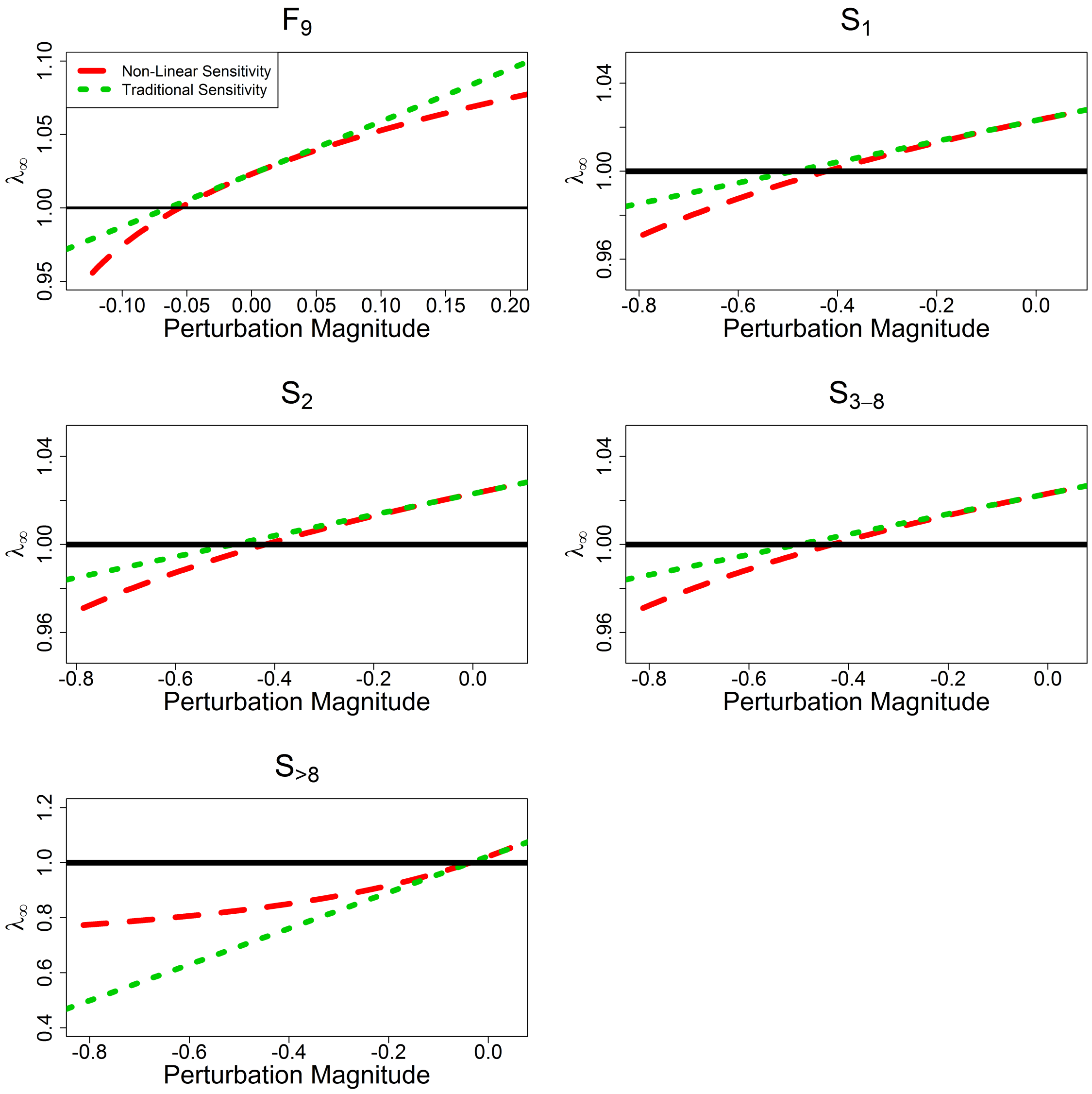

FIGURE 3.10. Non-linear perturbation analyses of vital rates of PPM2 and their affect on the asymptotic growth rate (λ_∞). Notice the y-axes are not scaled the same.

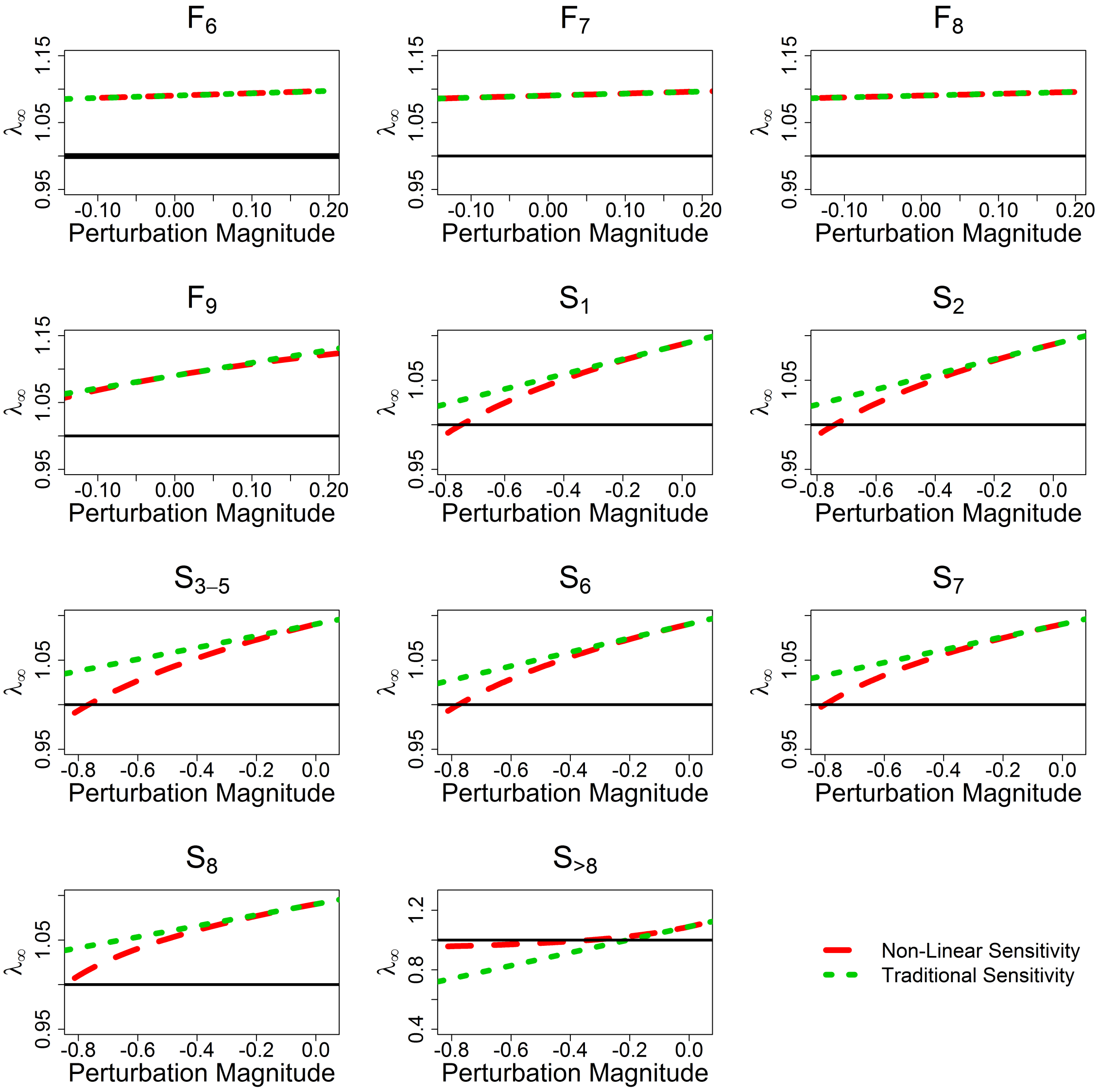

FIGURE 3.11. Non-linear perturbation analyses of vital rates of PPM3 and their affect on the asymptotic growth rate (λ_∞). Notice the y-axes are not scaled the same.

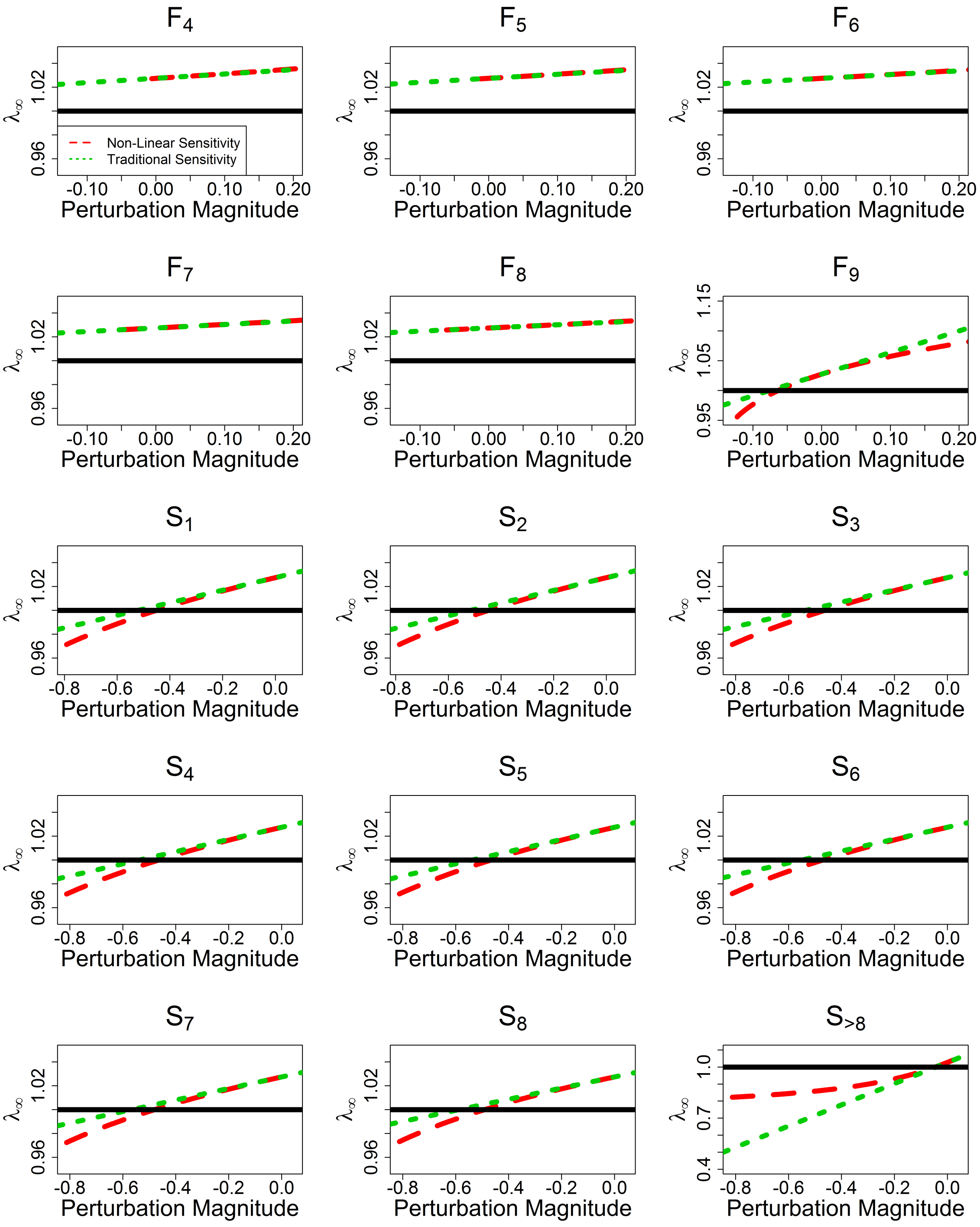

FIGURE 3.12. Non-linear perturbation analyses of vital rates of PPM4 and their affect on the asymptotic growth rate (λ_∞). Notice the y-axes are not scaled the same.

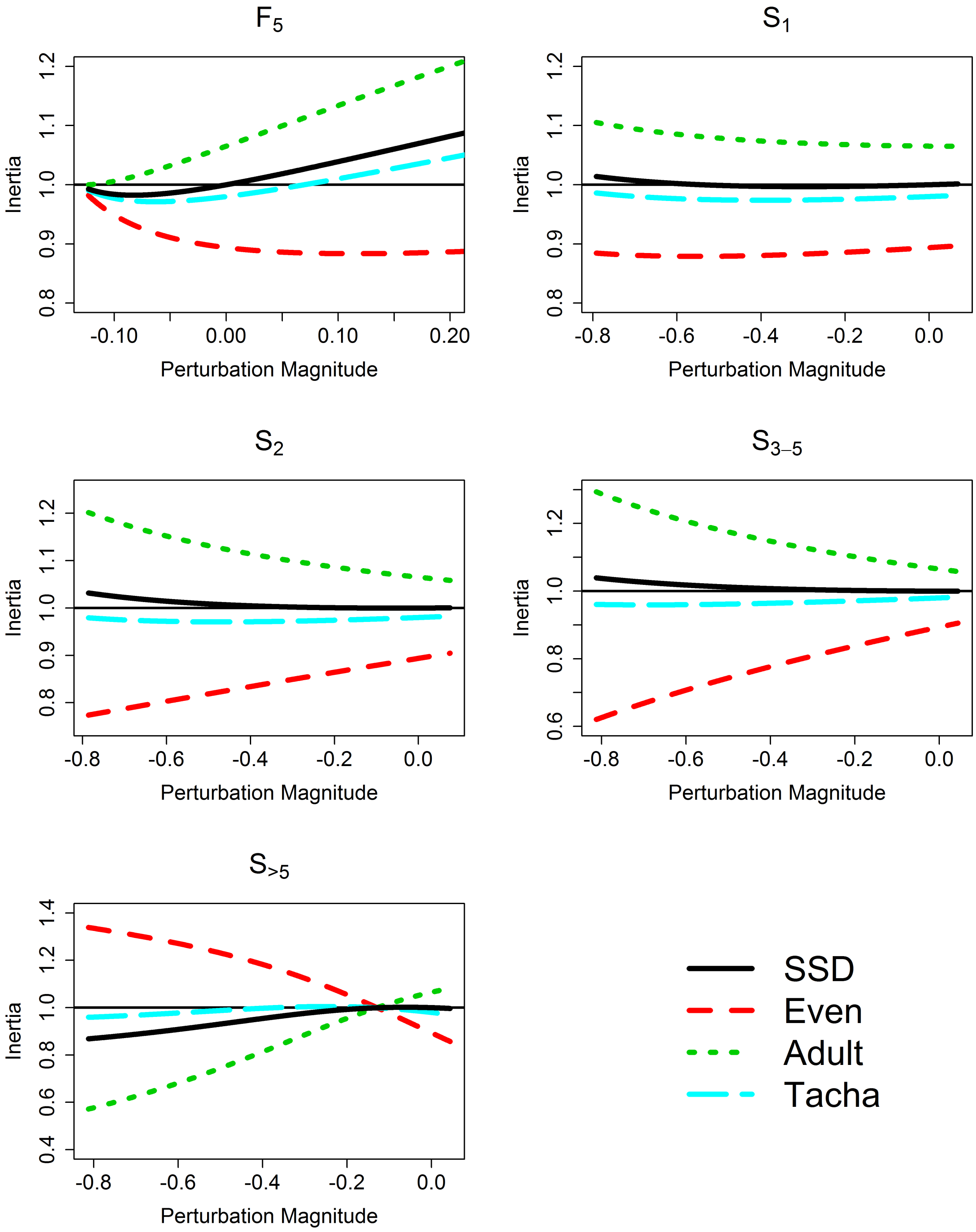

FIGURE 3.13. Non-linear perturbation analyses of vital rates of PPM1 and their effect on population inertia and initial stage distribution; Initial pre-perturbation stage distributions: "SSD" is stable stage distribution, "Even" is a stage distribution with individuals distributed evenly, "Adult" is a population with only individuals of the oldest stage, and "Tacha" assumes a stage distribution estimated from the mid-continent population of sandhill cranes (Tacha et al., 1989).

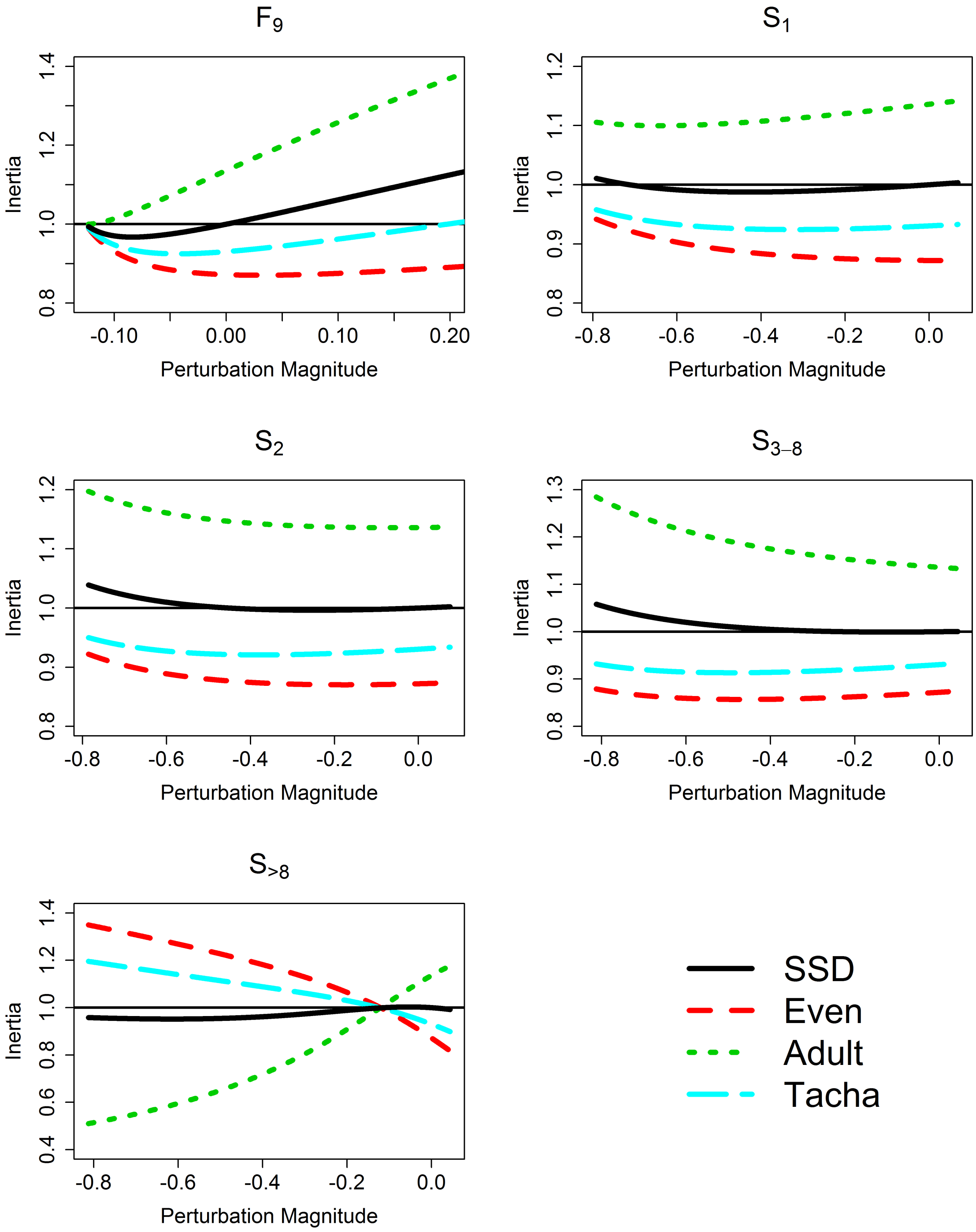

Figure 3.14. Non-linear perturbation analyses of vital rates of PPM2 and their effect on population inertia; comparison using different initial stage distributions: "SSD" is stable stage distribution, "Even" is a stage distribution with individuals distributed evenly, "Adult" is a population with only individuals of the oldest stage, and "Tacha" assumes a stage distribution estimated from the mid-continent population of sandhill cranes (Tacha et al., 1989).

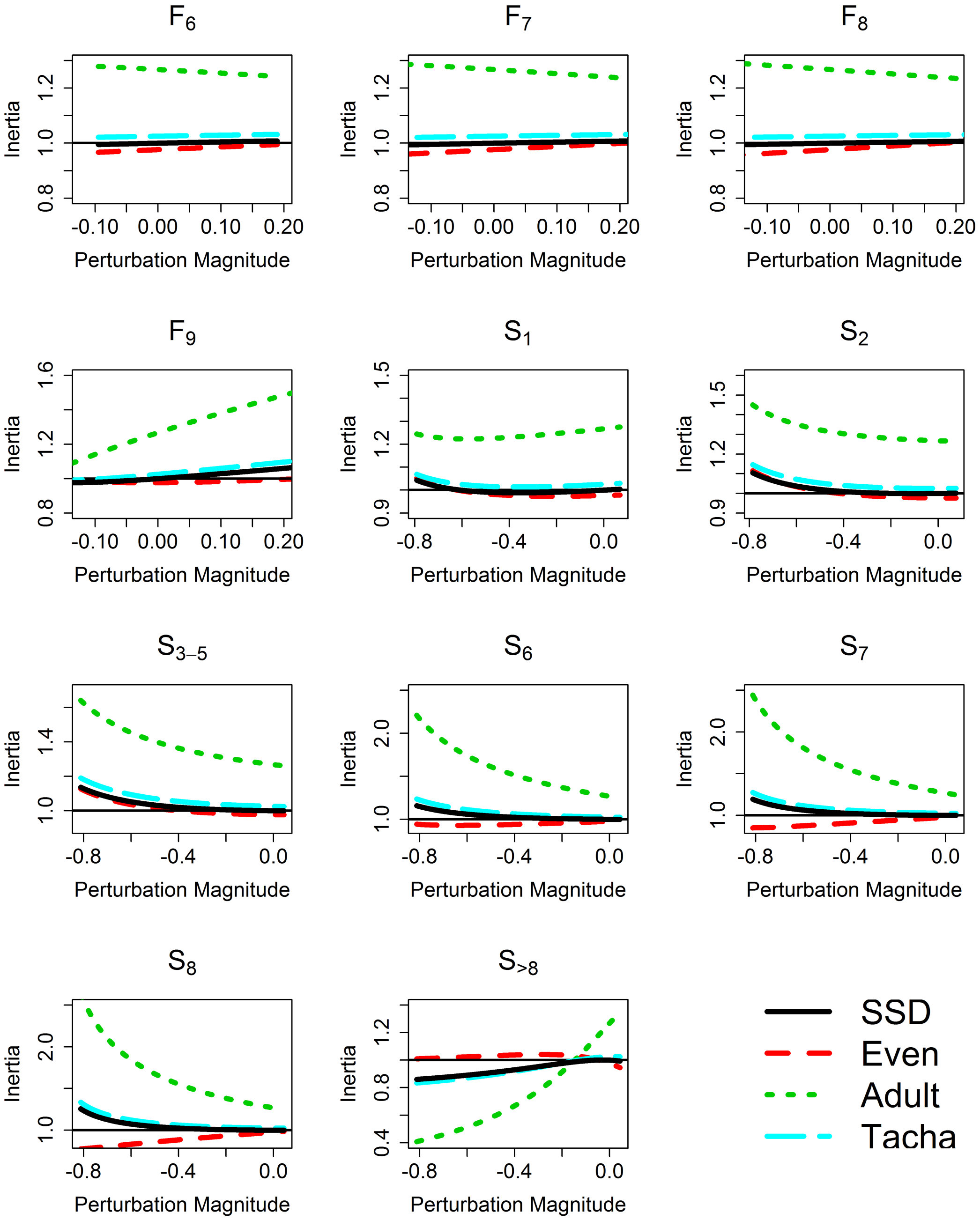

FIGURE 3.15. Non-linear perturbation analyses of vital rates of PPM3 and their effect on population inertia; comparison using different initial stage distributions: "SSD" is stable stage distribution, "Even" is a stage distribution with individuals distributed evenly, "Adult" is a population with only individuals of the oldest stage, and "Tacha" assumes a stage distribution estimated from the mid-continent population of sandhill cranes (Tacha et al., 1989).

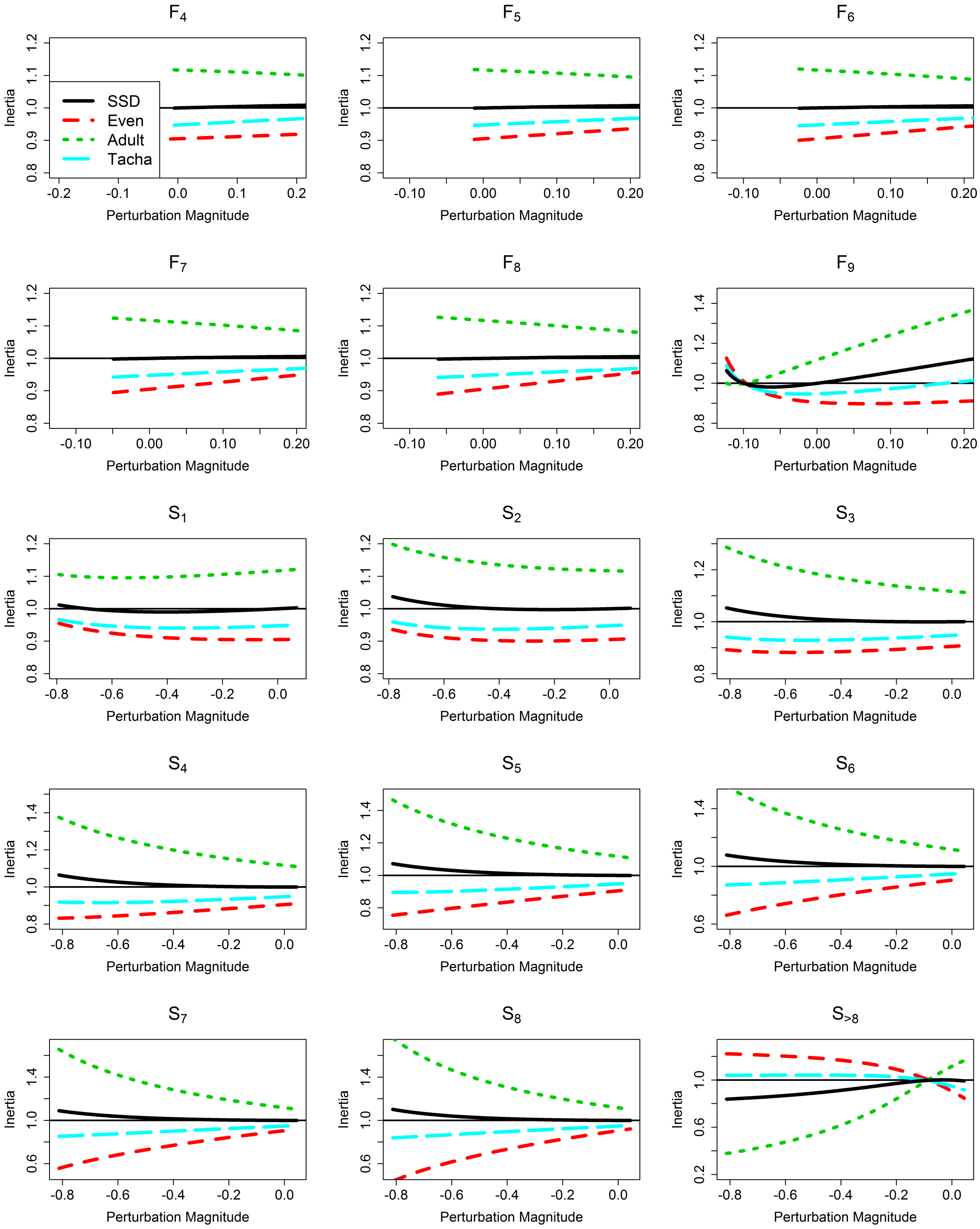

FIGURE 3.16. Non-linear perturbation analyses of vital rates of PPM4 and their effect on population inertia; comparison using different initial stage distributions: "SSD" is stable stage distribution, "Even" is a stage distribution with individuals distributed evenly, "Adult" is a population with only individuals of the oldest stage, and "Tacha" assumes a stage distribution estimated from the mid-continent population of sandhill cranes (Tacha et al., 1989).

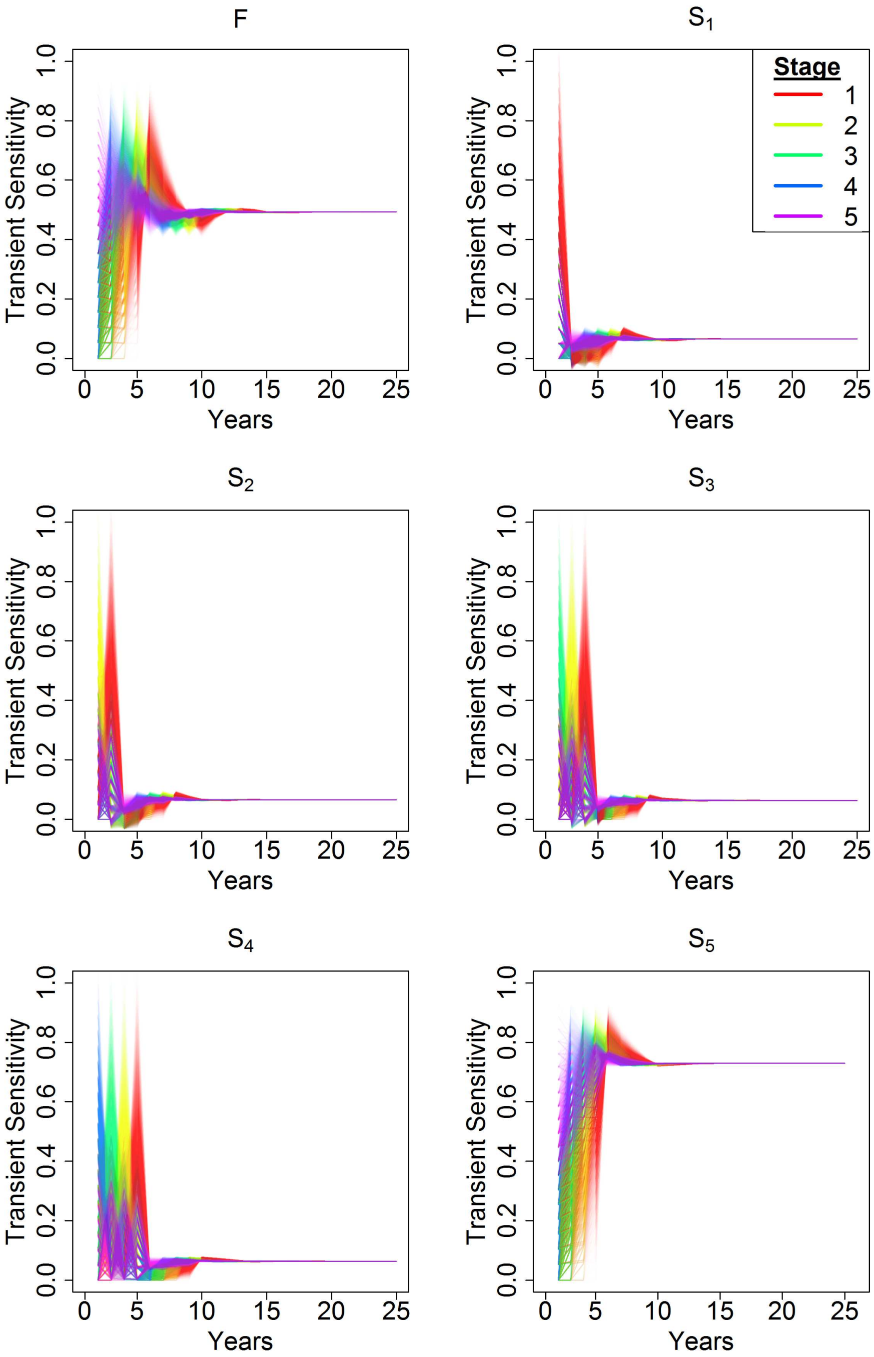

FIGURE 3.17. Transient population growth sensitivity of PPM1 vital rates through time under the complete set of permutations of the initial stage structure. The legend indicates the initial stage (1= juvenile, 5= oldest stage) with the majority of individuals ($\geq 50\%$).

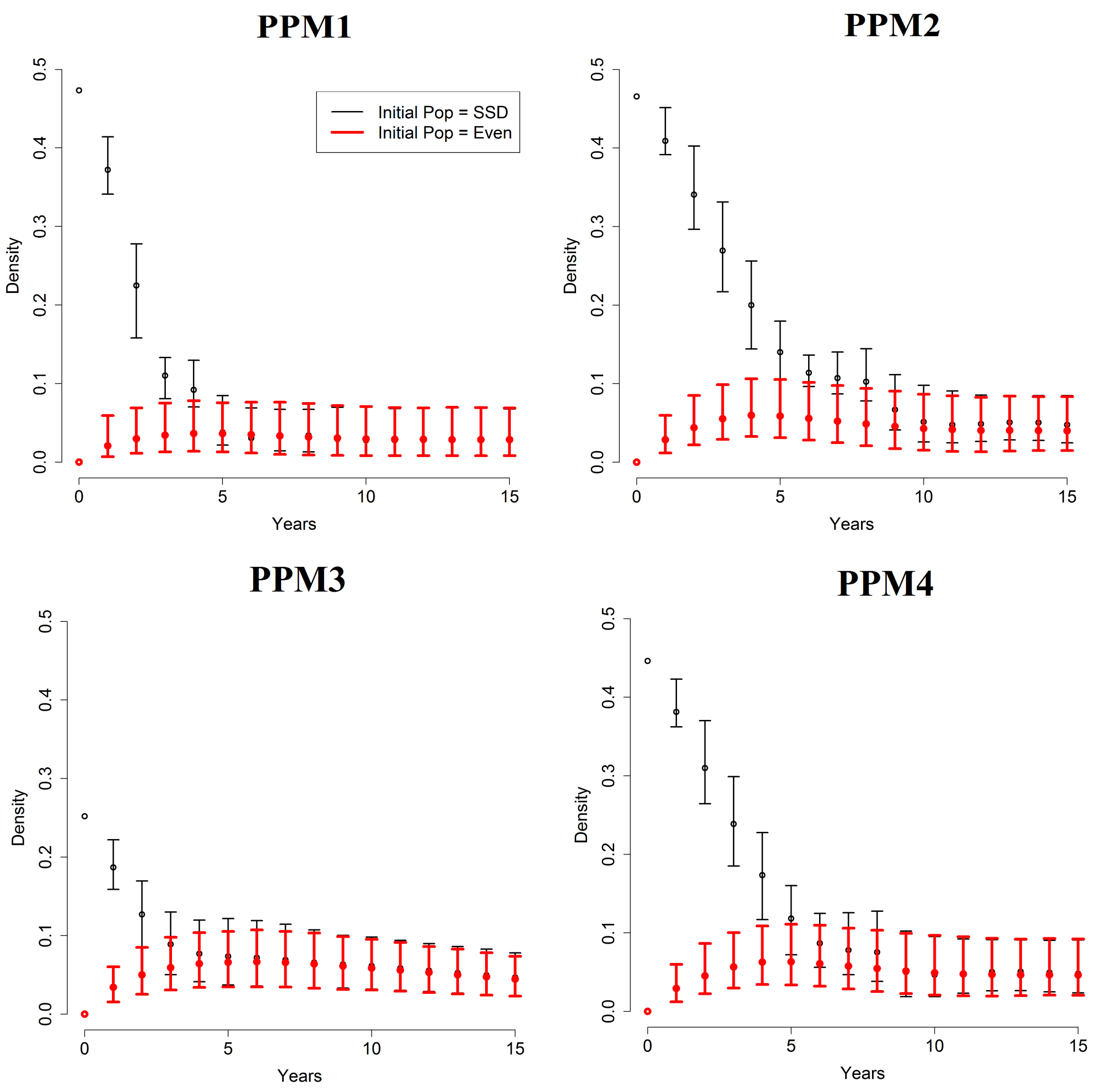

FIGURE 3.18. The Keyfitz's Δ between the stable stage distribution (SSD) of non-harvested and stochastically harvested populations, initialized at either the SSD of the non-harvested population or an even stage distribution; zero indicates no difference between two population stage structures. Harvest effected the stage structure on average in proportion to the number of individuals in each stage.

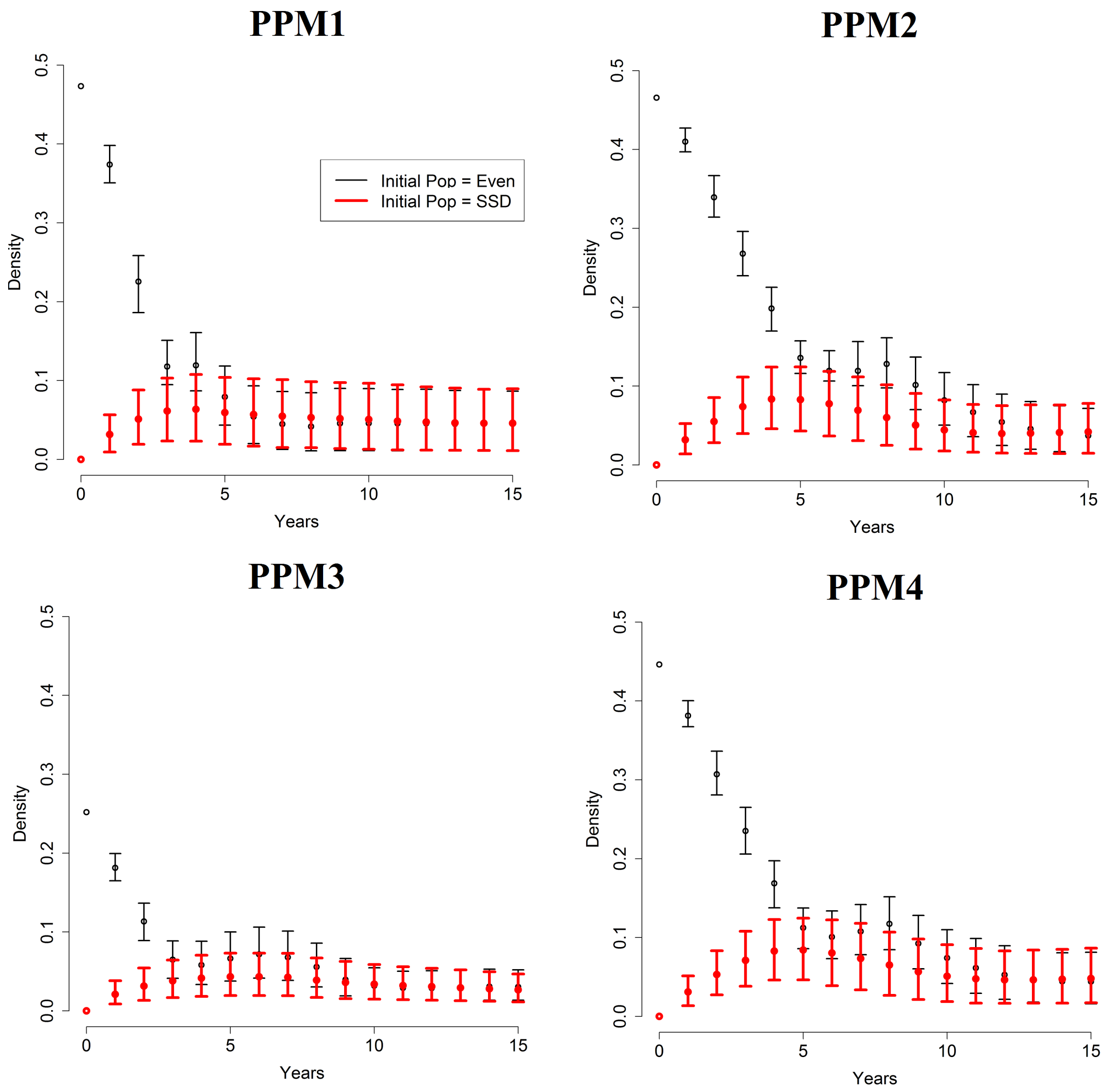

FIGURE 3.19. The Keyfitz's Δ between the stable stage distribution (SSD) of non-harvested and stochastically harvested populations, initialized at either the SSD of the non-harvested population or an even stage distribution; zero indicates no difference between two population stage structures and 1 indicates the maximum difference. Harvest effected the stage structure evenly, on average.

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CHAPTER 4

Monitoring with an index: investigating variation in the Rocky Mountain Population of sandhill cranes

4.1. Summary

Monitoring wild animal population abundances can be difficult. Many monitoring programs derive population indices from counts or use counts directly as an index to abundance. To dampen the effects of sampling variation, it is relatively common to smooth counts using a moving three-year average estimator; the derived population index may then be used to infer population changes and/or evaluate a population's status that has implications for conservation/management decisions (e.g., species delisting or annual harvest). We investigate the biological plausibility of the annual change in counts and population indices from a typical monitoring scenario: the Rocky Mountain Population (RMP) of sandhill cranes. We do this by integrating juvenile recruitment, harvest, and survival estimates into a stochastic stage-based population model, which is also used in a Bayesian framework to predict annual detection errors (i.e., under- and over-counting). We also fit a hierarchical Bayesian time series model (HBTS) to RMP counts to estimate observational and population process variance and predict population change; we considered observational processes where counts are symmetric around the true population (*symmetric*) or are strictly at or under the true population (*under*). We found spring migratory (1984-1996) and fall staging area (1997-2014) counts of the RMP to exhibit annual change that was biologically unrealistic (fall counts were less variable than spring counts), while the three-year average fall population index was largely biologically realistic. The HBTS model using *symmetric* suggests that the RMP

abundance has changed little over the current monitoring duration, but there is considerable uncertainty. Assuming *under*, the HBTS model predicted a slowly growing population from 1997-2007 and a slowly declining population from 2007-2014. We found the predicted population from 1997-2014 using the HBTS to be biologically plausible if observed crane harvest mortality was compensated up to natural mortality. In addition, a simulation demonstrated that the predicted mean of the HBTS is generally a more reliable estimate of the true population than using the moving three-year average estimator. Additional advantages of the HBTS compared to the moving three-year average are, we 1) obtain measures of uncertainty, 2) can use the entire time series of counts to jointly make inference on the population, 3) can incorporate prior information about the observational and population process, 4) can accommodate missing years of data, and, 5) it allows forecasting the population. Forecasting is especially advantageous when management decisions need to be made prior to current year data collection.

4.2. Introduction

A central topic in applied ecology is understanding population abundance to inform conservation and management of species (Mills, 2012; Nichols, 2014). Foundational laws relating to the conservation and management of species in the United States (e.g., Endangered Species Act of 1973, Migratory Bird Treaty Act of 1918, and the Marine Mammal Protection Act of 1972), as well as criteria used by international conservation agencies (e.g., International Union for Conservation of Nature), often reference the population status of species, leading to the common use of abundance and distribution as performance measures in recovery plans and delisting rules (Neel et al., 2012; Mace et al., 2008). Management of populations based on objectives around abundance and/or distribution for conserving species and sub-species is a logical outgrowth of societal and legal focus, as well as ecological theory relating to species extinction risk (Lande, 1993). As such, monitoring programs will logically often focus on population status (i.e., abundance and/or distribution), as well as population dynamics, and the effect of conservation/management decisions (Nichols, 2014). Knowledge of population status is especially important in evaluating decisions about anthropogenic take, either intentional (e.g., sport harvest, control of an overabundant species) or incidental (e.g., fishery bycatch, road or boat kills, wind turbine strikes). For sport harvested migratory bird species in the United States, it is the purview of the U.S. Fish and Wildlife Service to protect these species and ensure harvest regulations are appropriate for their current population status (U.S. Migratory Bird Treaty Act, 1918; U.S. Fish and Wildlife Service, 2013). In order to do so, monitoring populations is of paramount importance (U.S. Fish and Wildlife Service, 2004; Nichols and Williams, 2006).

Population monitoring is challenging (McComb et al., 2010). Monitoring migratory populations can be even more challenging. For example, for migratory birds, in the full annual migratory cycle of a population, there may be few opportunities to conduct a survey that is amenable to logistical and financial constraints, as well as appropriate statistical designs to make robust inference to population abundance (Ralph et al., 1981; Thompson, 2002). Reasons for these difficulties might include, 1) the breeding and wintering ranges cover a large geographic expanse, including remote areas across which birds may occur heterogeneously, at possibly low density, 2) multiple populations of the same species or different sub-species that are phenotypically similar mix during migration and/or at their wintering areas, making field-identification challenging, 3) migration timing is variable across years and perhaps by regional sub-populations, and 4) the species may occupy areas across international borders.

Due to the challenges of surveying many species or other logistical constraints, it is perhaps rare for long-term monitoring programs to obtain estimates of true population size (Pollock et al., 2002; Johnson, 2008).

Estimates of true population size require accounting for two aspects of sampling: spatial extent of a population (either through exhaustive coverage or through an appropriate sampling design, e.g., probabilistic design), and correction for imperfect detection/availability (Pollock et al., 2002; Nichols and Williams, 2006). While some population surveys purport to estimate true abundance (e.g., the annual waterfowl breeding population survey in North America, Smith 1995), many surveys result in only an index to population size, due to a lack of appropriate spatial coverage or adjustment for detection/availability. Population indices can be partitioned into two basic types. The first type is simple standardized periodic counts (e.g., roadside point counts of birds) that may or may not be spatially extensive, but cannot be reasonably converted to an estimate of population size (e.g., because roadside habitat is not representative of the full range of the population); indices of this type are usually limited to estimates of population change over time. The second type consists of surveys that are attempts to count the entire population, but are suspected to be incomplete, either due to a relatively small but variable component that is unavailable or counts are not corrected for visibility or counting bias.

Avian studies in general, overwhelming rely on indices to make inferences about populations (Rosenstock et al., 2002). Monitoring programs will often use counts as indices or derive an index of abundance based on the counts, of which the focus may be on the trend of the index over time and/or space. In North America, there are several non-species specific avian monitoring programs that derive population indices, including the North American

Breeding Bird Survey (Sauer and Link, 2011), the Breeding Bird Atlas (Smith, 1990), and the Audubon Christmas Bird Count (Link et al., 2006). Less formalized monitoring also includes the eBird program (Sullivan et al., 2009), which has been used in occurrence monitoring (Fink et al., 2010).

Whether an index is an appropriate estimator for population abundance, which may be used in making management decisions, will depend on the appropriateness of modeling assumptions (e.g., detectability; Williams 2009) and how well linked the management objective is to the monitoring strategy (Nichols and Williams, 2006; Nichols, 2014). A primary consideration in using an index as a surrogate for abundance is its relationship with true abundance; an index will be most useful when there is a constant and proportional relationship (i.e., linear). If this was an exact relationship without variation or at least very little, the index could be suitable to investigate population dynamics. However, this assumption may often be inappropriate due to sampling variation (e.g., the availability to be detected or probability of detection) across space and/or time (Anderson, 2001; Pollock et al., 2002). If interest is focused on the trend of an index, it is more important that sampling variation be much less than the variation in population abundance and not be dependent on the abundance (Johnson, 2008); detecting this trend statistically may however require a relatively long time series, depending on the strength of the sampling variation. Survey standardization is an often suggested way to minimize sampling variability, which is always a good idea, but is unlikely to reduce all the variation that is beyond the control of the researcher and thus there is still likely to be concern of sampling variation (Thompson, 2002).

For sport harvested migratory bird populations, there is often an operational taxa-focused monitoring program that directly informs annual harvest decisions using population indices, of which some are type one indices, including American woodcock (*Scolopax minor*; U.S. Fish and Wildlife Service 2014b), mourning dove (*Zenaida macroura*; U.S. Fish and Wildlife Service 2014c), and band-tailed pigeon (*Patagioenas fasciata*; U.S. Fish and Wildlife Service 2014d). In contrast, some monitoring programs attempt to estimate abundance but recognize sampling issues will lead to population indices (type two), such as for tundra swans (*Cygnus columbianus*, Pacific Flyway Council 2001), ducks (U.S. Fish and Wildlife Service, 2014b), and sandhill cranes (*Grus canadensis*; Kruse et al. 2014).

When monitoring a harvested species, it is particularly useful to not only understand the population trend, but the magnitude of the population, to be able to make appropriately scaled harvest management decisions. It is relatively common to attempt to dampen the effects of sampling variation in counts of migratory birds by deriving a population index using a moving three-year average (MTYA) estimator, $index = \frac{Count_{T-2}+Count_{T-1}+Count_{T}}{3}$, where T is the most current year (e.g., several species of geese, U.S. Fish and Wildlife Service 2014b, tundra swans, Pacific Flyway Council 2001, wood storks *Mycteria americana*, U.S. Fish and Wildlife Service 2014e, and sandhill cranes Kruse et al. 2014). This estimator is also used more generally in wildlife monitoring, often when relating the status of a population to an objective, such as with sea otter (*Enhydra lutris*) recovery (U.S. Fish and Wildlife Service, 2003), Utah prairie dog (*Cynomys parvidens*) recovery (Utah Division of Wildlife Resources, 2015), and furbearer harvest management (Lovallo and Hardisky, 2010; Erb, 2012). Despite the frequent use of the MTYA estimator, to our knowledge, there has yet to be a study that investigates its merits or a comparison with alternative model-based approaches.

Migratory populations of sandhill cranes are both challenging to monitor and are annually harvested. As part of the management strategy for the Rocky Mountain Population

(RMP) of greater sandhill cranes (*G. c. tabida*), there has been an annual survey of the population since 1984. The current survey produces a population count, in which the MTYA population index (referred to below as 'population index') is used to inform the allocation of allowable harvest in each year (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). We are interested in better understanding the components (i.e., biological and sampling) that make up the observed annual variation in the RMP counts. Primarily, this will help better understand the implications of the monitoring program's effect on making harvest management decisions, which has been identified as a priority in crane management (Case and Sanders, 2009). Secondly, it will also help elucidate whether there is a strong biological signal in the counts that could help lead to a better understanding of population dynamics. The development of statistical models that integrate multiple data sources can lead to important insights for migratory birds (Link and Royle, 2003; Hostetler et al., 2015), but these applications could be impeded by or lead to highly misleading results if data sources, such as population counts, contain sampling variation that is not considered (Strobel and Butler, 2014).

Our objectives are to evaluate whether annual changes in the spring migratory (1984-1996) and fall staging area (1997-2014) RMP sandhill crane counts (referred to below as 'count') and fall population index are biologically realistic and investigate ways to account for sampling variability when the survey design does not permit its estimation. We examine the annual changes in both the spring and fall population counts by integrating the counts with available data on RMP juvenile recruitment, harvest, and survival into stochastic stage-based population models. We also use these models in a Bayesian framework to estimate values of annual sampling error (i.e., detection/availability). Lastly, we use a hierarchical

Bayesian time series (HBTS) modeling approach to estimate RMP population abundance under different types of observational processes and prior information. We consider the biological plausibility of the predicted fall population from the HBTS model and compare the HBTS model to the MTYA estimator in simulation. Our findings have direct application to future monitoring and management decision making of the RMP of sandhill cranes and more generally to population monitoring programs, including the monitoring and recovery of threatened species (U.S. Fish and Wildlife Service, 2003; Utah Division of Wildlife Resources, 2015), as well as other crane populations that use the MTYA estimator (e.g., Mid-Continent Population (MCP) and the Eastern Population (EP); Kruse et al. 2014).

4.3. Materials and methods

4.3.1. Rocky Mountain Population. The RMP breeds within palustrine and riparian wetlands throughout the central Rocky Mountains, including Colorado, Wyoming, Utah, Montana, and Idaho (Drewien & Bizeau, 1974). During spring and fall migration, cranes stop-over in the San Luis Valley (SLV) in central-southern Colorado and winter throughout New Mexico, Arizona, and Mexico, but are primarily located in the Rio Grande Valley of New Mexico. Starting in 1981, the RMP has been annually harvested after 63 years of closed legal hunting since the passing of the Migratory Bird Act (U.S. Migratory Bird Treaty Act, 1918; The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). To help inform managers on harvest decisions a population survey was started in 1984, in which an aerial spring count (via transects) was conducted in the SLV. The count was adjusted for counting bias (via photographic-correction) and the proportion of lesser sandhill cranes (*G. c. canadensis*) of the MCP, which also stopover in the SLV (Benning et al., 1997; Kruse et al., 2014). However, because of sampling biases due to imperfect availability, the increasing number of MCP cranes over the years, and questions about the reliability of differentiating tracks by sub-species, the spring survey was discontinued in 1996 and a pre-migratory fall staging area survey became fully operational in 1997 and has continued since (Kruse et al., 2014).

The fall survey is coordinated across federal and state agencies and includes aerial and ground counts at 81 known staging sites throughout the breeding area states. There is no additional information collected to adjust the fall counts due to sampling variation. But, it is recognized that a 'poor' count can occur (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007), for example, due to survey conditions which impede the operations in conducting the complete survey; in these cases, the annual count may not be subsequently used in determining harvest allocation. The second way a 'poor' count could occur, is because of sampling variation caused by annual changes in the availability of cranes to be counted and counting biases, which ultimately could lead to annually under- or over-counting the population. The MTYA estimator of the most recent and reliable counts is used to reduce this variation, which is then used for allocating allowable RMP crane harvest in the following year (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). The current population objective of the RMP is to maintain a population index between 17,000 and 21,000 (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007).

4.3.2. (UN)REALISTIC ANNUAL VARIATION IN POPULATION COUNTS AND THE FALL INDEX? We evaluate whether the annual change in the RMP counts and fall population index are biologically feasible by developing stochastic stage-based population models using the spring and fall time series of counts, separately. Our aim is to develop models that are constructed around the available data, which do not require assumptions about additional age classes. We use the observed count data in year $t-1$ to predict three empirical distributions of the count in year t (*low*, *realistic*, and *high*). Each model incorporates data on annual juvenile recruitment ($<$ 1 year old), juvenile and adult survival, and estimated harvest. Juvenile recruitment (i.e., proportion of juveniles in the population) has been estimated since 1972 from an annual recruitment survey in the fall at the SLV (Brown, 2014); the survey covers all areas of the SLV that cranes are known to use, and entails substantial survey effort, with >4000 observations of cranes made using a systematic design. Harvest is estimated each year from hunter surveys (Kruse et al., 2014). We consider different survival parameters for each scenario, 1) unrealistically low survival with harvest mortality being completely additive (*low*), empirical survival from a 23-year mark-resight study and harvest that is compensated up to natural mortality (Drewien, RC, unpublished data; *realistic*), and an upper maximum survival where no death occurs (*high*).

We investigate biological plausibility of annual change in the counts by estimating the absolute difference between the *realistic* expected count with the observed $Count_t$ and whether $Count_t$ falls within the *realistic* empirical distribution or between the *low* and *high* distributions. When an observed count is either lower than the *low* distribution or higher than the *high* distribution, we suggest the change in the count is unlikely to represent true population change. If the observed count falls between these distributions, it is feasible, but not realistic unless it also falls within the *realistic* distribution. We constructed models in R (R Core Team, 2015) and simulated predicted counts from each model 50,000 times for each sequential comparison to obtain empirical distributions (*low*, *realistic*, *high*).

4.3.2.1. *Spring population model.* For each sequential comparison, we observe a spring (SP), adult (A), population count in year $t-1$ ($Count_{SP,A,t-1}$) that we consider has been observed perfectly ($\theta_{\forall t} = 1$). These adults survive with some probability ($\phi_A^{SP,F}$) to adults in the fall (F, $N_{F,A,t-1}$). During the fall, we observe the proportion of juveniles in the population (P_t) that we use to derive the juvenile population ($N_{F,J,t-1}$). The spring population in year t is a combination of adults and juveniles (J) in the fall ($N_{F,A,t}$, $N_{F,J,t}$, respectively) that survive to spring with some probability ($\phi_A^{F,SP}$, $\phi_J^{F,SP}$, respectively) and a portion of which is removed by harvest ($f(H_{t-1})$, where $f()$ is a function to indicate additive or compensatory mortality, depending on the scenario). We consider juveniles to become adults after the fall because they are no longer distinguishable in the following year. Lastly, we assume no counting error to then predict the spring population count in year t ($Count_{SP,A,t}$). The only parameters involve survival, which we define as beta distributed and time invariant ($\phi_A^{SP,F}, \phi_A^{F,SP} \sim Beta\left(\alpha_1, \beta_1\right), \phi_J^{F,SP} \sim Beta\left(\alpha_2, \beta_2\right)$). The complete spring stochastic population model is as follows (Figure 4.1),

$$
\begin{aligned}
N_{SP,A,t-1} &\sim \text{Poisson}\left(\frac{Count_{SP,A,t-1}}{\theta_{t-1}}\right) \\
N_{F,A,t-1} &\sim \text{Binomial}\left(N_{SP,A,t-1}, \phi_A^{SP,F}\right) \\
P_{t-1} &= \frac{N_{F,J,t-1}}{N_{F,J,t-1} + N_{F,A,t-1}} \\
N_{F,J,t-1} &\sim \text{Poisson}\left(\frac{N_{F,A,t-1}}{1 - P_{t-1}} - N_{F,A,t-1}\right), \text{which satisfies the definition of } P_t \\
N_{SP,A1,t} &\sim \text{Binomial}\left(N_{F,J,t-1}, \phi_J^{F,SP}\right) \\
N_{SP,A2,t} &\sim \text{Binomial}\left(N_{F,A,t-1}, \phi_A^{F,SP}\right) \\
N_{SP,A,t} &= N_{SP,A1,t} + N_{SP,A2,t} - f(H_{t-1}) \\
Count_{SP,A,t} &\sim \text{Poisson}\left(N_{SP,A,t} \times \theta_t\right)
\end{aligned}
$$

For the *high* scenario, we assume all survival parameters are exactly one and no harvest occurs. For *realistic*, we use an annual adult survival probability of 0.956 with a process variance of 0.025 and a 6-month juvenile survival probability of 0.848 with a process variance of 0.073. We re-scaled the adult survival to two 6-month periods and estimated the new variance using the delta method. We then used moment matching to obtain appropriate parameters for the beta distribution (e.g., $\phi_A^{F,SP} \sim Beta(\alpha_2, \beta_2)$). Harvest was considered to be compensated up to natural mortality, for which there is empirical evidence for most age classes (Kendall, W. L., Drewien, R. C., and Gerber, B. D., unpublished data). For *low*, we used a mean adult and juvenile survival for spring and fall of 0.90 and 0.70, respectively and harvest was additive to natural mortality; the process variances from *realistic* were used.

4.3.2.2. *Fall population model.* The fall count includes both the adults and juveniles ($Count_{F,AJ,t-1}$) on the pre-migratory staging grounds. To make an age structured model by incorporating juvenile recruitment, we have to assume that the recruitment and fall count surveys occur simultaneously. In actuality, there is, on average, a one month difference in these surveys. This may cause bias if the differential survival between the fall staging grounds and the SLV is largely different than for other months. We again assume no detection error. Here, we derive the adult and juvenile population in the fall using P_{t-1}. These fall adult and juvenile populations survive to the next year with some probability ($\phi_A^{F,F}$, $\phi_J^{F,F}$, respectively), with some being harvested. To add the new juveniles of year t, we use the recruitment survey again (P_t) and then lastly assume no detection error to predict the observed count in the year t ($Count_{F,AJ,t}$). Because we are adding juveniles into the predicted fall count based on $N_{F,A,t}$, rather than $N_{F,AJ,t}$ (see below), this will slightly underestimate the population of juveniles in the fall. We could use $Count_{F,AJ,t}$ as a substitute for $N_{F,AJ,t}$, but this could increase bias with uncertain direction. The complete fall stochastic population model is as following (Figure 4.2),

$$\begin{aligned}
N_{F,AJ,t-1} &\sim \text{Poisson}\left(\frac{Count_{F,AJ,t-1}}{\theta_{t-1}}\right)\\
N_{F,J,t-1} &\sim \text{Poisson}\left(N_{F,AJ,t-1} \times P_{t-1}\right)\\
N_{F,A,t-1} &= N_{F,AJ,t-1} - N_{F,J,t-1}\\
N_{F,A,t} &= \text{Binomial}\left(N_{F,J,t-1}, \phi_J^{F,F}\right) + \text{Binomial}\left(N_{F,A,t-1}, \phi_A^{F,F}\right) - f(H_{t-1})\\
N_{F,AJ,t} &= N_{F,A,t} + \text{Poisson}\left(N_{F,A,t} \times P_t\right)\\
Count_{F,AJ,t} &\sim \text{Poisson}\left(N_{F,AJ,t} \times \theta_t\right)
\end{aligned}$$

To investigate biological reliability of annual change in the fall population index (i.e., MTYA), we substitute counts with the fall population index.

4.3.3. Deriving annual counting variation.

To estimate the annual counting error, we use the spring and fall population models, assuming the same survival as the *realistic* scenario. The only unknown parameters are the annual detection process, for which we use relatively informative prior distributions of $\theta_t \sim Uniform\,(0.5, 1.5)$. The joint posterior distribution of the population model is defined as (square brackets indicate a probability distribution),

$$[\boldsymbol{\theta}|\mathbf{Count}, \mathbf{P}, \mathbf{H}, \alpha_1, \beta_1, \alpha_2, \beta_2] \;\propto\; [\mathbf{Count}, \mathbf{P}, \mathbf{H}, \alpha_1, \beta_1, \alpha_2, \beta_2|\boldsymbol{\theta}][\boldsymbol{\theta}]$$

However, the model is unidentifiable with as many unknown parameters as data. To remedy this, we assume one count is known with certainty, or at least the detection process is fully defined; thus, we conditioned on the first count of each time series and consider the detection process distribution for this year to be known with standard deviation of 0.1 and a mean of either 0.8, 1.0, or 1.2. We fit the model using Markov chain Monte Carlo (MCMC) by sampling from full-conditional distributions using R (R Core Team, 2015); 100,000 MCMC samples were used with a burn-in of 10,000 samples. Posterior convergence was assessed visually.

4.3.4. Hierarchical Bayesian time series population model. Fitting a population model without direct empirical information on the observational process (i.e., availability and detection probability) is challenging. We considered a hierarchical population model that includes a first-order autoregressive Gompertz population growth that separates population process and observational variability into distinct components. The parameters include an intrinsic population growth rate (β_0), a first-order autoregressive term that can be interpreted as a measure of density dependence (β_1) on population growth, process variance (σ_N^2), and observational uncertainty (σ_C^2). This type of observational process allows for symmetric under- and over-counting around the true population (*symmetric*). Negative density dependence would be indicated if β_1 was less than -1. We apply this model to spring and fall counts, separately. Parameters defined using subscripted dots (e.g, $\beta_.$) indicate the same distributional structure for all such parameters.

$$\text{Observation Process:} \qquad \log(Count_t) \sim \text{Normal}(N_t, \sigma_C^2)$$

$$\text{Population Process:} \qquad N_t = \beta_0 + (1 + \beta_1) \times N_{t-1} + \epsilon_t$$

$$\begin{aligned} &\text{Process Uncertainty:} && \epsilon_t \sim \text{Normal}(0, \sigma_N^2) \\ &\text{Prior Information:} && \beta. \sim \text{Normal}(0, 10000) \\ &\text{Prior Information:} && log(\sigma_.^2) \sim \text{Normal}(0, 10) \end{aligned}$$

We also considered a similar model by including relatively strong prior information on the observational and population process variances (fitting spring counts: $\sigma_C \sim$ Uniform(0, 0.4), $\sigma_N \sim$ Uniform(0, 0.05); fitting fall counts: $\sigma_C \sim$ Uniform(0, 0.2), $\sigma_N \sim$ Uniform(0, 0.05)). Prior distributions for the population process are fairly small to indicate limited variability in crane dynamics and prior observation processes that are fairly large to suggest the likelihood of high variation (Figure 4.3); the uniform distribution was preferred for informative priors because we can place constant probability support over a range of likely values.

Instead of allowing counts to occur symmetrically around the true population, it is also reasonable that counts can occur only at or below the true population. We consider this type of model by defining the observational process such that counts are the lower bound of the true population process (*under*; via a truncated normal distribution). We fit this model to the fall counts with relatively uninformative prior distributions (as shown in equation above) as well as using informative prior distributions on the variance parameters ($\sigma_C \sim$ Uniform(0, 0.2) and $\sigma_N \sim$ Uniform(0, 0.05)).

We attempt to evaluate the predicted population from the HBTS model using the fall population model. We initialize the fall population model using the posterior distribution of the predicted counts of the first year and project the model with the survival parameters from *realistic*. We considered harvest to be completely additive to natural mortality or compensated up to natural mortality.

We fit all models using the R package rjags, which interfaces with software JAGS (Plummer, 2013), in which MCMC is used to simulate samples from the full conditional distributions of unknown parameters of our statistical model. We initialized each model and obtained 1,000,000 MCMC samples, discarding the first 100,000 and thinning to every 10^{th} iteration. Each model was checked as to its adequacy in fitting the data using a posterior predictive check by calculating a Bayesian p-value (Gelman et al., 2004); values that are not extremely low (near 0) or large (near 1) suggest that model is able to give rise to new observations that resemble the original data. Unaccounted for temporal dependence was also checked by examining partial and full autocorrelations of model residuals (Box and Reinsel, 1994).

4.3.5. Evaluating the HBTS model vs. MTYA estimator. We investigate the reliability in estimating the fall population size of the RMP using the HBTS model compared to the MTYA estimator. We simulate a discrete-time exponential growth model that incorporates the estimated fall population process variance (via posterior distribution) and either consider the observational process to be *symmetric*, thus using the estimated fall observational process variance (via posterior distribution) or *under*, where we assume a random uniform process between a low under-count of 0.7 and a high under-count of 0.95. We initialized each population at 19,000 and projected for twenty years (similar time-span as the current fall counts) for 1,000 projections under an average annual population change of 5% decline, 2.5% decline, stable, 2.5% growth, 5% growth, and 5% growth for 10 years followed by 10 years of 5% decline. For each simulation, we calculate the MTYA and fit the

HBTS model where the observational process is correctly and incorrectly (observations are under-counts and we use the model with *symmetric* and vice-a-versa) assumed. We compare the mean population predictions of the HBTS model to the MTYA estimator by deriving empirical distributions of annual bias and correlation.

4.4. Results

4.4.1. Rocky Mountain Population surveys.

The spring population count was more variable than than the fall population count (SD(*Counts*): 3,200, 1,939, respectively; Figure 4.4). Only 5 out of 14 spring surveys were operationally characterized as 'good' (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007); there is no equivalent for the fall survey. The fall population counts and index have generally stayed within the population objective (17,000-21,000). Several counts have exceeded the upper population objective (2007, 2008, and 2010), which pushed the index out of the objective in 2008-2009, primarily due to the largest count observed of 22,822 in 2007. The largest annual difference between sequential years in the full time series (spring and fall counts) occurred between 1985-1986 with a drop in the counts of 7,227. The second largest difference in the full time series and the largest in the fall count occurred between 2012-2013 with an increase of 4,077. For the spring survey, 92% of counts indicated at least ±10% change, while for the fall counts only 44% demonstrated that much change. The fall population index had no changes that large and 77% of changes were less than ± 5%.

4.4.2. Annual spring and fall count variation.

The annual change of the spring counts appear to be extreme in most years (Table 4.1, Figure 4.5). The absolute differences between the expected count from *realistic* and the observed count ranged from 839 to 8,014.

Out of twelve comparisons, no observed counts were within the bounds of the *realistic* distribution and only three were between the most extreme low and high quantiles of the *low* and *high* empirical distributions, respectively. These three occurrences did not correspond to only 'good' operational survey years.

We found the annual change of the fall count to be less extreme than the spring, but still not largely biologically realistic (Table 4.2, Figure 4.6). The absolute differences between the expected count from *realistic* and the observed count ranged from 98 to 3,807. Out of 14 comparisons, three were within the bounds of *realistic* and seven were between the most extreme low and high quantiles of the *low* and *high* empirical distributions, respectively. We did find the annual change in the fall population index to be generally biologically reasonable (Table 4.3, Figure 4.7). The absolute differences between the expected population index from *realistic* and the observed index ranged from 20 to 1,493. Out of 16 comparisons, 12 fell within the bounds of *realistic* and all were between the most extreme low and high quantiles of the *low* and *high* empirical distributions, respectively.

4.4.3. ESTIMATES OF ANNUAL COUNTING VARIATION. The assumption of the error associated with the initial count (i.e., under-detecting, no mean-detection error, and over-detecting) has a significant influence on the posterior distributions of the subsequent detection for both the spring and fall models. If we assume the 1984 spring count had no mean-detection process, the subsequent posterior counting variation mostly indicated that the counts over-estimated population size in most years (Figure 4.8). In contrast, if we assume the 1997 fall count had no perfect mean detection, the subsequent posterior counting process were mostly symmetrically distributed on either side of no detection variation, with three exceptions with large under-detection occurring in 2001, 2011, and 2012 (Figure 4.8).

4.4.4. Hierarchical Bayesian time series population model. We found no evidence that the HBTS models did not fit our data ($0.4 >$ all Bayesian p-values < 0.8) or indicate additional temporal dependency (Figure 4.9). Considering the *symmetric* observation process with relatively uninformative priors, we found no evidence of mean population change over the duration of the spring or fall surveys, although there was considerable uncertainty (Figure 4.10). We also found no evidence of negative density dependence (Spring: mode and 95% highest point density intervals, β_1, of -1.16 and -1.96 to -0.11; Fall: mode and 95% HPDI, β_1, of -0.73 and -1.56 to -0.10). The observational variance was greater in the spring counts than in the fall with 80% probability density of the spring observational process variance greater than the fall observational process variance (Spring: mode and 95% HPDI of 0.16, 0.00-0.25; Fall: mode and 95% HPDI of 0.09, 0.00-0.12). We did not find a difference in the process variance with 57% probability density of the spring process variance greater than the fall process variance (Spring: mode and 95% HPDI of 0.001, 0.00-0.24; Fall: mode and 95% HPDI of 0.001, 0.00-0.14). There is minor evidence that the spring observational variance is greater than the process variance (66% probability density of observational variance is greater than process variance) and no evidence that this is true for the fall (49% probability density of the observational variance is greater than the process variance).

The population index was inconsistent with the HBTS predicted population mean for the spring and fall, with the population index being much more variable (Figure 4.10). There is a high probability that the RMP has stayed within the population objective since the start of the fall population survey (assuming *symmetric*), with the probability density of the annual fall population prediction between 17,000 and 21,000 ranging from 87 to 100%. There was less certainty for the duration of the spring population survey, with probability densities between 17,000 and 21,000 ranging from 52 to 78%. Fitting the population model with informed prior knowledge on the variance parameters produced moderate dampening of the population prediction mean and associated uncertainty (Figure 4.11). Lastly, assuming the population can only be under-detected (*under*), we found the population mean to exceed the RMP objective to a small degree, but with a large amount of uncertainty that exceeded the population objective (Figure 4.12).

We found the predicted population of the HBTS model using the fall counts to be biologically-reasonable using the fall population model, but only when harvest mortality was compensated up to natural mortality (Figure 4.13). Results were more reasonable when observations were considered to be symmetric around the population. Harvest that was completely additive to mortality caused a declining population, which was not the case for the predicted population using the fall counts.

4.4.5. Evaluating the HBTS model vs. MTYA estimator. In our simulation comparison, we found using the *symmetric* observation process that there was small expected bias for the predicted mean population from the HBTS model and MTYA estimator, but the HBTS predicted mean was less biased on average and had a higher expected correlation with the true population, for all scenarios of population growth, decline, and mixed combinations (Figure 4.14). The expected bias of the MTYA was positive when the true population was increasing and negative when the population was decreasing. When the true population was stable, there was a small expected bias for the HBTS model and MTYA estimator, but the variation was slightly less extreme for the HBTS model. When we assumed counts were *under*, the average bias from the HBTS model was considerably less than the MTYA estimator for all scenarios, while the correlation was similar between the two methods (Figure 4.15). When the counts were only under-detecting the population (*under*) but the observational process of the HBTS model was *symmetric*, we found both the HBTS model and MTYA estimator were highly biased low with the HBTS model having higher correlation with the true population (Figure 4.16). The expected bias was slightly lower for the MTYA estimator when the population was decreasing and slightly higher when the population was increasing. When the counts were *symmetric* but the observational process of the HBTS model was *under*, we found the MTYA estimator to have less expected bias while the correlation was mostly similar but varied by population change (Figure 4.17).

4.5. Discussion

Monitoring migratory populations can be challenging. Ecological and life history complexity of migratory species incur logistical challenges that are not easily overcome with limited budgets, which may impede the design of an appropriate statistical design to make inference to true population size. Even with considerable effort put towards monitoring a population, an index to a population may be inevitable (e.g., mallards (*Anas platyrhynchos*), U.S. Fish and Wildlife Service 2014b; Johnson et al. 2015). Population monitoring programs that count animals and then smooth these counts using the MTYA estimator to derive a population index (Utah Division of Wildlife Resources, 2015) may find a more formal time series modeling approach, such as the HBTS model, beneficial. This includes the monitoring of the MCP of sandhill cranes, which uses the MTYA to evaluate the status of the population and hunting opportunity (Central Flyway Webless Migratory Game Bird Technical Committee, 2006), and the EP of sandhill cranes, which also uses the MTYA and has had growing interest in hunting as the index increases (Kruse et al., 2014). Recovery plans that monitor a population using the MTYA may benefit from being able to express uncertainty about their population estimate and recast population objectives as meeting a lower confidence/credible interval of the population estimate so as to not be overly optimistic, as with using the MTYA, which does not express uncertainty (U.S. Fish and Wildlife Service, 2003; Utah Division of Wildlife Resources, 2015).

We should recognize that both the MTYA, HBTS, and other timer-series models are simplistic, non-mechanistic approaches that do not contain real population parameters (i.e., age-specific survival and reproduction). However, they may still be useful and produce biologically reasonable population predictions, as was found for both when compared with the RMP fall population model. In comparing the MTYA estimator to the HBTS model, we found the HBTS model to demonstrate overall better performance, as long as the correct observational process was used. Understanding this process is clearly important, as RMP predictions under *symmetric* and *under* were noticeably different and have implications on the annual probability of meeting the management objective. The HBTS model allows knowledge of population dynamics and how the counts vary to directly inform the model and thus help specify more realistic population predictions. While we provided a limited exploration of using prior knowledge to inform both the observational and population process, a more rigorous brain-storming among managers could lead to significant improvements when applied, that may reduce the large uncertainties in population predictions seen here. In addition, the HBTS model provides measures of uncertainty, makes use of information for the entire time series to make inference about parameters, can easily handle missing years of data, can be used to forecast the population, and time series models in general have a long history of practical applications. Being able to forecast the population may be especially useful, depending on the timing of data availability and decision making (U.S. Fish and Wildlife Service, 2013).

There are many alternative approaches to estimating population trends (Humbert et al., 2009; Hosack et al., 2012). Each is usefulness will to some degree depend on what is known about sampling variability and how this is translated into modeling the observational process. One approach that has recently shown promise is using the flexible normal inverse Gaussian distribution to describe observations, which combined with prior knowledge could help specify a useful population model (Hosack et al., 2012); preliminary investigations of fitting the RMP crane data did not produce largely different population predictions than the HBTS model (Gerber, B., unpublished data). Another approach is to exploit spatial replication of some surveys within years, such that detection probability can be estimated via an N-mixture model that is then linked to a population model (Hostetler and Chandler, 2015); preliminary investigations of fitting the RMP crane data using this approach found results to be highly sensitive to prior specification (Royle, 2004) and necessitate unlikely assumptions about the detection process across space and time that produced unrealistic predictions (Gerber, B., unpublished data).

When monitoring is directly linked to an explicit objective, such as in a structured decision making framework, whether an index is an appropriate measure will depend on the objective(s). Here, we have implicitly taken the view that an accurate and precise estimate of population size is best when monitoring a population. For investigating population dynamics, this will almost universally be true. But for decision-making, one does not necessarily require perfect information in order to achieve a good decision. Simply, the decision needs to be robust to uncertainties, one of which, is the state of the population. One should ask whether decisions made using an index would be the same, similar, or completely different if the population state was known with certainty (Moore and Kendall, 2004). However, to do so, we must understand the observational process, which for some species, such as RMP sandhill cranes, may not be understood well.

An important consequence of monitoring a population with an index that does not have a strictly linear relationship with true abundance is that it will likely lead to a reactive management strategy (Thompson, 2002). This is in contrast to a proactive and anticipatory approach to management decisions as through an adaptive resource management (ARM) framework (Kendall, 2001). An ARM framework links predictive models with new observations of the population (via monitoring) in a learning process whereby insights into population dynamics can iteratively improve management decisions (Kendall, 2001; Conn and Kendall, 2004; Johnson et al., 2015). However, if a monitoring program can only inform managers of a population index, there may be a decrease in the probability of meeting management objectives (Moore and Kendall, 2004); in addition, this unknown sampling variation may also limit the potential for learning in an ARM process and thus limit its benefits to making increasingly better decisions. Instead, a common strategy is a simplistic threshold approach (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007), where a decision threshold (when to make changes in regulations) is equated with an objective threshold (acceptable population index), which can lead to unintended outcomes (Martin et al., 2009). Instead of anticipating future dynamics to make a decision, this approach reacts to past observations or smoothed ones (via the MTYA), which has a tendency to try and push the population into an acceptable range as it approaches the limits of the range (Gerber, B., unpublished data). Without predictive population models (representing hypotheses of population processes), there is no learning about the mechanisms governing population change, such as the effects of management decisions, and thus this type of reactive management strategy does not lead to learning that can improve management decision making.

4.5.1. Sandhill crane populations. The RMP objective is to maintain a MTYA fall pre-migratory staging area index between 17,000 and 21,000 (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). This objective is intended to balance recreational opportunities and population growth with minimizing major agricultural crop depredation, which is thought to be achieved when the population is within 10% of 19,000 cranes. As such, the implicit population objective is to maintain 19,000 cranes ±10%. However, because of monitoring uncertainties, the population is understood to be observed imperfectly and the fall counts are thought to be 'minimum' estimates of population size (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). The reason for this is not explicit in the management plan and while our results demonstrate non-biological change in spring and fall counts, the main sources of variability are unknown.

There are many reasons why RMP counts might not reflect realistic population change. First, because the count relies on surveying traditional staging areas, the count may vary annually due to the migration phenology from breeding area to staging area and staging area to migration stop-over in the SLV. Also, distributional shifts in staging areas likely occur because of shifting agricultural practices, increasing development pressure near staging areas, and the timing of hunting seasons (Drewien et al., 1996; Lockman et al., 1987). The fall counts will likely always be an underestimate of population size if some proportion of the population does not use the fall staging areas and thus is never available to be counted.

Moreover, if this availability changes annually, maybe due to environmental conditions, it may cause significant variation that obscures any signal of population dynamics. In addition, counting large flocks accurately can be difficult and many small flocks can easily be obscured by topography or vegetation. Lastly, while the fall survey is aimed at reducing multiple counts of the same flocks by restricting operations within a short time span, there is always the possibility it could occur. Little empirical evidence is currently available on the movements of RMP cranes leaving the breeding and staging areas, which could aid understanding of the above mentioned sources of sampling variation. The one study that has followed telemetered RMP cranes did identify variation among individuals and years in the timing of movements from the breeding to the staging areas (Drewien et al., 1999). A telemetry study currently underway (Collins, D., pers. comm.) could help in understanding movement patterns in association to the fall survey, similar to what has been done for the MCP (Pearse et al., 2014).

Relying on counts and the assumption of proportionality to abundance can lead to considerably misleading conclusions about spatial and temporal variation in abundance, population dynamics, habitat relationships, and effects of management decisions on populations (Thompson, 2002). For the RMP and other populations monitored using an index, it is critical to understand significant sources of variation, or at least some understanding of the relationship between the index and true abundance. Otherwise, it is difficult to know what a population index or predictions from a model, such as the HBTS, actually represent. For example, we may predict the RMP to be declining over the most recent few years. The reason for the decline could be due to a number of possibilities, 1) an actual population decline, 2) a constant over-counting at the staging areas followed by a constant under-counting, 3) a shifting distribution of staging areas away from traditional areas, 4) poor survey conditions, or 5) a fall survey that occurred too early or too late for the migration of the majority of RMP cranes. Future directions that may help clarify the variation in the fall counts and the meaning of the population index are a better 1) understanding of the timing of RMP crane movements from the breeding area to the staging areas and from the staging areas to the SLV, 2) understanding of the variability in the proportion of cranes that do not use traditional staging areas, and 3) understanding of counting biases by flock size, habitat type and topography for both ground and aerial surveys.

If we assume the RMP fall counts vary annually by under-estimating the true population, the use of the MTYA estimator is not logical because it does not strictly assume the population is always at or above the counts. If the under-estimation was constant, we can expect the MTYA to be lower than the counts when the counts are increasing and above the counts when the counts are decreasing. As such, the MTYA will further exacerbate this under-estimation when the population is increasing. Conversely, if the population is decreasing, the MTYA will either reduce the under-detection of the true population or exceed it and thus over-estimate the true population, depending on the amount of under-detection. However, if we consider the proportion of the population that uses the staging area to be constant, but the timing of movement from the breeding areas is variable and occurs at different rates, the population index or HBTS predictions may still be reasonably in proportion to the population, albeit lower. If both the proportion of the population using the staging areas and the timing of movement are relatively constant, but counts vary due to counting biases, the population index or HBTS predictions may still be in proportion to the population, but again always lower. If we imagine variation in the proportion of the population that uses the staging areas, the timing of movements, and the counting biases on the staging areas, the population index will reflect a composite of these factors including the population dynamics, of which, the dynamics and relationship with true abundance are likely completely obscured.

We found that the spring and fall counts vary beyond what is biologically realistic, such that their use in exploring spatial or temporal dynamics should not be considered without some form of adjustment for annual sampling variation. Interestingly, we did find the annual variation in the fall population index to be largely biologically realistic, as well as the HBTS model when harvest was compensated, suggesting simple time series approaches may be useful in characterizing population dynamics. As expected, we found the variance of the spring observational process to exceed that of the fall, suggesting an improvement in transitioning from the spring to the fall survey. Despite uncertainties about the relationship between the fall population index and true abundance, there is good reason to believe the current RMP objective is being met.

What would it take to lead to either estimating RMP crane abundance or improve confidence that the fall population index is appropriate in making annual harvest decisions? To estimate RMP sandhill crane abundance, it would be necessary to deal with two main sources of variability in counts, 1) spatial and 2) detectability (Yoccoz et al., 2001). Previous knowledge of crane breeding and staging area distribution could be combined with a predicted map of potential crane habitat that included wetland and agricultural features to design a probabilistic sampling scheme. At selected sampling sites, multiple counts could be conducted by different observers, which could be analyzed in a binomial mixture modeling approach (Kèry et al., 2004). Lastly, certain assumptions about movement among sites and out of the study area would have to be made or some explicit empirical evidence be collected. Such an approach would not have to be done annually if it was not cost effective, but perhaps done on some regular interval, such that a reliable annual correction factor to the fall population index could be made. Alternatively, monitoring the population via the fall population index could be abandoned all together and annual resources pooled to estimate population size on a longer interval, such as every second or third year. Years that were not monitored could be predicted either based on the HBTS or fall population model. Of course, institutional flexibility would be needed to manage such finances. We could expect this to be an effective approach when the population predictions do not have large uncertainty (Hauser et al., 2006).

However, ultimately the costs of estimating abundance may exceed the decrease in the risks of not meeting the population objective for the RMP. Whether these costs are worth while, depends on the risks of not knowing abundance or it's relationship with the population index. Understanding the risks depends largely on the magnitude and variability of the sources of variation in the counts and thus what the population index actual represents, as well as the tolerance of the managers to the probability of not meeting the population objective in a given year. Is it possible for a count to under-estimate the population size by 50 or 75%? If this occurred for several consecutive years, annual harvest may be severely limited or even closed when the population was in fact still within the population objective. While harvest is not an explicit objective in the RMP management plan, several states with active crane hunters are likely to find the above situation far from ideal. Knowing population size is likely to lead to better management decisions, especially when predictive population dynamics models are used in an ARM framework. Managers and likely the general public may find it useful if managers and stakeholders clarified their risk tolerance in connection with beliefs about the magnitude and variance of the sampling variation of fall population counts and indices and ultimately not meeting their defined population objective. Future research is needed to clarify the risks of not meeting annual population objectives using the current decision framework and possibly alternative frameworks, such as adaptive resource management.

TABLE 4.1. Evaluation of the biological plausibility of the spring count of the Rocky Mountain Population of sandhill crane.

Year	P_t [1]	Spring Count	Low Expected Count	Realistic Expected Count)	High Expected Count)	Diff [2]	Survey Cond.	Cov1 [3]	Cov2 [4]
1984	0.08	14112					Poor		
1985	0.09	20382	12215	14531	15356	5851	Good	0	0
1986	0.06	13155	17781	21168	22398	8014	Poor	0	0
1987	0.05	14660	11167	13252	13965	1408	Poor	0	0
1988	0.03	16403	12401	14713	15497	1690	Poor	0	0
1989	0.04	17004	13649	16165	16980	839	Good	0	1
1990	0.06	21496	14227	16861	17731	4635	Good	0	0
1991	0.05	16220	18354	21795	22990	5575	Good	0	0
1992	0.05	20008	13709	16262	17128	3746	Ground	0	0
1993	0.06	17738	16898	20043	21106	2305	Poor	0	1
1994	0.04	15266	15096	17918	18890	2652	Fair	0	1
1995	0.06	20229	12756	15110	15885	5119	Good	0	0
1996	0.09	23747	17259	20496	21612	3251	Good	0	0

1) recruitment survey, 2) the absolute difference between Realistic expected Count and observed count, 3) = coverage of the observed count within the 95% quantiles of the realistic prediction, 4) = coverage of the observed count within the lower 95% quantile of the lower prediction and upper 95% quantile of the upper prediction.

TABLE 4.2. Evaluation of the biological plausibility of the pre-migratory fall count of the Rocky Mountain Population of sandhill crane.

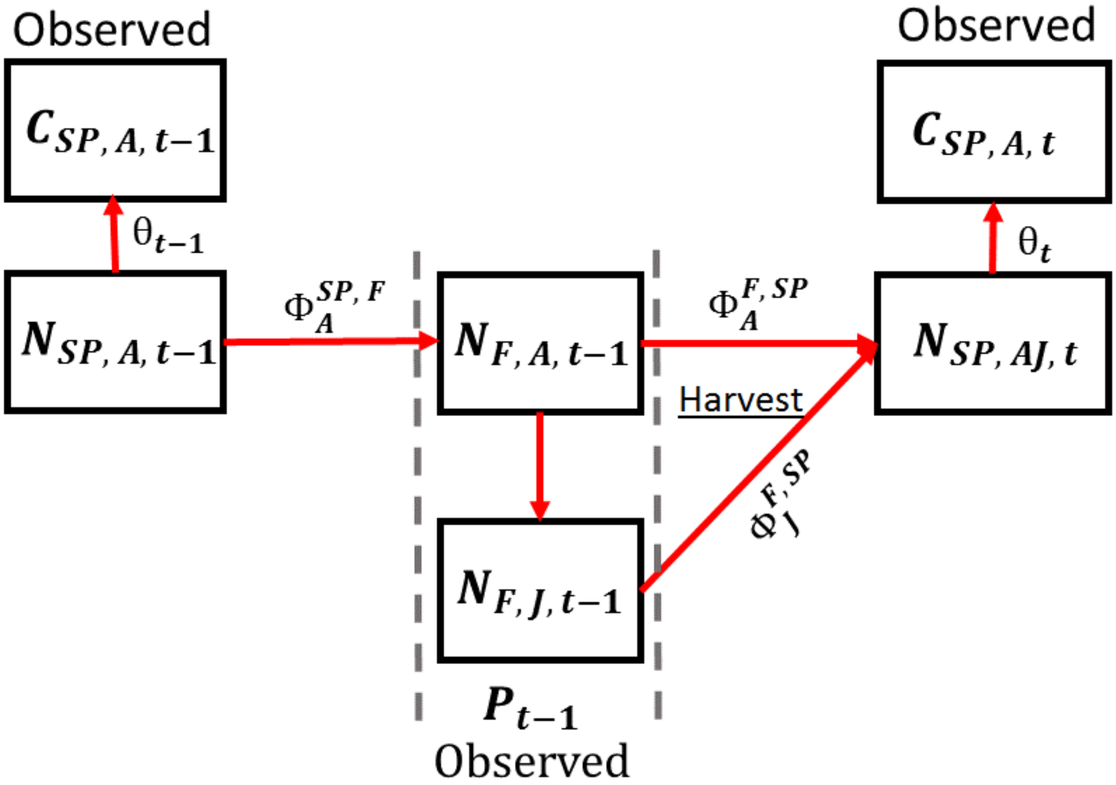
Year	P_t [1]	Fall Count	Low Expected Count	Realistic Expected Count	High Expected Count	Diff [2]	Cov1 [3]	Cov2[4]
1997	0.10	18036						
1998	0.11	18102	15231	18270	19551	168	1	1
1999	0.08	19501	14952	17982	19315	1519	0	0
2000	0.07	19990	16162	19338	20632	652	1	1
2001	0.06	16559	16583	19786	21029	3227	0	1
2002	0.05	18803	14041	16722	17735	2081	0	0
2003	0.07	19523	16319	19425	20570	98	0	0
2004	0.09	18510	17031	20336	21632	1826	0	1
2005	0.11	20865	15870	19017	20343	1848	0	0
2006	0.10		17523	21056	22597			
2007	0.08	22822						
2008	0.09	21156	19933	23854	25446	2698	0	1
2009	0.12	20321	17897	21449	22923	1128	1	0
2010	0.08	21064	16656	20038	21540	1026	0	1
2011	0.06	17494	17803	21301	22728	3807	0	1
2012	0.08	15417	14744	17573	18645	2156	0	0
2013	0.07	19668	13349	15959	17006	3709	0	0
2014	0.10	20360						

1) recruitment survey, 2) absolute difference between Realistic expected count and observed count, 3) coverage of the observed count within the 95% quantiles of the realistic prediction, 4) coverage of the observed count within the lower 95% quantile of the lower prediction and upper 95% quantile of the upper prediction. Counts in 1995-1996 were considered a test-phase.

Table 4.3. Evaluation of the biological plausibility of the pre-migratory fall three-year moving average population index of the Rocky Mountain Population of sandhill crane.

Year	P_t[1]	Fall Index	Low Expected Index	Realistic Expected Index)	High Expected Index)	Diff[2]	Cov1[3]	Cov2[4]
1997	0.10	20671						
1998	0.11	19962	16971	20498	22408	536	1	1
1999	0.08	18546	15910	19556	21299	1010	1	1
2000	0.07	19198	14666	18079	19622	1119	0	1
2001	0.06	18683	15069	18728	20196	45	1	1
2002	0.05	18451	14873	18029	20010	422	1	1
2003	0.07	18295	15312	18505	20186	210	1	1
2004	0.09	18945	15374	18611	20271	334	1	1
2005	0.11	19633	15582	19107	20821	526	1	1
2006	0.10	19633	15725	19106	21262	527	1	1
2007	0.08	20732	15683	19077	21419	1655	0	1
2008	0.09	21614	17197	21383	23117	231	1	1
2009	0.12	21433	17277	21324	23419	109	1	1
2010	0.08	20847	16089	19690	22719	1157	0	1
2011	0.06	19626	16177	19646	22494	20	1	1
2012	0.08	17992	15201	19486	20917	1493	0	1
2013	0.07	17757	14326	17557	19847	200	1	1
2014	0.10	18482						

1) = recruitment survey, 2) = absolute difference between Realistic expected fall index and fall population index, c3) = coverage of the population index within the 95% quantiles of the realistic prediction, 4) = coverage of the population index within the lower 95% quantile of the lower prediction and upper 95% quantile of the upper prediction. Counts in 1995-1996 were considered a test-phase.



$$P_{t-1} = \frac{N_{F,J,t-1}}{N_{F,A,t-1} + N_{F,J,t-1}}$$

Figure 4.1. Spring population model that links observed data (spring count, juvenile recruitment, and harvest) and survival parameters to assess the reliability of the annual change in the spring sandhill crane count in the San Luis Valley, CO from one year to the next (1984-1996).

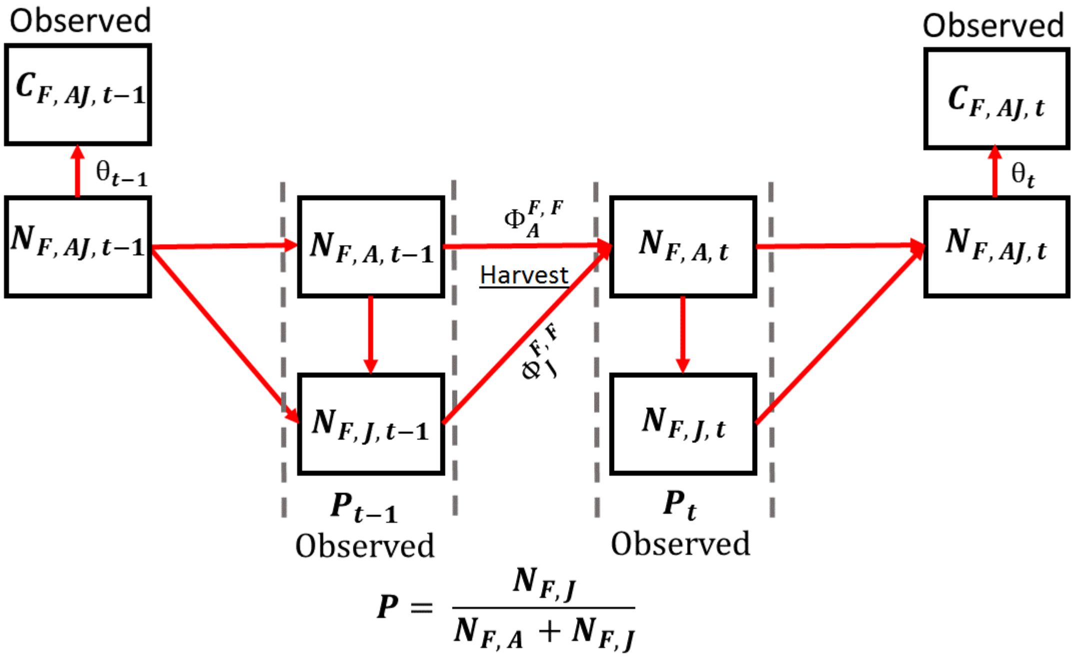


FIGURE 4.2. Fall population model that links observed data (fall count, juvenile recruitment, and harvest) and survival parameters to assess the reliability of the annual change in the spring sandhill crane count in the San Luis Valley, CO from one year to the next (1997-2014).

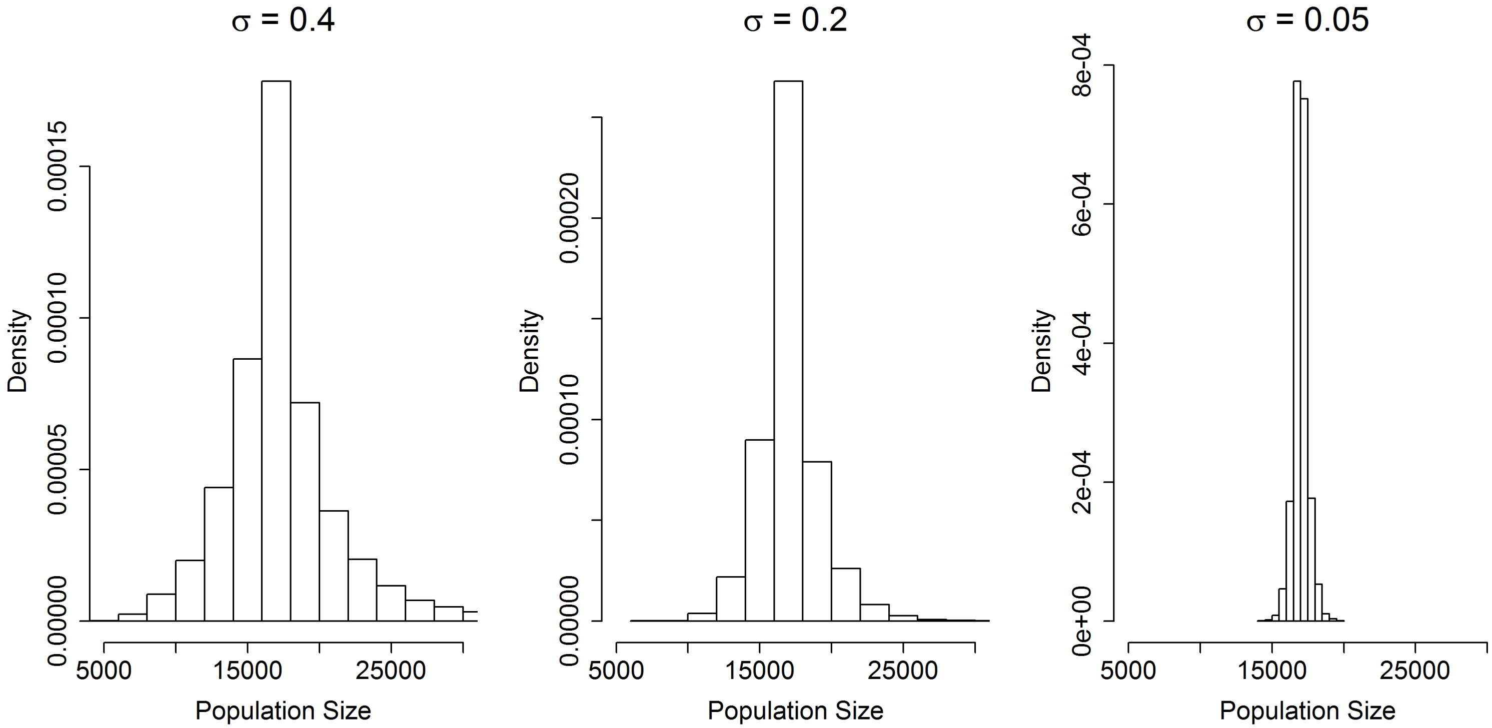


FIGURE 4.3. Maximum realized variability due to either the observation or population process variance of a population with mean 17,000; σ's pertain to variation on the log-scale of the population.

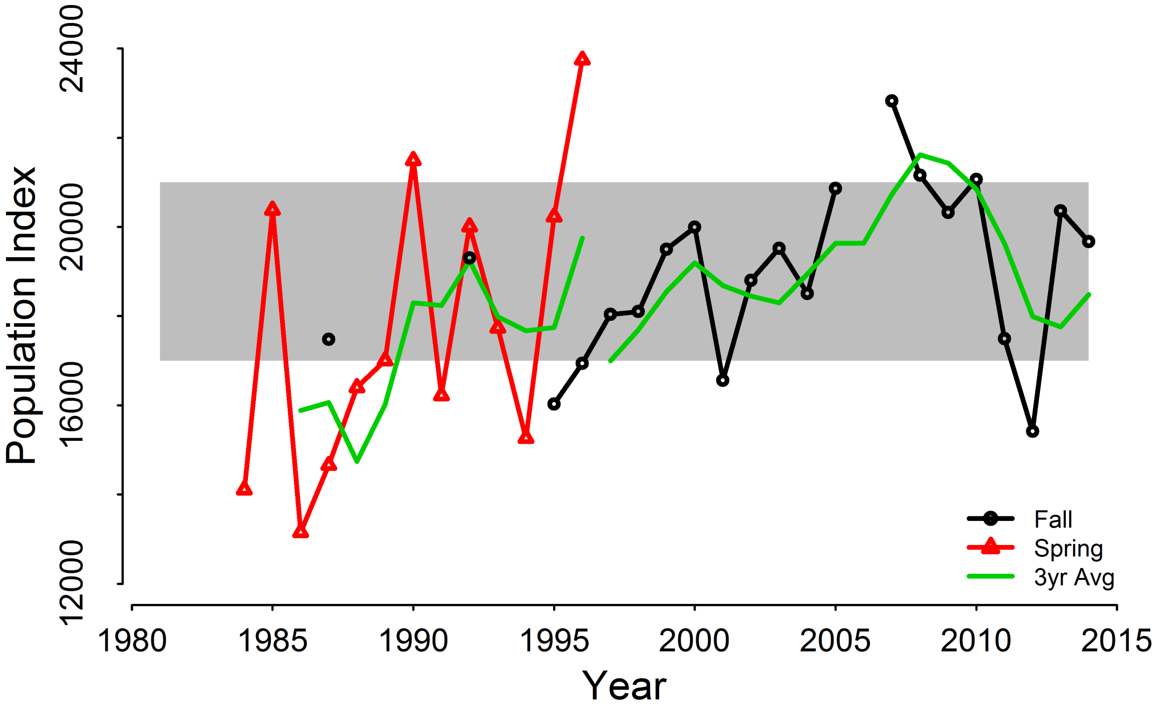


Figure 4.4. Annual population counts and population indices (3yr Avg) of the Rocky Mountain Population of sandhill cranes. The gray area indicates the range of the population objective for the 3yr Avg. The 3yr Avg is calculated separately for the spring and fall counts.

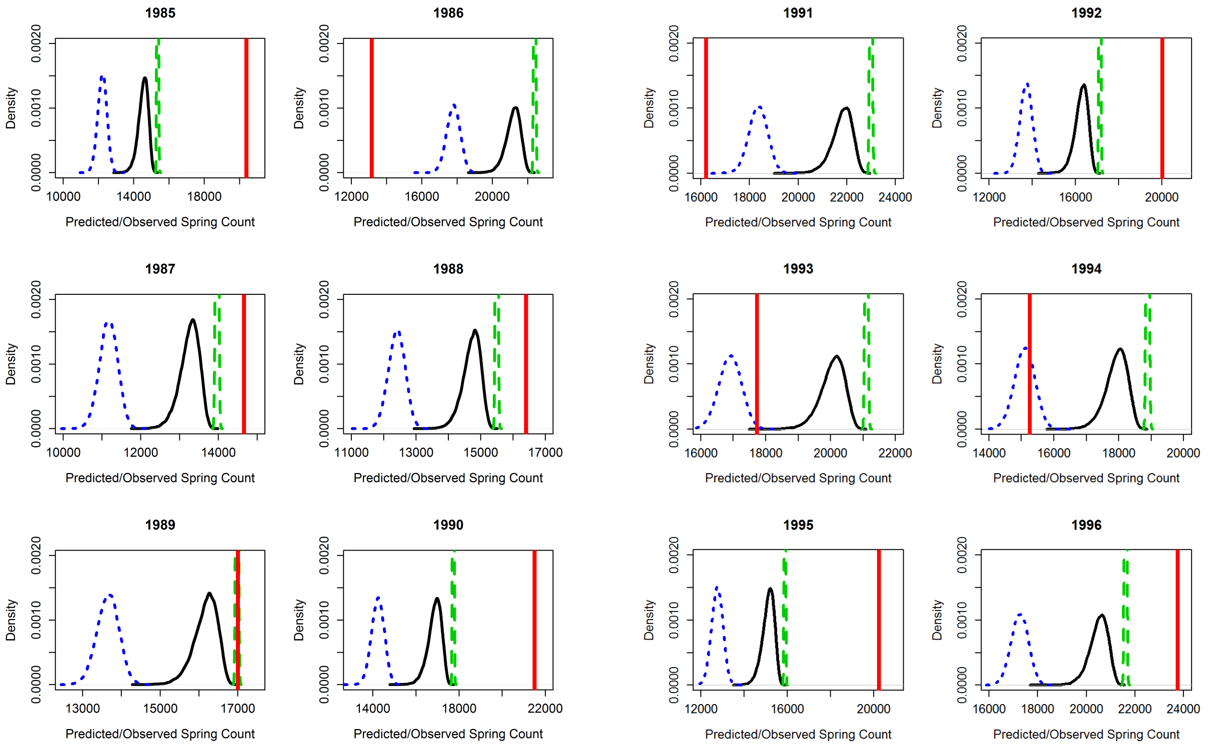


FIGURE 4.5. Comparing predicted spring counts (low (dotted), realistic (solid), high (dashed)) in year t with the observed count in year t (solid vertical line).

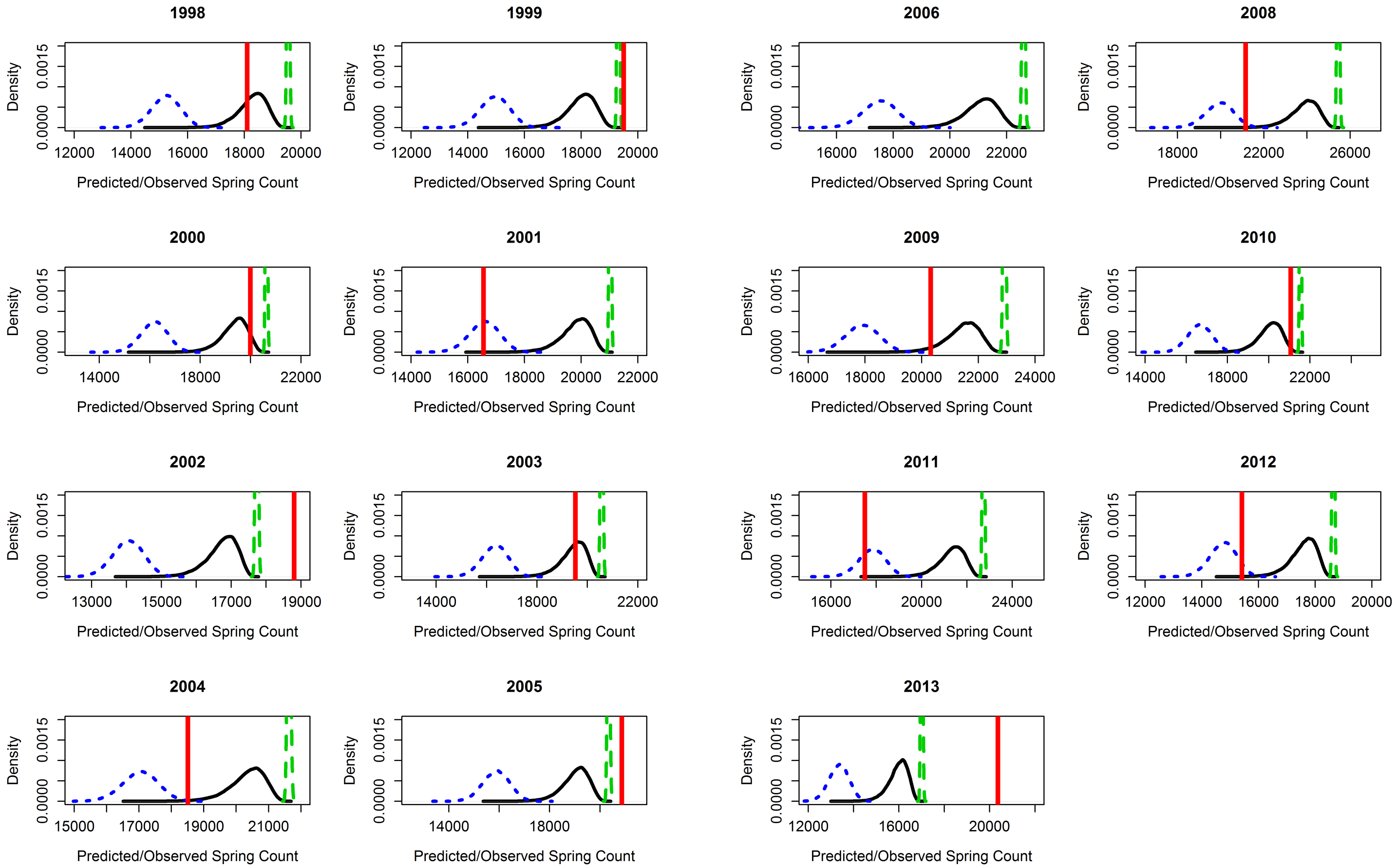


FIGURE 4.6. Comparing predicted fall counts (low (dotted), realistic (solid), high (dashed)) in year t with the observed count in year t (solid vertical line). There was no count in 2006; thus, no vertical line in that plot and no prediction for 2007.

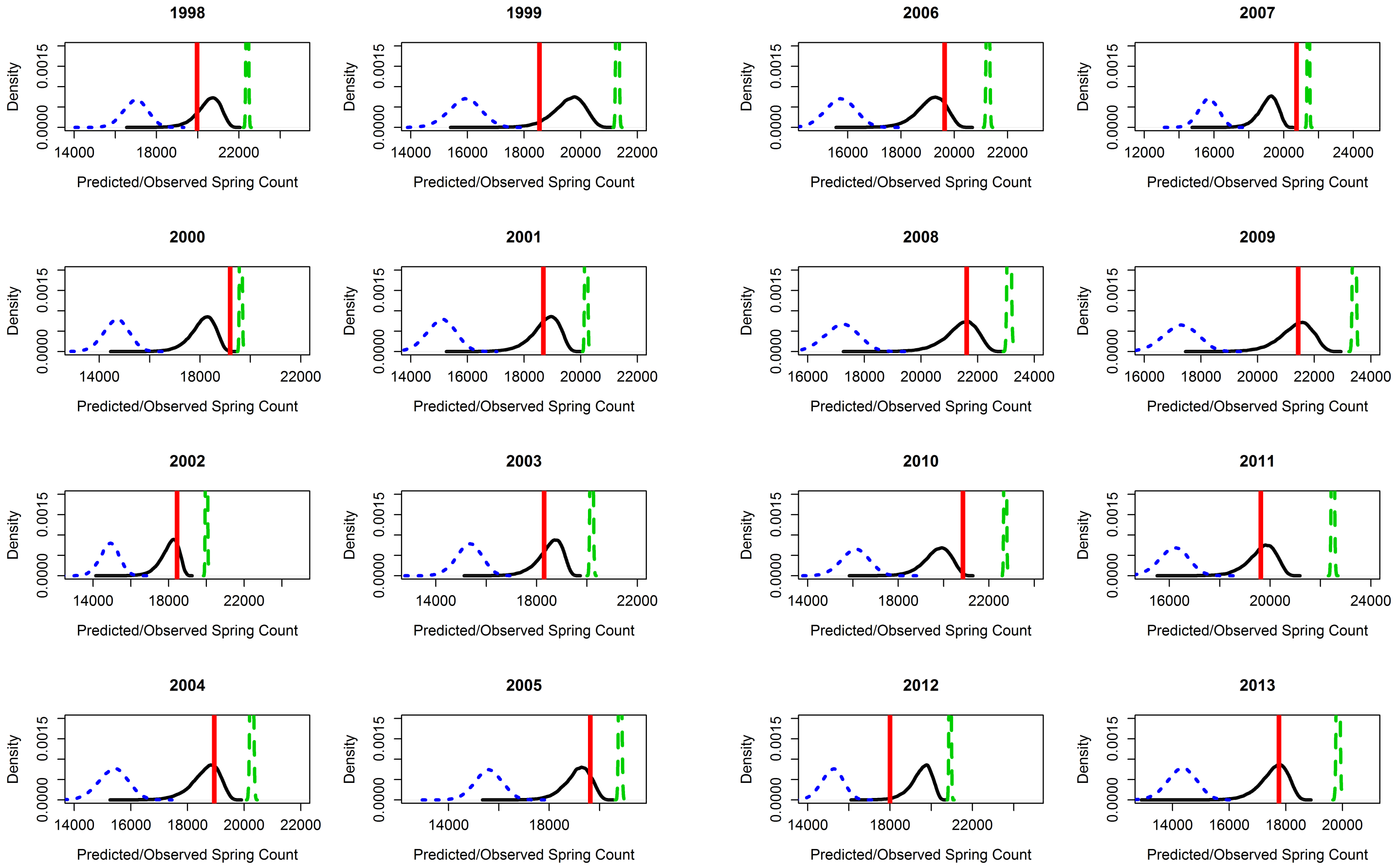


FIGURE 4.7. Comparing predicted fall indices (low (dotted), realistic (solid), high (dashed)) in year t with the observed population index in year t (solid vertical line).

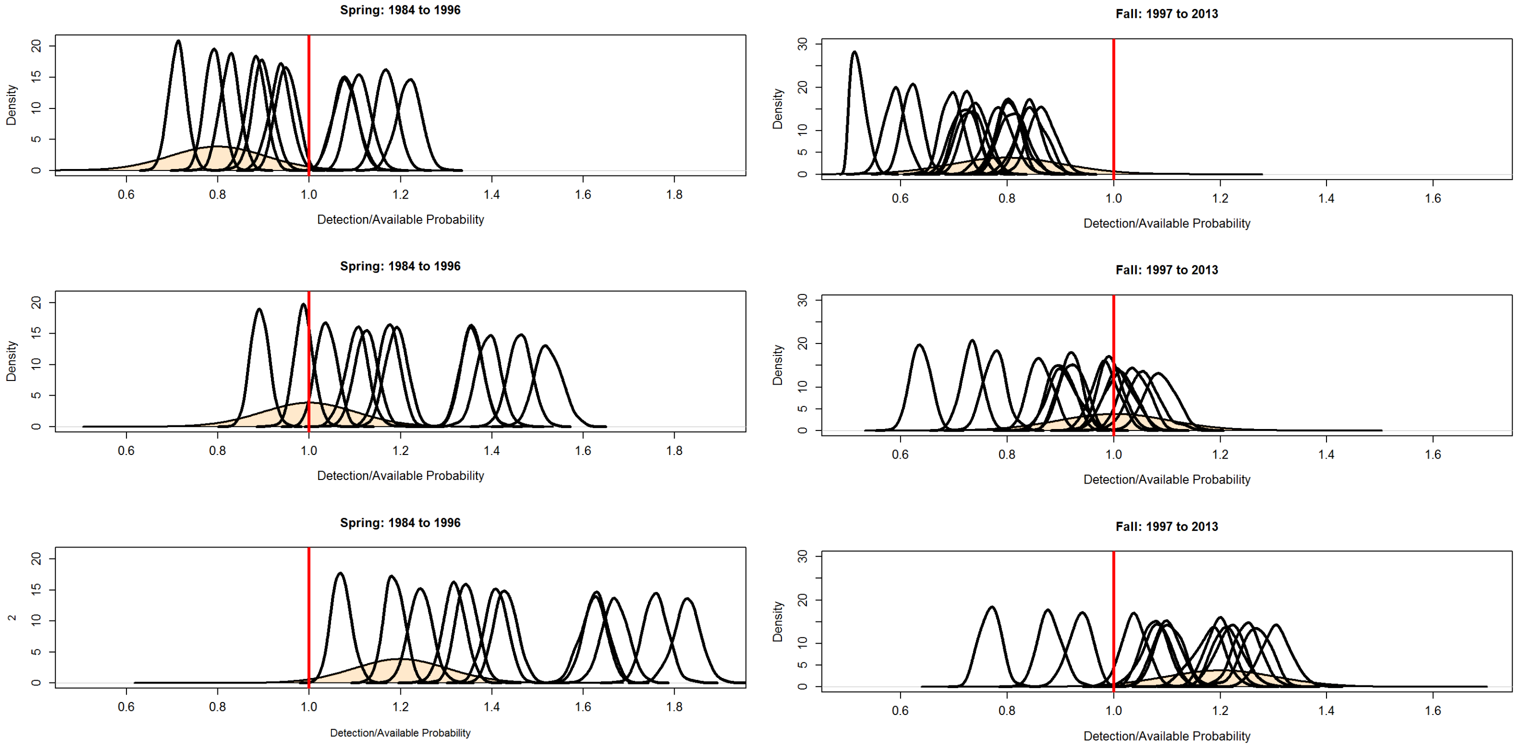
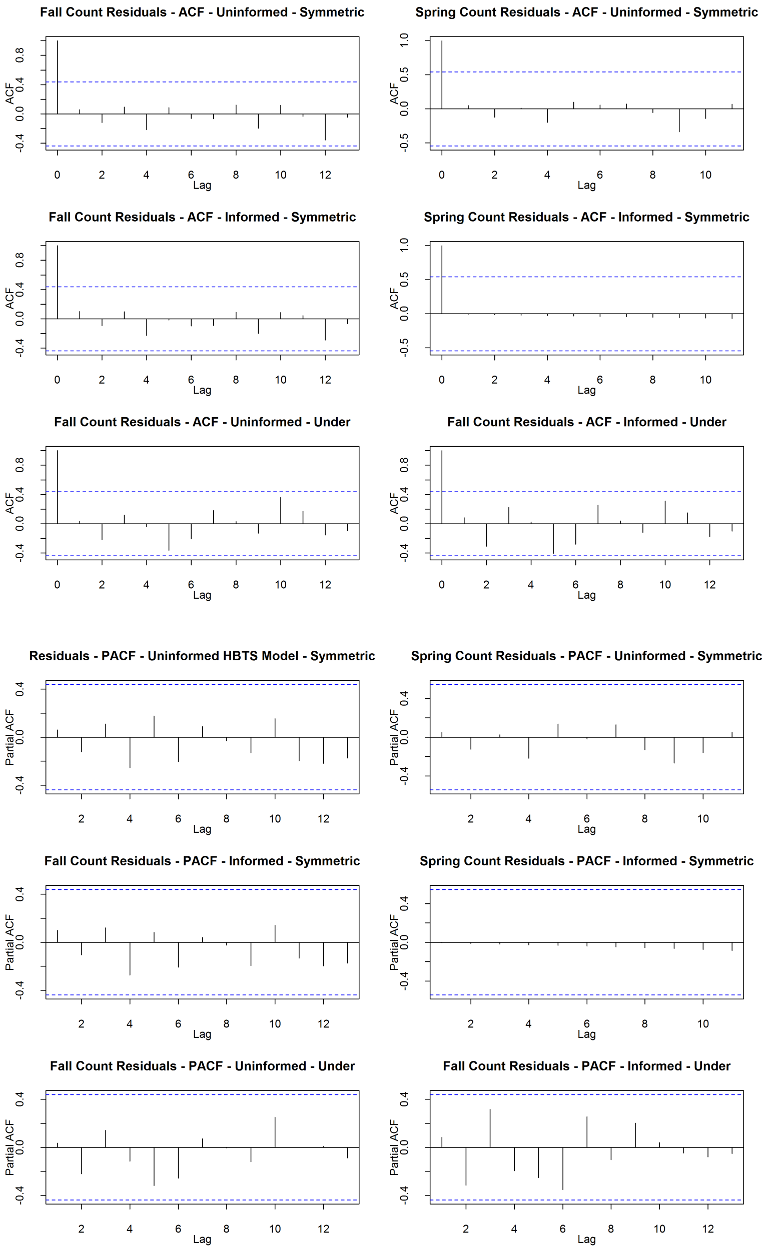


FIGURE 4.8. Posterior distributions of detection/availability parameters from the fall and spring population model. The first count in the time series is defined by a known probability distribution with a mean of 0.8, 1.0, and 1.2, respectively for rows A, B, and C (displayed as the shaded distribution). The vertical line at 1 indicates no error in detection.


Fall Count Residuals - ACF - Uninformed - Symmetric

Spring Count Residuals - ACF - Uninformed - Symmetric

Fall Count Residuals - ACF - Informed - Symmetric

Spring Count Residuals - ACF - Informed - Symmetric

Fall Count Residuals - ACF - Uninformed - Under

Fall Count Residuals - ACF - Informed - Under

Residuals - PACF - Uninformed HBTS Model - Symmetric

Spring Count Residuals - PACF - Uninformed - Symmetric

Fall Count Residuals - PACF - Informed - Symmetric

Spring Count Residuals - PACF - Informed - Symmetric

Fall Count Residuals - PACF - Uninformed - Under

Fall Count Residuals - PACF - Informed - Under

Figure 4.9. Autocorrelation function (ACF) and partial autocorrelation function (PACF) of Pearson residuals from hierarchical Bayesian time series model predictions of fall and spring observed counts, where variance parameters were informative or relatively uninformative, and the observational process was either symmetric around the true population process or strictly undercounting.

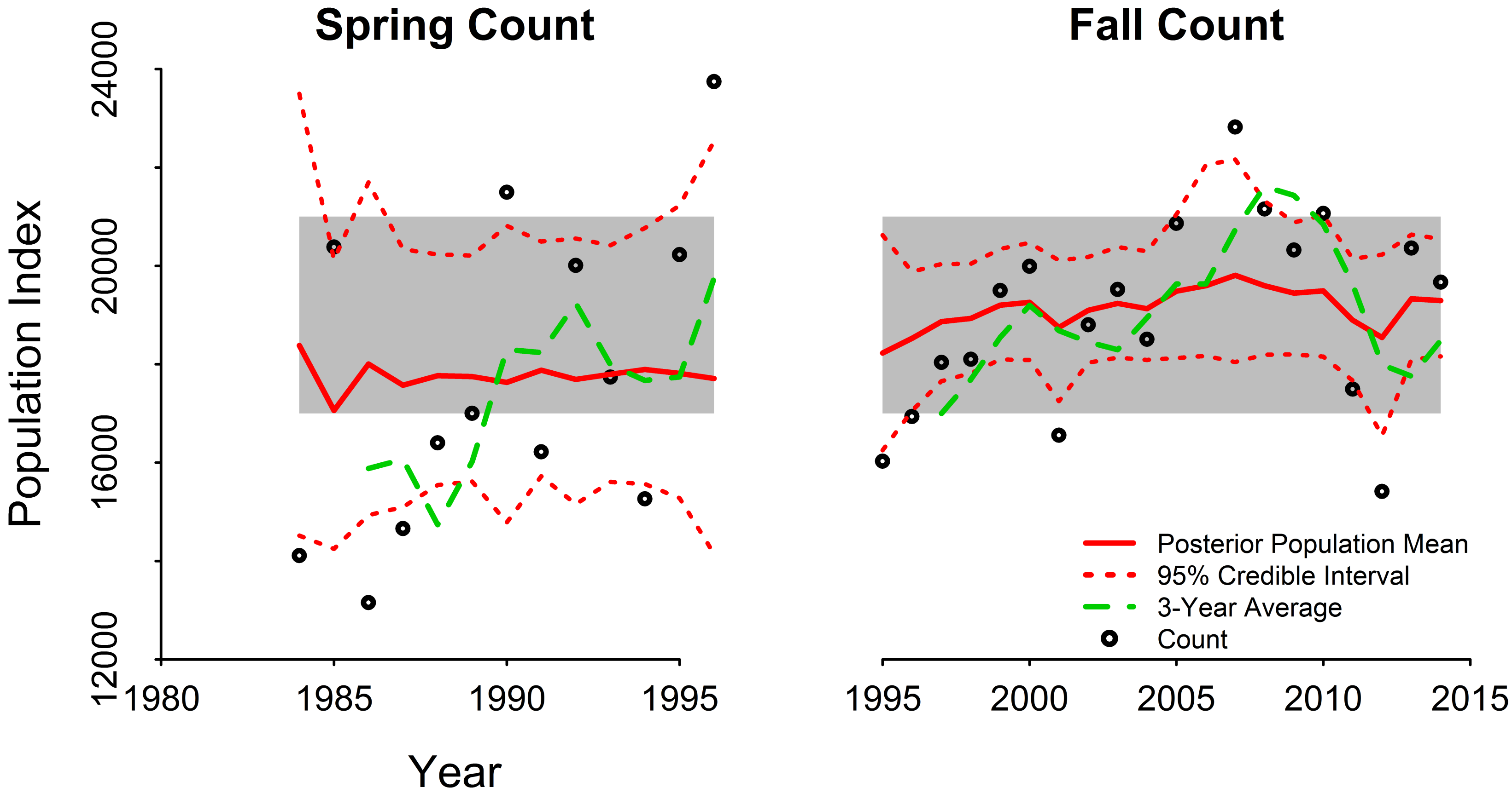


FIGURE 4.10. Predicted population mean with 95% credible intervals from a hierarchal Bayesian time series model, observed fall and spring counts, and population indices (3-Year Average) of the Rocky Mountain Population (RMP) of sandhill cranes. The gray area indicates the population objective. Prior probability distributions are relatively diffuse.

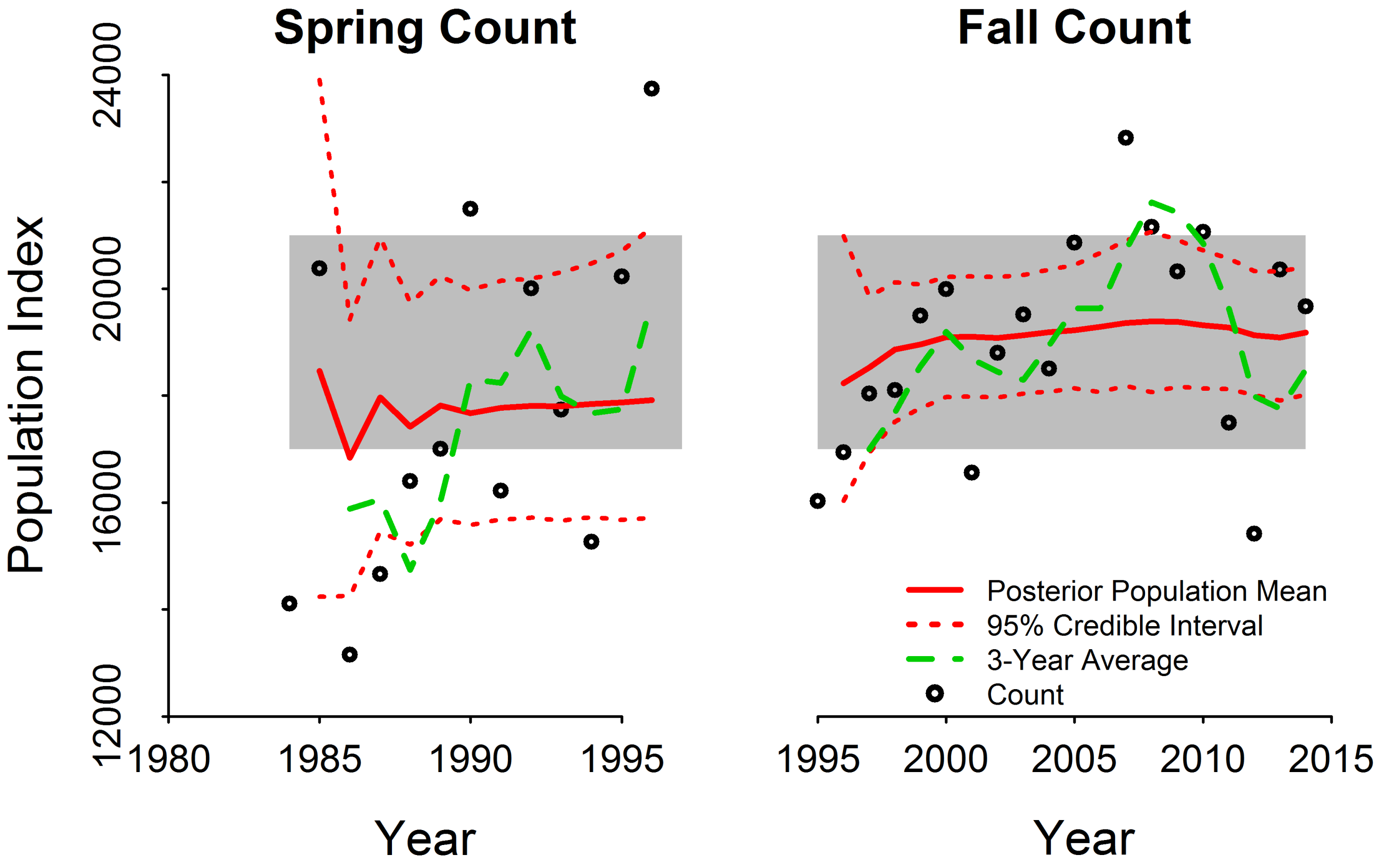


FIGURE 4.11. Predicted population mean with 95% credible intervals from a hierarchal Bayesian time series model, observed fall and spring counts, and population indices (3-Year Average) of the Rocky Mountain Population (RMP) of sandhill cranes. The gray area indicates the population objective. Prior probability distributions on σ_C and σ_N are defined using a uniform distribution with lower bounds of zero and informative upper bounds: Spring Counts uses of 0.4 and 0.05, respectively, Fall Counts uses 0.2 and 0.05, respectively.

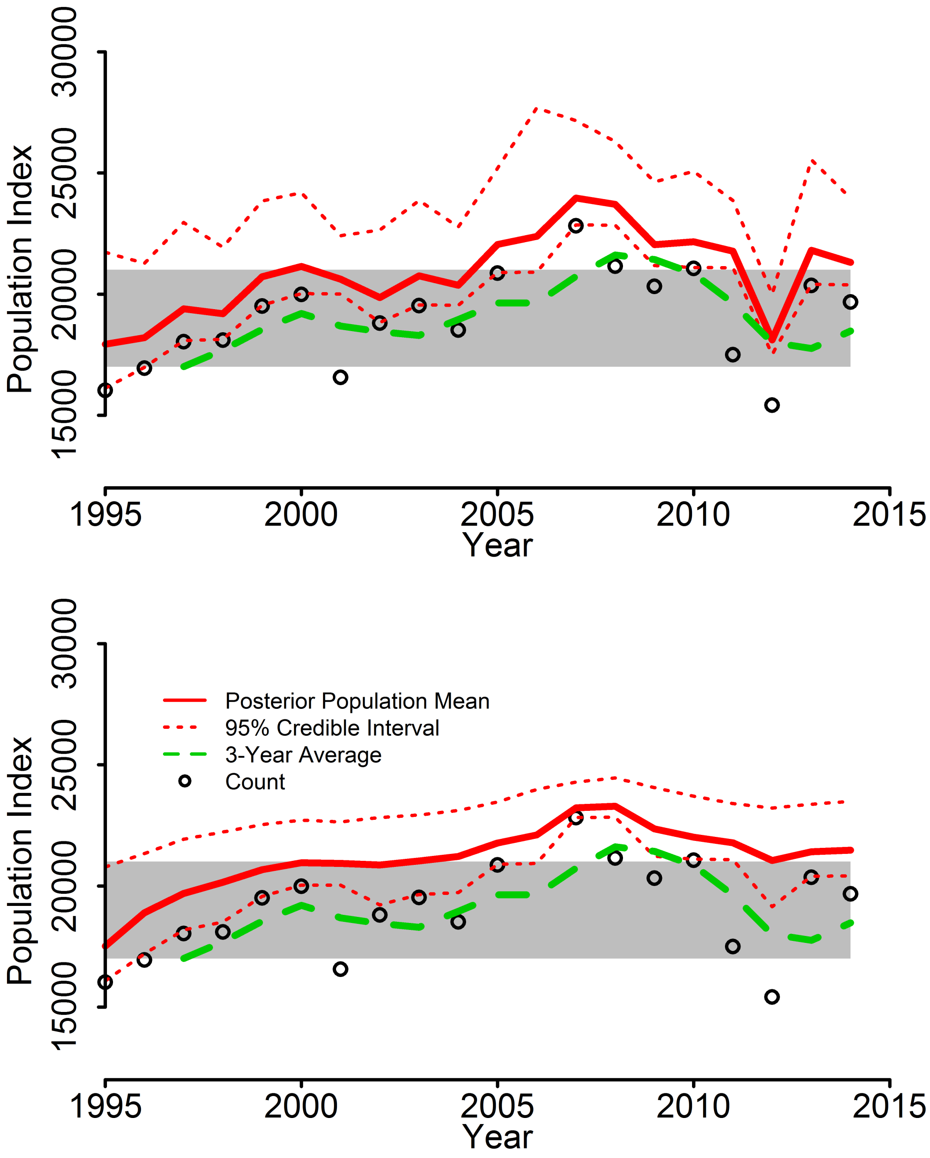


FIGURE 4.12. Predicted population mean with 95% credible intervals from a hierarchal Bayesian time series model, observed fall counts, and population index (3-Year Average) of Rocky Mountain Population (RMP) of sandhill cranes. The observational process is assumed to only be able to under-detect the population; the top figure uses relatively uninformative prior information, while the bottom figure uses informative uniform priors, $\sigma_C \sim Uniform(0, 0.2)$ and $\sigma_N \sim Uniform(0, 0.05)$. The gray area indicates the population objective.

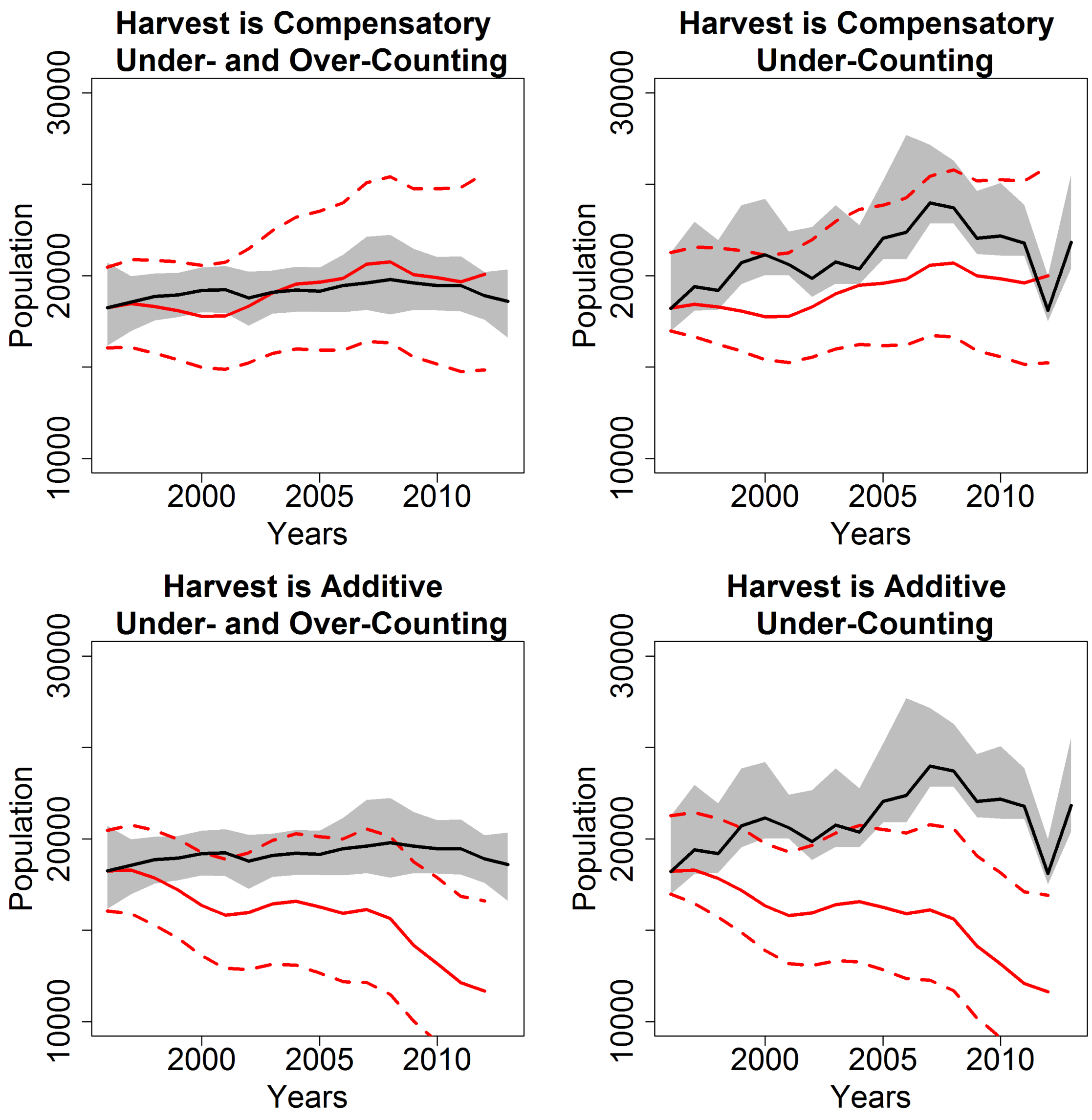


FIGURE 4.13. Predicted population mean (solid black line) with 95% credible intervals from a Bayesian hierarchical time series model (gray area) and projected fall population model initialized with population predictions from the time series model (mean as solid red line and 95% quantiles as dashed red lines). Scenarios included observational processes that were either symmetric around the true population (under- and over counting) or only under-counted, and where harvest was either compensated up to natural mortality or completely additive.

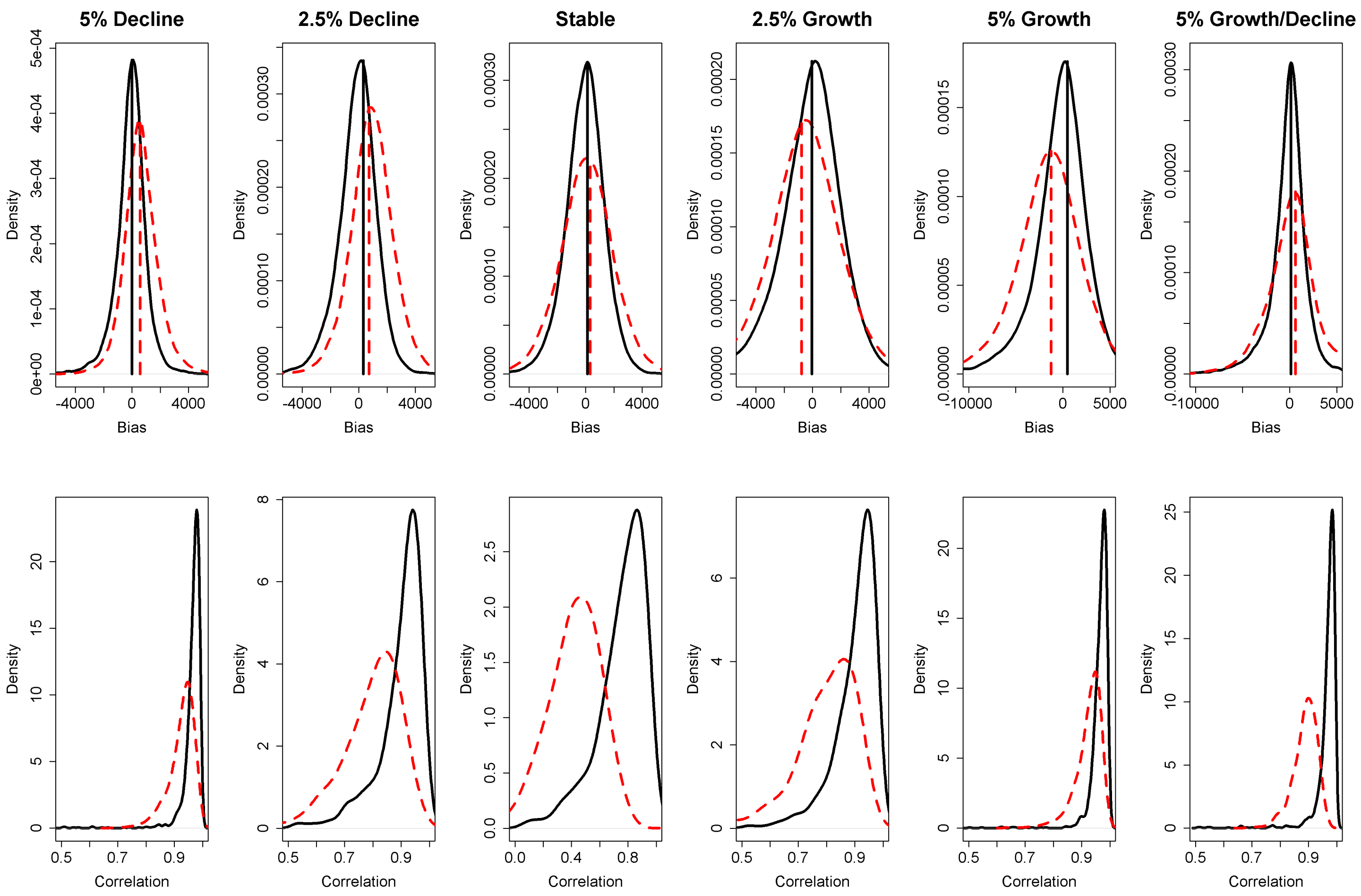


FIGURE 4.14. Empirical distributions of annual bias and correlation of the mean predicted population from a hierarchical Bayesian time series model (solid lines) that considers counts to be symmetric around the true population and using the moving three-year average estimator (dashed lines) for different scenarios of population growth, stability, decline, or combination over a 20 year period. The true observational process is symmetric around the true population. Note, axes are not consistent.

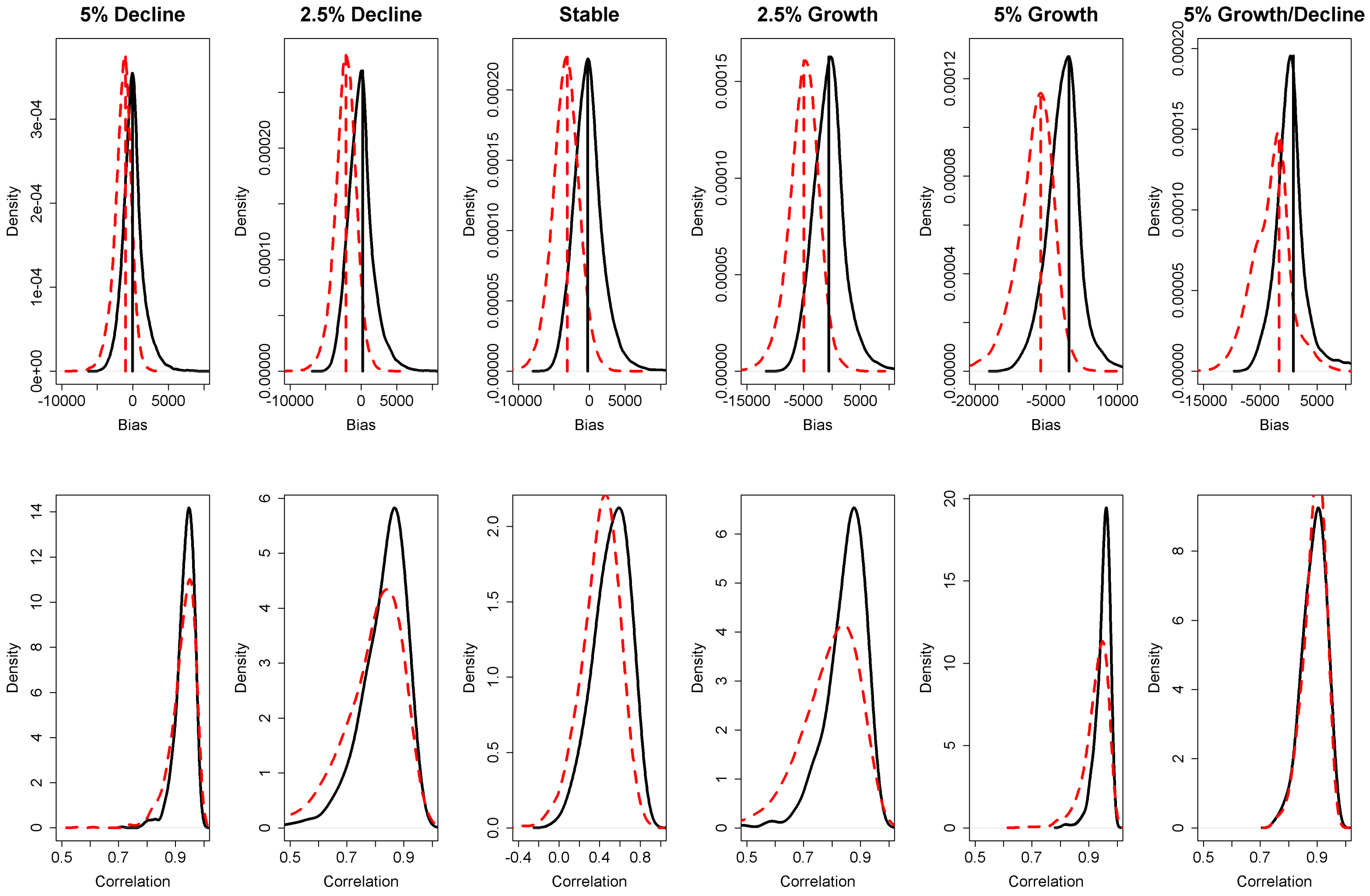


FIGURE 4.15. Empirical distributions of annual bias and correlation of the mean predicted population from a hierarchical Bayesian time series model (solid lines) that considers observations as only under-counting and using the moving three-year average estimator (dashed lines) for different scenarios of population growth, stability, decline, or combination over a 20 year period. The true observational process is equal probability of under-detection between 0.7 and 0.95. Note, axes are not consistent.

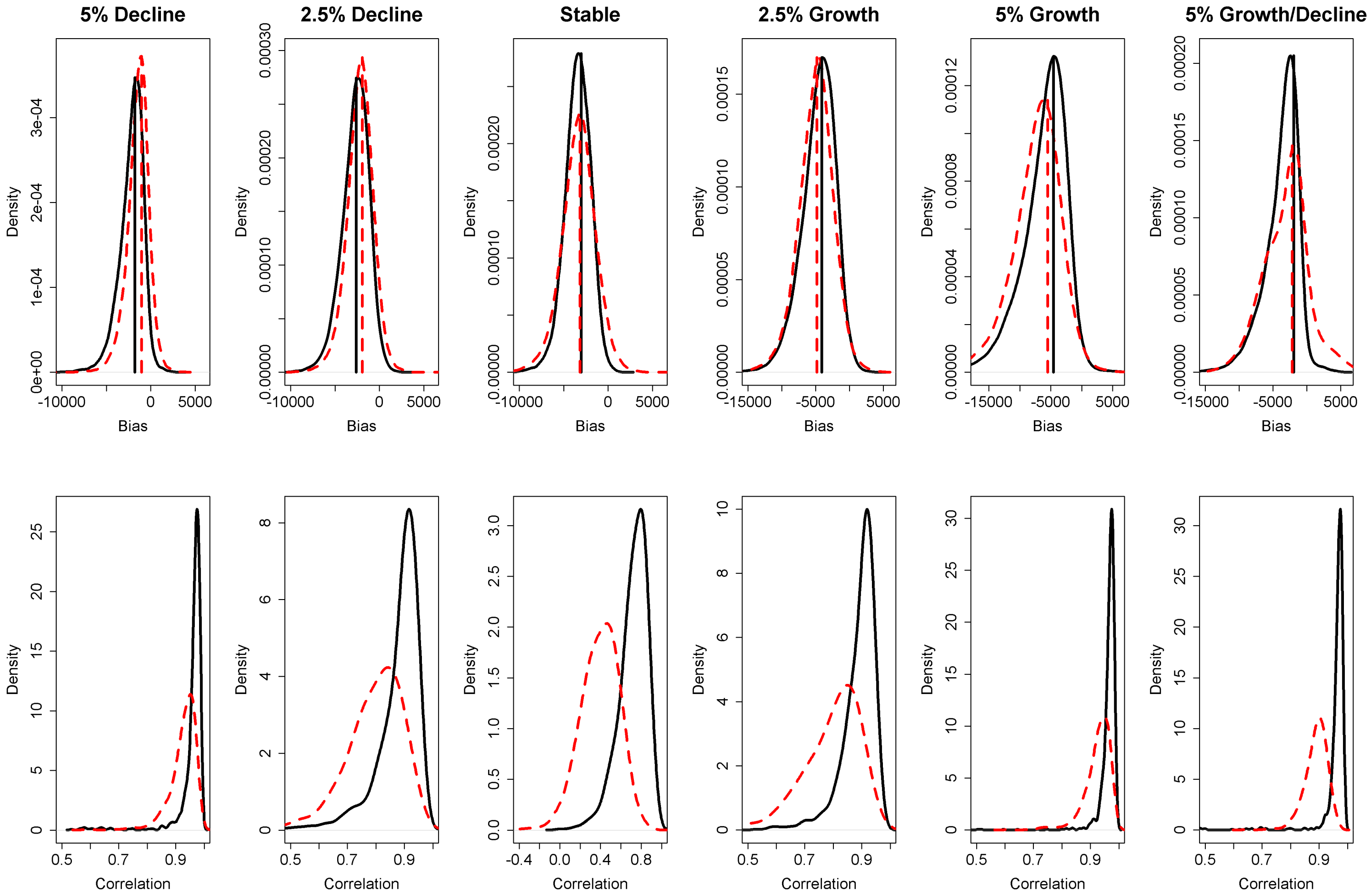


FIGURE 4.16. Empirical distributions of annual bias and correlation of the mean predicted population from a hierarchical Bayesian time series model (solid lines) that considers observations as symmetric around the true population and using the moving three-year average estimator (dashed lines) for different scenarios of population growth, stability, decline, or combination over a 20 year period. The true observational process is equal probability of under-detection between 0.7 and 0.95. Note, axes are not consistent.

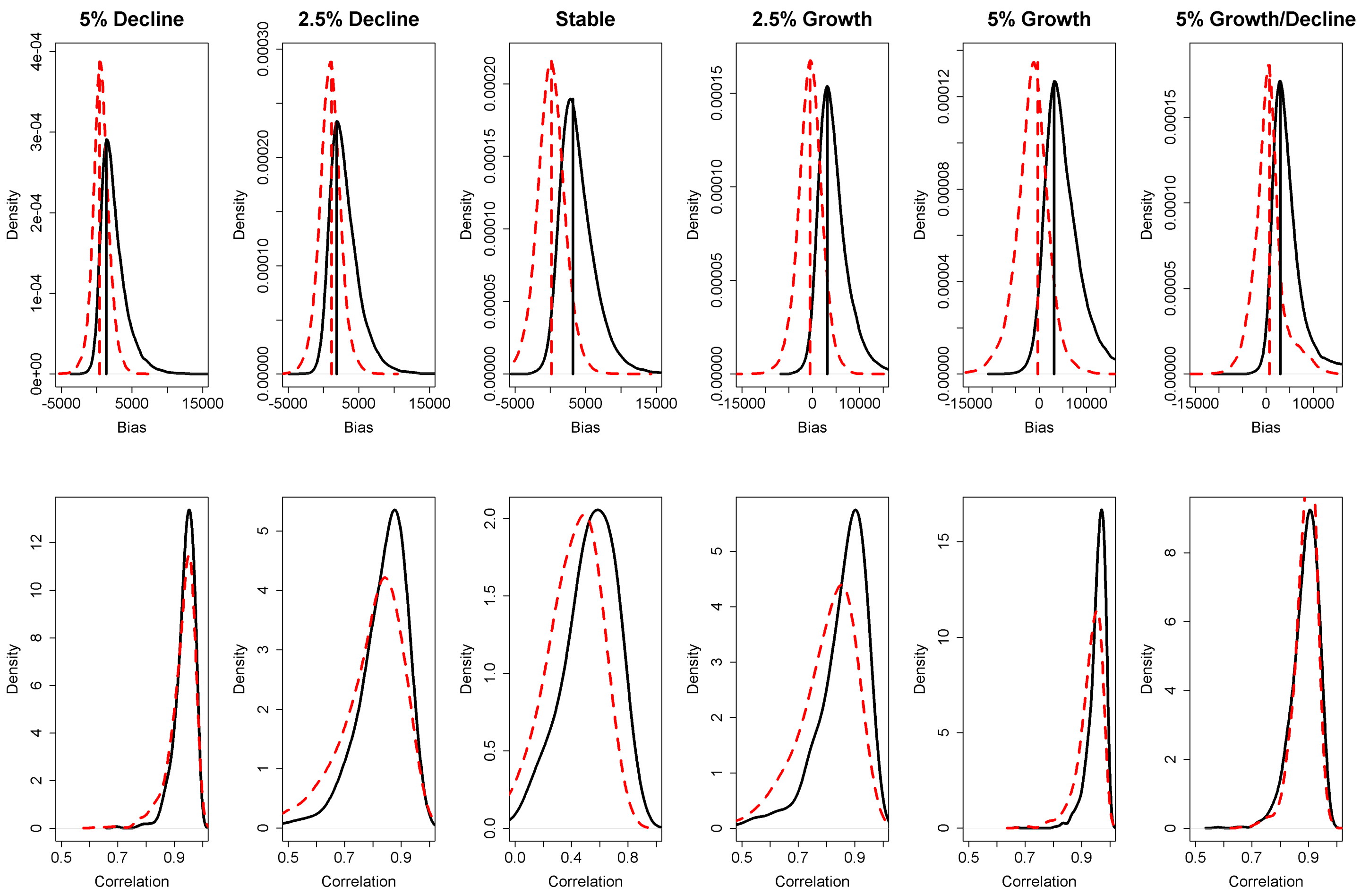


FIGURE 4.17. Empirical distributions of annual bias and correlation of the mean predicted population from a hierarchical Bayesian time series model (solid lines) that considers observations to be under-detections of the true population and using the moving three-year average estimator (dashed lines) for different scenarios of population growth, stability, decline, or combination over a 20 year period. The true observational process is symmetric around the true population. Note, axews are not consistent.

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CHAPTER 5

‘ADAPTIVE’ VERSUS ‘REACTIVE’ MANAGEMENT STRATEGIES: IMPLICATIONS FOR SANDHILL CRANE AND OTHER HARVESTED SPECIES

5.1. SUMMARY

Making management decisions in natural resources in the face of uncertainty is common. Adaptive resource management (ARM) is a formal process to making logical and transparent recurrent decisions when there are uncertainties about system behavior. The ARM process has an explicit, built-in learning component, where the relative belief in models of system dynamics is updated based on their predictive performance. Over time, this process of ‘learning while doing’ can reduce uncertainty about system dynamics and thus lead to improved management decisions to meet stated objectives. Despite wide recognition and calls for implementing adaptive natural resource management, applications still remain limited. To better understand how common uncertainties affect the population management of species, we evaluate the potential risks of an adaptive harvest management process compared to a more common decision threshold or reactive approach to management, where harvest decisions are based on a simple prescriptive function. We focus on the migratory Rocky Mountain population (RMP) of sandhill cranes, as a case study, where the management objective is to maintain the population between 17,000 and 21,000. We evaluate an ARM framework and the current reactive RMP decision strategy using simulation, where the underlying population dynamics follow a complex stochastic stage-structured, density-dependent population model. We consider nine different scenarios with varying levels of

monitoring and modeling uncertainty. We found that using a model set of relatively simple models in an ARM framework to make annual harvest decisions, on average, out performed the current RMP decision process in meeting the population objective across a wide array of scenarios. The primary limitation of the RMP harvest framework occurred when the population without harvest is stable or declining, such that harvesting was large enough to push the population to the lower bound of the population objective. We also found that when harvest decisions are made using the RMP framework, there is only a small improvement in meeting the population objective when resolving monitoring uncertainty, such that the population size was observed without error. In contrast, when using an ARM framework, resolving the uncertainty about the population size meant that the population objective was always maintained, regardless of the model set. We found that stage-specific optimal harvest decisions are not always necessary to meet a population objective when population dynamics are stage structured. As sandhill crane populations continue to expand, there may be increasing interest in additional harvest within already harvested populations or in additional populations. Lastly, when there is considerable uncertainty in estimating annual population size and/or population models are expected to be relatively simple compared to the true population process, learning in an ARM process may be best viewed as a way to identify reasonable predictive models for the current time period, rather than potential to learn about ecological processes. Sandhill crane managers and stakeholders could benefit from decreased risks to managing sandhill cranes by adopting an ARM framework, as well as benefit from its logical, transparent, and theory-driven process that is highly adaptable as new challenges arise.

Key-words: adaptive resource management, hunting, learning, optimal decision, population monitoring, sport harvest, stage-structured

5.2. Introduction

Natural resource managers routinely have to make decisions in the face of multiple uncertainties (Holling, 1978; Hillborn and Mangel, 1997; Kendall, 2001; Regan et al., 2002; Williams et al., 2002). Decisions are often aimed at manipulating ecological systems, as a means to reach a specific state and/or to provide value from the system (e.g., non-consumptive or consumptive utility; Holling 1978). Management decisions are commonly context-specific/state-dependent. Ecological system dynamics are highly complex and thus making a 'good' decision (that will lead to meeting objectives) for a given system state can be complicated (Holling, 1978; Mangel et al., 1996; Kendall, 2001). Logical questions arising from this process include, 1) what are the most important factors governing system dynamics, 2) how will management actions affect the system, and 3) what state is the system presently in?

Recurrent decisions add additional complexity because decisions made today can affect the future state of the system and thus future decision making (Williams et al., 2007). It may be desirable to balance outcomes dependent on the relative utility gained today and in the future. To do so requires some understanding of system behavior and the effects decisions have on the system. Recurrent decision making also allows for a unique opportunity to learn about system behavior while managing, which is explicitly directed at improving future decisions by decreasing uncertainties related to management (Williams et al., 2007; Williams, 2011). Considering current and future decisions simultaneously with uncertain system dynamics, makes the decision process highly unintuitive and can benefit from a formal application of optimal decision making (Williams, 2011). The paradigm that outlines a formal procedure to make recurrent optimal decisions, in the face of uncertainty, with respect to explicit objectives and constraints is adaptive resource management (ARM; Holling 1978; Walters 1986).

The basics of the ARM process include, 1) explicit specification of management objectives through collaboration among managers and stakeholders, 2) developing a set of acceptable management options, 3) defining alternative predictive models of system dynamics, often based on mathematical or statistical representations of hypotheses, 4) implement a decided course of management actions, 5) monitor the system response such that management objectives can be evaluated, and 6) adjust management practices in response from monitoring results via updating relative beliefs in hypotheses of system dynamics (Williams et al., 2007; Williams, 2011).

The basis of making decisions is using models to anticipate future dynamics and the effects of the suite of management actions. Since, it is common to have multiple working hypotheses about system dynamics (Chamberlin, 1890; Burnham and Anderson, 2002), decisions may be based on the weighted average of each model's prediction of system change under each alternative management action. A model's weight represents the relative degree of faith in its predictions, which can change through time. This process is highly dependent on a well-designed monitoring program (Moore and Kendall, 2004; Nichols and Williams, 2006; Lyons et al., 2008; Kendall and Moore, 2012) to provide the necessary information for, 1) making state-dependent decisions, 2) evaluating management performance (as outlined by the objectives), and 3) facilitating learning of system dynamics by comparing predicted and observed states to improve future management decisions. Ideally, the monitoring program accounts for sampling variability, including spatial and detection/availability variation (Pollock et al., 2002; Nichols and Williams, 2006).

ARM is widely considered the most effective, efficient, and formal paradigm for making recurrent management decisions for ecological systems in the presence of uncertainty (Williams et al., 2002, 2007; Williams, 2011; Westgate et al., 2013). ARM is a special case of structured decision making, which is a general framework for making informed decisions in a logical and transparent process (Williams et al., 2007). ARM's appeal is its evidence-based approach to management (Walker, 1998; Sutherland et al., 2004). Despite much support for ARM and calls for its implementation (U.S. NABCI Committee, 2007; Williams et al., 2007; Wilson and Woodraw, 2013), operational ARM programs are still uncommon, but likely growing (Atlantic States Marine Fisheries Commission, 2009; Gannon et al., 2011; Westgate et al., 2013).

The longest running, most spatially extensive, and perhaps the most successful ARM program is the harvest management of mallards (*Anas platyrhynchos*) in North America (Nichols et al., 1995; Johnson et al., 1997; Westgate et al., 2013). Over time, harvest management for an increasing number of waterfowl species has evolved into an ARM process (U.S. Fish and Wildlife Service, 2014a). However, many waterfowl and game bird management, as well as general national and local natural resource management frameworks, have yet to make the transition. Despite the appeal of the ARM process, one reason for slow adoption or even resistance to its use could be that managers, stakeholders, and researchers desire explicit demonstration that compare ARM to the current management strategy, so that realistic expectations for each are better known (Hall et al., 2010). Theoretical expectations are less meaningful than realistic ones when responsible for difficult decisions about a public resource.

In contrast to ARM's anticipatory type of process for making management decisions, it is perhaps more common for management strategies to follow a reactive approach that equates the decision with the current state and thus utility of the system (Martin et al., 2009) and does not recognize future system changes. For example, conservation actions may precipitate if the finite rate of population change (λ) is detected to be less than 1.00 for a threatened wild animal population or hunting of a game species is restricted or closed if the population is detected to fall below a certain threshold. Management actions following an ARM approach try to keep the system state away from these decision thresholds that precipitate low utility value according to the management objective(s) (Martin et al., 2009). However, to do this, models (or at least the model set) must be adequate to make reasonable predictions of system behavior and the effect of alternative management decisions, such that an appropriate management decision for the current state of the system can be made. Supporters of ARM have often noted that conservation/management decisions need not be impeded by a lack of consensus with regard to understanding system dynamics (Nichols and Williams, 2006; Martin et al., 2009; Marescot et al., 2013). An ARM process will enable learning about the system while managing. A logical question is whether there is more or less risk in making decisions based on a model set of potentially poor models (i.e., are limited in their structure and parameterization due to limited available data) or decisions from a non-model based, reactive approach to management?

We are interested in comparing the potential risks of long-term management using an ARM program versus a reactive strategy, in the face of common uncertainties in population management. We are specifically interested in evaluating decision frameworks for recurrent decision making to manage a highly complex stage-structured animal population. We consider scenarios where there are uncertainties about population dynamics (i.e., structural uncertainty), including the effect of management decisions on the population. We also consider monitoring uncertainties, where we are unable to estimate the annual stage-structure of the population and/or estimate the true population size, and thus only observe a count of the total population (i.e., partial observability). As such, decisions have to be made with uncertainty as to the state of the true population and short- and long-term effects of management actions. We use the sandhill crane (*Grus canadensis*) of the Rocky Mountain Population (RMP) as a case study to examine the risks of an adaptive harvest management process to making annual decisions and compare them to the current (reactive) decision framework.

The slow life history of sandhill cranes (sensu Sæther and Bakke 2000; long-lived and slow reproducing) makes harvest decisions challenging. Even if harvest mortality is compensated up to natural mortality there is little room for additional annual mortality before causing a decline in survival and perhaps the population. Harvested sandhill crane populations are currently restricted to migratory populations, which breed across large spatial extents at low densities, making population monitoring challenging. Migratory sandhill crane populations are currently monitored using population indices, such that there is concern that annual sampling variation may mask a population trajectory heading outside the bounds set by management objectives, and thus recovering from a decline may be long, given their slow life-history (Case and Sanders, 2009). Sandhill crane harvest decisions for the RMP and the much larger Mid-Continent Population (MCP) are both made using a reactive management approach via a prescriptive function that does not account for age-structured dynamics or consider the trade-offs in recurrent decisions. Given sandhill cranes' slow life-history, there is concern whether the current harvest decision frameworks and monitoring programs for the RMP and MCP are appropriate and will be able to sustain population levels within the stated objectives of their respective management plans (Case and Sanders, 2009).

Our objective is to consider an array of scenarios to better understand the risks associated with making sandhill crane harvest decisions using the current RMP framework versus an ARM framework. We do so by taking a virtual-ecologist approach (Zurell et al., 2010) and simulating stochastic stage-structured population dynamics with variable vital rate density-dependence coupled to environmental variability. There is an explicit objective for the RMP to maintain a population between 17,000 and 21,000. We investigate the potential for each framework in meeting this management objective. For each scenario (which varies in its structural and monitoring uncertainty and decision framework), we investigate the expected value of perfect information (EVPI) and the expected value of partial perfect information (EVPXI), which represents the value of completely or partially eliminating uncertainty, respectively (Yokota and Thompson, 2004). We are specifically interested in how the decrease in one or all uncertainties changes the annual probability of meeting the RMP objective and the expected annual harvest. We also evaluate the potential for learning in the ARM framework and how this affects decisions.

Our approach aims to make the benefits and costs of current and alternative management practices clearer for managers to decide on appropriate future changes to harvest management of wild animal populations (Hall et al., 2010). Our findings have direct implications to the harvest management of sandhill crane populations. More generally, our findings are important to both ecologists and resource managers interested in understanding the comparative risks of ARM versus reactive strategies to making management decisions, as well as the potential for learning about complex ecological systems while managing.

5.3. Methods and materials

5.3.1. Sandhill crane life History and harvest management.

Sandhill cranes are among the oldest extant species of the class Aves (≈ 2.5 million years old; Emslie 1992). They are large, vocal, birds that are sought after as a harvested species, as well as admired as an icon throughout North America. Crane festivals at traditional migratory stop-over areas attract numerous visitors annually, providing an economic boon to local communities (Lingle, 1991; Case and Sanders, 2009; The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). A cost of large crane populations is agricultural crop damage, which in some areas can be as high as 50-60% loss (Schramm et al., 2010), and the possibility of increased risk to human health via food and water fecal contamination (Gardner et al., 2011; Vogel et al., 2013). Most migratory crane populations allow sport harvesting mitigate crop damages and to provide recreational opportunity.

Migratory populations are harvested, at varying levels, throughout Russia, the United States, Canada, and Mexico depending on the state/province and crane population (Kruse and Dubovsky, 2015). The Central Valley population of the Pacific Flyway is not currently hunted, while the Pacific Flyway population, also of the Pacific Flyway, has limited sport and subsistence hunting in Alaska (Case and Sanders, 2009). The smallest sandhill crane migratory population is the Lower Colorado River Valley population of the Pacific Flyway, which has allowed a limited experimental hunt for only a few years (Kruse and Dubovsky, 2015). Two of the larger populations, the MCP of the Central Flyway and the RMP, which spans the Central and Pacific Flyways, are harvested across multiple states and countries, starting legally in 1961 and 1981, respectively (Central Flyway Webless Migratory Game Bird Technical Committee, 2006; The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). Lastly, the Eastern Population of the Mississippi and Atlantic flyways has recently seen substantial population growth, which has also increased interest in hunting, with limited hunting beginning in Tennessee and Kentucky (Kruse and Dubovsky, 2015).

Life history characteristics of sandhill cranes include an average clutch size of 1.9 (see, Gerber et al. 2014), high annual adult survival (>0.92 Johnson and Kendall 1997; Drewien et al. 1995, 2001), and first attempted breeding by 2-3 years of age with most productive birds greater than 7-8 years of age (Drewien et al., 2001; Tacha et al., 1989). Sandhill cranes have the lowest known juvenile recruitment of any sport harvested bird in North America (Drewien et al., 1995), which for the RMP appears to be driven by climate (Gerber et al., 2015).

5.3.2. RMP current monitoring and harvest decision framework.

The RMP is monitored annually via a fall pre-migratory staging area population survey that results in an aggregated count pertaining to the whole population (*Count*); the survey is coordinated across federal and state agencies and includes aerial and ground counts at 81 known staging sites throughout the breeding area states (Colorado, Utah, Wyoming, Montana, Idaho; The Subcommittee on Rocky Mountain Greater Sandhill Cranes 2007; Kruse and Dubovsky 2015). This count began operationally in 1997. There is no additional information collected to adjust the *Count* due to sampling variation (e.g., detectability/availability). In addition to the population survey, an annual recruitment survey of the proportion of juveniles (< 1

year old) in the population (P_t) during the fall migration in the San Luis Valley (SLV) of south-central Colorado has been conducted since 1972 (Brown, 2014). The current allowable harvest for the entire RMP is allocated based on the following function (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007),

$$H_t = \mathrm{g}(C_t, P3_t, R, L) = \begin{cases} 0 & , C_t < 15,000 \\ C_t \times P3_t \times R \times L \times (\frac{C_t}{16,000})^3 & , C_t \geq 15,000 \end{cases}$$

where H_t is the allowable harvest in year t, C_t is an index to the population based on the annual fall pre-migratory fall population counts ($C_t = \frac{Count_{t-3}+Count_{t-2}+Count_{t-1}}{3}$), $P3_t$ is an index to juvenile production as measured by the proportion of juveniles in the population during the fall migration ($P3_t = \frac{P_{t-3}+P_{t-2}+P_{t-1}}{3}$), R is an assumed recruitment of fledged chicks to breeding adults (R = 0.5), and L is an assumed retrieval rate of cranes shot by hunters (L = 0.8, thus an assumed 20% crippling loss). The increase in either or both $P3_t$ and C_t increases allowable harvest non-linearly (Figures 5.1, 5.2). The observed allowable harvest between 1997-2014 has averaged 1132 (range, 632-1970), which translated into an estimated mean annual realized harvest of 852 (range, 446-1392; Kruse and Dubovsky 2015). The realized scenarios (C_t and $P3_t$) for harvest allocation have not explored much of the total potential decision-space, thus leaving questions as to how the function g will operate under a sizable range of possible future conditions (Figure 5.2). The harvest function is relatively most sensitive (i.e., based on partial-derivatives of g with respect to each input parameter, evaluated at the normal operating point; Smith et al. 2008) to changes in C_t.

5.3.3. RMP ADAPTIVE HARVEST MANAGEMENT FRAMEWORK.

5.3.3.1. *The decision process.* To outline an adaptive harvest management framework for sandhill cranes, we require one or more models that can predict crane populations in year $t+1$ based on the population in the current year t and a harvest decision (H_t). By summarizing these models as a discrete Markovian process (i.e., population transitions depend only on the current population state and harvest decision), we can evaluate an optimal state-dependent harvest management policy using stochastic dynamic programming (Bellman, 1957; Walters, 1978; Marescot et al., 2013). We defined the six essential elements to solve our Markov-decision problem (Marescot et al., 2013) by first specifying our objective to follow the RMP management plan (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007) to maintain a population within 17,000 and 21,000 in perpetuity. Second, we defined a vector of possible states of the population from 10,000 to 40,000 at an interval of 500 (length NS). Third, we defined a vector of possible actions as harvest from 0 to 4000 at an interval of 100 (length NH). Fourth, for each population model, we characterized the probability of transitioning from the current state (N_t) to a population state in year $t+1$ (N_{t+1}) based on the previous year's state and action ($P(N_{t+1}|N_t, H_t)$). As such, for each population model, we defined an array with dimensions of $NS \times NS \times NA$.

For population models that are stage-structured, we assume the current stage structure is known (see *Simulation*), but do not find stage-specific optimal decisions because stage-specific control on harvest is not logically feasible with sandhill cranes. In the best of circumstances, individuals can only be aged in the field as less than or greater than one year old (Drewien et al., 1995). However, there are fundamental differences of optimal harvest strategies for specific stages versus an optimal harvest for the whole population (Hauser et al., 2006). Non-optimal stage-specific harvest can cause population momentum that may jeopardize meeting one's defined management objectives (Hauser et al., 2006).

To incorporate uncertainty about the relative belief in each model and its ability to predict crane population dynamics, we weight each model's probability transition array based on each model's weight or relative belief (see *Simulation*). Fifth, we define the utility function for each year t (also called a reward function) that represents the desirability of a given action for each possible state over time,

$$U(N_t, H_t)_t = \begin{cases} 1 & , 17,000 \leq N_t \leq 21,000 \\ 0 & , \text{otherwise} \end{cases}$$

Notice that we only give utility to the state of the population and not to the action, harvest. An alternative utility function that captures the desirability of crane harvest may also only provide utility within the population objective, but also increasing utility with increasing harvest. The sixth element is finding the optimal solution or the optimal policy, which provides us with a harvest decision, depending on our current state, that maximizes our chance of achieving our objective. We do so by solving the problem,

$$V(N_t) \quad = \max_{H(N)} \textstyle\sum_{\tau=0}^{\infty} \beta^{\tau-t} U(N_\tau, H(N_\tau))$$

where $V(N_t)$ is the state-dependent value, and β is the discount rate, which characterizes the value of the utility gained in the next time period relative to the utility obtained in the current time period. Because we are interested in sustaining the population, we see no value in changing the importance of meeting our objective today versus anytime in the future and thus set no discount ($\beta = 1$). We solve this problem using the policy iteration algorithm as implemented in the R package 'MDPtoolbox' (Chadés et al., 2013).

5.3.3.2. *Learning.* Once we have an optimal policy, a harvest decision is implemented based on the current population state (N_t), which may or may not be observed with error (see *Simulation*). In order to update the support for each model, we observe the population state (N_{t+1}) after implementing the harvest decision, which again may be observed with error. We then update the relative weight of evidence (i.e., model weight) for each model i in the subsequent year $t+1$ based on the new observation of the population (N_{t+1}) using Bayes theorem,

$$P(Model_{i,t+1}|N_{t+1}) \quad = \quad \frac{P(N_{t+1}|Model_i) \times P(Model_{i,t})}{\sum_{j=1}^{n} P(Model_{j,t}) \times P(N_{t+1}|Model_{j,t})}.$$

The $P(Model_{i,t})$ is the model weight of $Model_{i,t}$ in the previous year (also know as the prior) and $P(N_{t+1}|Model_i)$ is the probability density of the monitoring data under a given model (also known as the likelihood). For each model, we approximate the $P(N_{t+1}|Model_{i,t})$ using the normal probability density function, which allows us to use any model type without having to derive the likelihood (joint probability density) of each model; approximations are believed to be accurate because model empirical distributions are highly symmetric and unimodal. Our approach to learning can be considered passive (Williams, 2011), such that the focus is on meeting our management objective, while learning still occurs but as a by-product of the iterative decision process. This is in contrast to an active approach to ARM, which explicitly pursues the reduction of structural uncertainty through management actions to explore the system behavior and discriminate among hypotheses (Williams, 1996).

Updating model weights using Bayes theorem is a logical and powerful approach. However, there are may be unintended consequences that should be noted. First, if the probability $P(N_{t+1}|Model_{i,t})$ is approximated (e.g., rounding or discretization of an empirical distribution) at zero, the updated weight for model i will be zero, ensuring its effective removal from the model set. If all models of a set poorly predict in a given year and the probability density of each model for the new observation is approximated at zero, no model weight update can be performed as the numerator and denominator of Bayes theorem will be zero. By characterizing the probability of an observation using the normal probability density function, zeros will not occur unless the predicted variance is zero. Another implication is that the $P(N_{t+1}|Model_i)$ accounts for both the accuracy and precision of a model's prediction, which may lead to giving models that are highly imprecise and inaccurate increasing weight, compared to other models that are more accurate, but also more precise (Figure 5.4). Throughout, we refer to model updating using this process as 'Prob'. We consider two alternative, ad hoc, model weighting strategies that ameliorate this issue by evaluating the discrepancy between a model's expected prediction and an observation.

The first strategy is to exploit Bayes formula and replace the $P(N_{t+1}|Model_{i,t})$ with the probability density of the Laplace distribution using the new observed data N_{t+1} and the expected prediction from $Model_i$ (Laplace); the scale parameter is estimated using a minimax estimator under the quadratic loss function (Al-Noor and Rasheed, 2008). As such, this only evaluates the accuracy of a model's prediction and ignores the uncertainty, so that the more accurate a prediction, the more weight of evidence goes to that model (Figure 5.4). The second strategy is to update model weights based on the mean-squared error (MSE) of the expected model predictions (U.S. Fish and Wildlife Service, 2014a), where for a given $Model_{i,T}$ in current year T,

$$MSE_{Model_{i,T}} = \tfrac{1}{T}\textstyle\sum_{t=1}^{T}\left(N_{t+1} - E[N_{t+1}|N_t, H_t, Model_i]\right)^2$$

and the weight for each model is,

$$W_{Model_{i,T}} = \tfrac{(MSE_{Model_{i,T}})^{-1}}{\sum_{\forall i}(MSE_{Model_{i,T}})^{-1}}$$

Under this approach (1/MSE), squared error in each year is carried through the weighting across years and weighted equally. This approach penalizes poor predictions more harshly than the Laplace probability density approach (Figure 5.4). The fundamental difference between using the Laplace density and the MSE can be best understood as the differences between an L_1-norm and L_2-norm penalty function, respectively. Under all model weight updating strategies (Prob, Laplace, 1/MSE), initial model weights in year $t = 1$ were made equal among all models within each set per scenario.

5.3.4. THE 'TRUE' (GENERATING) CRANE POPULATION MODEL. We evaluate management scenarios using simulation. We define the 'true' sandhill crane population dynamics to follow a complex stochastic stage-structured, density-dependent population model. The motivation of this model is a hybrid of empirical estimates of stage-specific vital rates, natural history interpretations of cranes, and common regulating factors in populations expressed by phenomenological functions. Currently, available data does not support a fully empirically parameterization of the model. Most importantly, we try to capture the potential dynamics of a long-lived, slowly reproducing species in a changing environment. Specifically, the generating model is defined by eight stages with stage-specific mean and process variances that are density-dependent. Harvest mortality ($f(H_{k,t})$ for stage k and year t) is compensated up to natural mortality. We considered density-dependent processes to negatively affect vital rates due to changing environmental conditions, characterized as the annual carrying capacity (K_t). As the population approaches K_t, vital rates are affected negatively in the following order, 1) juvenile survival, 2) proportion of breeders, 3) reproductive rate, and 4) adult survival, (Eberhardt, 2002). Only individuals of stages 6-8 attempt breeding and most production comes from individuals of stage 8.

We first describe phenomenological functions that are used to derive carrying capacity, stage-dependent survival parameters, the annual proportion of breeders, and per capita fecundity of pairs that do breed. Parameters and some mathematical functions (e.g., *log*) are noted in italic, while phenomenological functions and statistical distributions are not. We consider crane habitat conditions to vary annually, affecting the year-specific carrying capacity of the population (Figure 5.6), as

$$\text{Kfunc}(A, B, C, D, t) = \{A * sin(B \times (t - C)) + D\}$$

$$log(K_t) \sim \text{Normal}(log(\text{Kfunc}(5000, 0.1, 1500, 25000, t)), 0.05)$$

We defined phenomenological density-dependent functions for the proportion of breeding individuals and per capita fecundity, where $PrBreed_{init} = 0.25$ and $Fecundity_{init} = 1.24$, as (Figure 5.6)

$$\text{PropBreeding}(PrBreed_{init}, N_t, K_t) = \begin{cases} PrBreed_{init} & , N_t/K_t < 4/5 \\ PrBreed_{init} + 0.12 - 0.2 \times N_t/K_t & , \text{otherwise} \end{cases}$$

$$\text{Fecundity}(Fecundity_{init}, N_t, K_t) = \begin{cases} Fecundity_{init} & , N_t/K_t < 1 \\ Fecundity_{init} + 0.7 - 0.7 \times N_t/K_t & , \text{otherwise} \end{cases}$$

We defined juvenile (1st year) survival (S_1), as

$$\text{JuvSDD}(S_{1-init}, N_t, K_t) = \begin{cases} S_{1-init} & , N_t/K_t < 3/4 \\ S_{1-init} - (0.7 \times N_t/K_t)^3 & , \text{otherwise} \end{cases}$$

$$
\begin{aligned}
\mu_{S_1} &= \text{JuvSDD}(S_{1-init} = 0.73, N_t, K_t).\\
\sigma_{S_1} &= 0.07\\
\alpha_{S_1} &= -1 \times (\mu_{S_1} \times (\sigma^2_{S_1} + \mu^2_{S_1} - \mu_{S_1}))/\sigma^2_{S_1}\\
\beta_{S_1} &= ((\sigma^2_{S_1} + \mu^2_{S_1} - \mu_{S_1}) \times (\mu_{S_1} - 1))/\sigma^2_{S_1}.\\
S_1 &\sim \text{Beta}(\alpha_{S_1}, \beta_{S_1})
\end{aligned}
$$

Adult survival (S_{2-8}) is defined similarly, where S_{k-init} for $k = 2$ to 8 is 0.80, 0.90, 0.93, 0.94, 0.95, 0.96, 0.97, while the process variances are 0.06, 0.05, 0.04, 0.03, 0.02, 0.01, 0.01, and an alternative function for density-dependency is used,

$$
\text{AdultSDD}(S_{2-8-init}, N_t, K_t) = \begin{cases} S_{k-init} & , N_t/K_t < 1.5 \\ S_{k-init} - S_{k-init} + 0.3 - (0.1 \times N_t/K_t)^{1/2} & , \text{otherwise} \end{cases}
$$

The generating population model is defined following the population size of each stage k in year t ($N_{k,t}$), the proportion of breeders ($z_{k,t}$), and survival (S_k). The model is defined using the explicit functions, PropBreeding and Fecundity (see above), while the the density-dependent survival functions (JuvSDD, AdultSDD) are implicitly assumed for each survival parameter.

$$z_{8,t+1} \sim \text{Binom}\left(N_{8,t+1}, \text{PropBreeding}(PrBreed_{init}, N_t, K_t)\right)$$

$$z_{7,t+1} \sim \text{Binom}\left(N_{7,t+1}, \text{PropBreeding}(PrBreed_{init}/2, N_t, K_t)\right)$$

$$z_{6,t+1} \sim \text{Binom}\left(N_{6,t+1}, \text{PropBreeding}(PrBreed_{init}/3, N_t, K_t)\right)$$

$$z_{5,t+1} \sim \text{Binom}\left(N_{5,t+1}, \text{PropBreeding}(PrBreed_{init}/5, N_t, K_t)\right)$$

$$N_{1,t+1} \sim \text{Poisson}\left(\sum_{i=6}^{8} \frac{\text{Fecundity}(Fecundity_{init}, N_t, K_t)}{2} \times z_{i,t+1}\right)$$

$$N_{2,t+1} \sim \text{Binom}\left(N_{1,t}, S_1\right) - \text{f}(H_{1,t})$$

$$N_{3,t+1} \sim \text{Binom}\left(N_{2,t}, S_2\right) - \text{f}(H_{2,t})$$

$$N_{4,t+1} \sim \text{Binom}\left(N_{3,t}, S_3\right) - \text{f}(H_{3,t})$$

$$N_{5,t+1} \sim \text{Binom}\left(N_{4,t}, S_4\right) - \text{f}(H_{4,t})$$

$$N_{6,t+1} \sim \text{Binom}\left(N_{5,t}, S_5\right) - \text{f}(H_{5,t})$$

$$N_{7,t+1} \sim \text{Binom}\left(N_{6,t}, S_6\right) - \text{f}(H_{6,t})$$

$$N_{8,t+1} \sim \text{Binom}\left(N_{7,t}, S_7\right) + \text{Binom}\left(N_{8,t}, S_8\right) - \text{f}(H_{7,t}) - \text{f}(H_{8,t})$$

$$N_{t+1} = \sum_{\forall k} N_{k,t+1}$$

The harvest function ($f(H_{i,t})$) is defined generally and indicates either additive mortality or mortality that is beyond what is allowed by compensation.

5.3.5. ALTERNATIVE POPULATION MODELS. In our simulation, we considered a maximum of seven models for each ARM scenario. Any type of model that can predict the future population state, given the current state (N_t) and harvest decision (H_t), can be considered;

this includes mechanistic or descriptive/phenomenological models, simple or complex models that range in degree of integrated parameters (Nichols et al., 2001), or purely predictive models that include no representation of processes (e.g., time-series models). Here, we focus on the importance of developing a model set that on average can provide useful predictive models to make harvest decisions, thus considering all types of models. By doing so, the process of learning is not strictly focused on discriminating among hypotheses of ecological processes, but on identifying useful predictive models.

5.3.5.1. *Model 1.* We defined Model 1 as an autoregressive time-series model (AR1); it incorporates a 1^{st} order Markovian process, where the population in year t (N_t) depends on the autocorrelation parameter ρ, the previous year's population (N_{t-1}; may be observed with error, depending on the scenario), and noise (ϵ), which has a mean of zero and variance of σ^2,

$$\begin{aligned} N_t &= \rho \times N_{t-1} + \epsilon_t \\ \epsilon_t &\sim \text{Normal}(0, \sigma^2) \end{aligned}$$

In the simulation, we fit the current data (N_{1-T}) and project a single time step using the R package 'FitAR' (McLeod and Zhang, 2008). We considered harvest to be additive to natural mortality.

5.3.5.2. *Model 2.* We defined Model 2 as a discrete logistic growth model,

$$N_{t+1} \quad = \quad N_t + r \times N_t \left(1 - \frac{N_t}{K_t}\right)$$

We assume that carrying capacity is not annually estimated but is assumed to be fixed at 30,000. The intrinsic growth rate (r) is defined based on juvenile recruitment (P_t), which is observed annually without error and differential survival of juveniles and adults. Survival is stochastic and based on estimates from a 23-year mark-resight study (Kendall, W.L., Drewien, R.C., and Gerber, B.D., unpublished data; see *Appendix*).

5.3.5.3. *Models 3 and 4.* Model 3 is a density-independent 5-stage stochastic population model, where harvest mortality is additive, while Model 4 is the same population model but harvest is compensated up to natural mortality. Survival is stochastic with means for stages 1, 2, and 3-5 as 0.85, 0.94, and 0.96, respectively. In both models, only individuals of stage 5 breed and only a proportion of them annually produce young (ee *Appendix*).

5.3.5.4. *Model 5.* Model 5 is the generating model, but harvest is assumed to be additive to mortality, rather than compensated up to natural mortality.

5.3.5.5. *Model 6.* Model 6 is a moving three-year average (MTYA) estimator, $N_{t+1} = \frac{N_{T-2}+N_{T-1}+N_T}{3}$, where T is the most current year. This estimator is often used to smooth counts in population monitoring of harvested species, including several species of geese (U.S. Fish and Wildlife Service, 2014b), tundra swans (*Cygnus columbianus*; (Pacific Flyway Council, 2001)), and sandhill cranes (Kruse and Dubovsky, 2015).

5.3.6. SIMULATION.

5.3.6.1. *Simulation scenarios.* We consider nine scenarios, which vary by model set, whether the monitoring process observes the true population perfectly or imperfectly, whether the population structure is known or assumed, and decision framework (RMP decision strategy or ARM; Table 5.1). For scenarios in which the population stage-structure is assumed, we use the same stage-structure, which was accurate ten years prior to the start of harvest decisions. Since, it is costly and often logistically infeasible to characterize the population structure of many long-lived species, we imagine the situation where a study characterized stage-structure only once, and represents the best available data. We also use this stage-structure to distribute total harvest among the stages, thus assuming harvest is in proportion to the assumed availability of each stage. Actual harvest does affect the population in proportion to the availability of the stage, but following the true stage structure. For scenarios where the population is observed imperfectly, in any given year, the population may be over- or under-counted,

$$Count_t \sim exp(\text{Normal}(log(N_t), 0.07))$$

For each scenario, we initialize the population at 20,000 cranes with a stage structure biased towards older individuals [0.08 0.06 0.05 0.04 0.04 0.04 0.03 0.66]. We then simulate a single realization of the population for 20 years using the Generating Model, as well as a single realization of observations of the population. These data are fixed for all scenarios and considers the present situation where we have some data available and are interested in either implementing an ARM process or the current RMP decision process. Next, we simulate an ARM process (Figure 5.3) or the current RMP crane decision strategy. For both, we project the population and decision process for eighty years (t = 20 to 100) for 1000 iterations. The current RMP crane decision strategy is implemented using the harvest allocation function (g) directly on the Generating Model, where we annually observe either $Count_t$ or N_t and the proportion of juveniles in the population (P_t), which is observed without error. For all scenarios, the annual allocated harvest is equal to the harvest on the population (see *Discussion* for comments on partial controllability).

5.3.7. THE VALUE OF INFORMATION.

We compare scenarios by evaluating how different uncertainties affect outcomes of managing, such as the probability of meeting our management objective and harvesting sandhill cranes. We do so by calculating the EVPI, which is the expected improvement in management performance if all uncertainty about the system being managed was resolved. We do so by calculating the difference between the expected probability of meeting our objective or expected annual harvest over the time frame management decisions were made (years $t = 20$ to 100) when there is no uncertainty and when there is one or more uncertainties (Yokota and Thompson, 2004; Maxwell et al., 2015). We also investigate the EVPXI, which is the difference between the expected probability of meeting our objective or expected annual harvest, where one scenario has resolved one or more uncertainties, but not all (Yokota and Thompson, 2004; Maxwell et al., 2015). For our scenarios, we consider management using the RMP decision framework as an uncertainty, as it not based on population theory or decision theory, thus we calculate EVPI and EVPXI where there is change from using the RMP decision framework to an ARM framework.

5.4. Results

5.4.1. Managing under an ARM framework. We found ARM scenarios (scenarios 1-6) varied in their expected annual probability of maintaining the RMP crane population between 17,000 and 21,000 by whether the population was observed with error (scenarios 1,4-5) or was observed perfectly (scenarios 2-3, and 6; Table 5.2, Figures 5.7, 5.8, 5.9, 5.10). The overall expected probabilities of maintaining the population objective over the duration of harvest when the population was observed with error ranged from 0.74 to 0.90, while the minimum values ranged from 0.43-0.64 (Table 5.2). The minimum and expected annual probability of meeting the objective was generally lowest under scenario 5. The variability in population observations combined with potentially non-optimal harvest decisions due to the unknown current state and population dynamics led to more variable population trajectories than compared to scenarios that observed population size without error (Figures 5.7, 5.8, 5.9, 5.10). Scenarios where the population was observed with error led to differences in the extent of populations going under- or over the objective, depending on the model weighting strategy and model set. The overall expected annual harvest over the duration of harvest decision varied, but not largely (range, 629-731).

In all scenarios where the population was monitored without error (scenarios 2-3, and 6), we found the minimum expected annual probability of maintaining the population objective was 0.98, regardless of model weighting strategy (Table 5.2). Besides, scenario 6 when updating model weights with Laplace or Prob, all other scenarios and updating model strategies did not consistently rely on the Generating Model for predictions, but still consistently met the population objectives (see *Learning*). The overall expected annual harvest over the entire duration of harvest decisions varied among scenarios and updating strategies (range, 651-820; Table 5.2). When there was no monitoring or structural uncertainty (scenario 7), such that the only model considered was the Generating Model (Figures 5.7), the probability of meeting the objective was always 1.00. We found annual predictions for scenario 7 to be highly accurate, despite not having stage-specific optimal harvest decisions (Figure 5.11). Scenario seven's expected annual harvest was found to vary from a low of 391 and a high of 1363, corresponding to the changes in the environmental limitations and thus the effects of density-dependence on vital rates.

5.4.1.1. *Learning.* We found significant differences in the evolution of model weights among the three model updating strategies (Prob, Laplace, 1/MSE; Figures 5.12, 5.13, 5.14). Using the Prob strategy, Model 1 quickly gained all model weight when was present in the model set and the population was observed with error (scenarios 1 and 4; Figure 5.12). This led to adequate performance overall in meeting the population objective (Table 5.2), but did not consistently maintain the population objective, largely due to Model 1's inability to respond quickly when the carrying capacity increased; as such, the population could move beyond the upper population objective because harvest was not adequately increased during this time period (Figure 5.12). Otherwise, when Model 1 was not in the set, Model 2 slowly accumulated most of the weight and performed similarly overall. When the population was observed without error and the Generating Model and Model 5 were not in the set, Model 3 accumulated most weight in most years, except for a five year period where Model 1 dominated (Figure 5.12); regardless of not having a model that captured the true population dynamics, the probability of meeting the population objective was almost always 1.00. In the scenarios where the Generating Model and Model 5 were present in the set, the Generating Model quickly accumulated almost all model weight, but while this was maintained throughout when the population structure was known annually (scenario 6), its weight quickly declined with carrying capacity when the population structure was assumed (scenario 3); regardless, the population objective was almost always met in either scenario 5 or 6.

Using the Laplace model weight updating strategy, there was no model that accumulated all weight when the population was observed with error (Figure 5.13). When the Generating Model and Model 5 were included in the set, Model 5 slowly accumulated the majority of weight (scenario 1), which led to a high overall expected probability of meeting the population objective (0.90). When the Generating Model and Model 5 were not included, Model 6 held the majority of weight throughout the years, which still led to a high overall expected probability of meeting the population objective ($\geq$0.86). Even when the population was observed perfectly but the Generating Model and Model 5 were not included in the set, Model 6 accumulated a large proportion of model weight temporarily when the carrying capacity was stable, but declined when it increased and decreased, where Model 3 eventually accumulated almost all the weight (Figure 5.13). However, this scenario (scenario 2) still led to almost always meeting the population objective (minimum annual expected probability of 0.97). In the scenarios that both had perfect observations of the population and included the Generating Model and Model 5 in the set (scenarios 3 and 6), the Generating Model accumulated a large amount of model weight (Figure 5.13). However, in scenario 3, the Generating Model's weight began to decline and shift to Model 5 when the carrying capacity was increasing, likely due to the assumption of the stage structure. Regardless, both scenario 3 and 6 using the Laplace strategy led to almost a guarantee of meeting the population objective (Table 5.2).

The 1/MSE strategy resulted in quickly changing model weights in the first few years but then was slow to change (Figure 5.14). When the population was observed with error (scenarios 1, 4-5), model weights did not vary much from their initial equal weights. However, these scenarios still lead to relatively high overall expected probabilities of meeting the population objective and making this strategy comparable to the other model updating strategies (Table 5.2). When the population was observed without error but the model set included neither the Generating Model nor Model 5 (scenario 2), Model 3 had the most weight across years, but did not exceed 0.5 probability in any year. In contrast, when the Generating Model and Model 5 were in the model set (scenarios 3 and 6), the Generating Model initially accumulated the most weight, but presumably due to the incorrect stage structure assumption it's model weight declined in scenario 3, but not so for scenario 6.

5.4.2. Managing under the RMP decision framework. We found that making harvest decisions based on the RMP framework (scenarios 8 and 9) led to the lowest annual overall expected probability of meeting the management objective and the highest overall expected annual harvest (Table 5.2). In addition, both scenarios 8 and 9 led to the lowest overall minimum expected annual probability of meeting the population objective (<0.05). The overall expected probability of meeting the population objective was slightly better when the population was observed perfectly (Table 5.2). When the carrying capacity was either stable or decreasing, the RMP decision framework called for harvest at a level that caused the population to be maintained near the lower boundary of the population objective (Figures 5.15, 5.16). We found that when the population was observed with error, this lead to observed counts that were below the allowable harvest level (15,000) and thus harvest was closed in rare circumstances (Figure 5.16). In years the carrying capacity was increasing, the RMP decision framework appropriately allocates harvest to maintain the population within the bounds of the objective, regardless of whether the population is observed with error.

5.4.3. EVPI AND EXPXI. The largest EVPI for meeting the population objective is when resolving all uncertainties associated with managing under the RMP decision framework while observing the population with error (scenario 8; Table 5.3). This includes changing to an optimal decision process where the population size and structure is observed perfectly and there is no model uncertainty. While the EVPI of meeting the objective is 0.28 and thus a guarantee of always meeting the objective, there is a loss of annual allowable harvest by 171 cranes. Within the ARM scenarios, we found the largest improvement (i.e., EVPI) when resolving all uncertainties in scenario 5 and using the model weighting strategy Prob. There is almost no improvement in meeting the population objective when the only monitoring uncertainties that require resolution are stage structure and structural uncertainty (i.e., choosing the best model). The expected benefit of resolving monitoring uncertainties in meeting the population objective but not changing to an ARM framework is moderate

(EVPXI = 0.05). In contrast, within an ARM process, we found that by improving monitoring such that the population is observed perfectly, there is a relatively large increase in the probability of meeting the population objective (0.10-0.15, Table 5.3).

Changing from the RMP to an ARM decision process always increases the probability of meeting the population objective, regardless of resolving any additional uncertainties (Table 5.3). The lowest EVPXI when only changing the decision process from the RMP to ARM is when there is still monitoring and model uncertainty and the model set does not include models 2-4 and 6 (EVPXI = 0.07, 0.14 and 0.03 for 1/MSE, Laplace, and Prob, respectively). In all cases of shifting from the RMP decision process to an ARM process, there is a decrease in annual expected harvest (Table 5.3).

5.5. Discussion

Decision making in natural resource management can be complicated. Natural system processes and dynamics are often highly complex, varying across both spatial and temporal scales and individual-level variability. Species population dynamics is relatively simple in its most fundamental form (N_{t+1} = N_t + Births - Deaths + Immigrants - Emigrants). However, processes that govern additions and losses from a population can be driven by spatial and age population structuring, which interacts jointly with environmental variation that can cause highly temporal dynamics (Mills, 2012). For harvest management scenarios, harvest mortality can also be spatially and age-specific, as well as be completely, partially, or not at all compensated by a decrease in natural mortality. Characterizing these complex mechanisms is challenging. It is even more challenging when life-history characteristics (e.g., migration) make empirical studies and monitoring programs practically infeasible due to necessary logistics and finances, thus inhibiting a clear understanding of how vital rates vary according to life-history characteristics, including the effects of harvest management decisions. Despite such complexity, abstract representations or models of system behavior are routinely used and often useful in natural resources research and management (Williams et al., 2002). In accordance with the philosophical stance that "all models are wrong, but some are useful" (Box, 1976), we found that even relatively simplistic crane population models (that are "wrong", in that they are simply poor characterizations of the true governing processes) within an ARM can be useful in meeting the stated population objective over a diverse set of environmental conditions and population trajectories.

5.5.1. CRANE MANAGEMENT. We found several important and perhaps surprising findings in regard to adopting an ARM framework for making recurrent population management decisions. First, even with a model set of relatively simple predictive population models and considerable uncertainty about population status (including the total population size and stage structure), an ARM process that evaluates optimal state-dependent harvest decisions can increase expected annual probability of meeting a population objective compared to a reactive decision framework (e.g., RMP decision process; scenario 4 and 5). For sandhill crane management, there is a higher risk to not meeting the RMP population objective by managing under the current framework, compared to an ARM framework. By explicitly recognizing the uncertainty about how the population will change from one year to the next, there is an inherent conservatism in harvest decisions compared to a reactive decision process.

The primary concern of using the RMP harvest framework occurs when the population without harvest is stable or declining. In either of these scenarios, the population is harvested to a degree that causes the population to be pushed to and sometimes beyond the lower bound of the population objective (17,000), regardless of whether the population is monitored without error. This occurs even with compensation up to natural mortality and the incorporation of a measure of annual juvenile productivity (i.e., juvenile recruitment data, P_t). We might expect the population to decline even more sharply and to a greater extent outside of the population objective if harvest mortality was less compensatory or was strictly additive to natural mortality. For scenarios with monitoring uncertainty, whether an ARM scenario allowed the population to be mainly below or above the population objective depended on the model set and the model updating strategy. The advantages of the ARM process are even more clear if the monitoring process could remove a significant amount of variation, such that population size was accurately estimated. Within the RMP decision framework, the three-year moving average population index effectively reduces the sensitivity of the harvest decisions to fluctuations in the observed population, but is still a reactive decision process that does not anticipate decision thresholds and thus can not reduce harvest to ensure the population is far from low utility population states.

We found that the RMP decision framework performed well when the carrying capacity increased, thus dampening negative density-dependent processes, which caused increases in survival and juvenile productivity and led to population increases beyond the population objective when unharvested. Both with perfect and imperfect monitoring of population size, the RMP decision framework kept the population from exceeding the upper population objective. This was not the case for ARM scenarios when the population was observed with error. However, the simulated RMP decision process relied on accurate knowledge of juvenile recruitment (P_t). If P_t was biased low, it would decrease harvest and thus allow the population to exceed the upper population objective, depending on the level of bias, while the reverse is true if P_t was biased high (Gerber, B., unpublished data).

As with many harvested animal populations, management decisions of how many individuals to harvest or how the type of regulations (e.g., daily bag limit, season length) translates into the number of individuals that are harvested is not exact nor even straightforward (Nichols et al., 1995). As such, managers only have partial controllability over their decisions (Williams, 2011). While we did not investigate the effects of partial controllability in our simulation, it should be noted that the RMP annual harvest is often lower than the total allowable annual harvest. By evaluating the rate at which individuals are harvested, given the allocated harvest, there are some important differences across breeding and wintering states (see *Appendix*). Most states in most years harvest less than their allocation; Wyoming is the only state to have harvest exceed their allocation in more than 2 years. But overall, the total allocation is not annually fulfilled, suggesting that even under the current RMP crane decision framework, the effect of harvest on the population is lessened, thus potentially increasing the probability of meeting the population objective in years the population is stable without harvest. Conversely, this may also lead to some probability that the population exceeds the population objective in some years. In contrast to the current RMP decisions framework, by using population models, it is straightforward to incorporate this additional type of uncertainty, such that a high probability of meeting the population objective can still be maintained, while issuing additional allocation to the states. This could increase revenue for state-wildlife research/management.

The annual allocation of sandhill crane harvest for the RMP follows according to the harvest function (g), which pertains to the whole population. However, this harvest is then unequally divided among all states the RMP ranges, except Colorado, which has continually declined their harvest allocation. State allocation is based on the relative abundance by seasonal range (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). While we did not explicitly examine the effects of state-level harvesting, it should be recognized that shifting distributions of relative abundances and variability in partial controllability across states may add considerable variability to the impact harvest has on the whole population. Relative abundances are currently estimated using the fall three-year moving average population index. Whether variability in detectability/availability among states masks changes in these relative abundances is unknown, but is highly possible. An important future question that needs to be explored is how distributional shifts of cranes among the RMP states affects harvest allocation and effects of harvest on the whole population. However, to do so, detailed information on spatial variation in abundance and especially production is necessary, both of which are unknown.

For all scenarios we investigated, we implemented an explicit and simplistic objective of maintaining the RMP population within a given range (17,000 to 21,000). We did so for two reasons: it is outlined in the management plan for the RMP (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007); and it is currently the sole measure of success for each year (Kruse and Dubovsky, 2015). However, the RMP management plan also includes objectives to, 1) maintain and protect suitable habitat to support the population objective, 2) provide for consumptive and non-consumptive recreational uses of RMP cranes, and 3) minimize crop depredations by RMP cranes (The Subcommittee on Rocky Mountain Greater Sandhill Cranes, 2007). It is generally believed that if the population objective is met, than so are the objectives for recreation and crop damage. Whether this is true has yet to be assessed.

A future avenue that crane managers may find useful to explore, is the integration of all four objectives more explicitly within the decision making process. This may entail monitoring hunter and birder satisfaction, as well as the number of crop damage complaints and requests of depredation permits from the U.S. Department of Agricultural-Animal Plant Health Inspection Service-Wildlife Services and state agencies. To incorporate the objective to maintain suitable habitat, an evaluation of available and protected habitat could be derived from the Intermountain West Joint Ventures work, which is quantifying the magnitude and distribution of available sandhill crane habitat (Donnelly and Vest, 2006). Lastly, it is by the means of using a logical and transparent approach to management, such as ARM, which we can explicitly and logically represent each objective, so as to make annual decisions that will be satisfactory to both managers and stakeholders. However, it may be that meeting the population objective truly satisfies the other RMP objectives. In that case, simplicity has significant benefits. Regardless, there may still be considerable benefits to add transparency and additional logic to the RMP decision process (and other migratory bird management processes) by following a structured decision process (Conroy and Peterson, 2013). This process can help clarify the thought process behind the RMP objectives, thus refining these objectives in terms of fundamental and means objectives, as well as open a dialogue about alternative approaches to management, including the decision process.

5.5.2. ADAPTIVE MANAGEMENT. Learning is an important component of ARM (Williams, 2011). Through the process of iterative decision making and comparing observed and predicted values, there is a natural process for identifying useful predictive models. Whether an ARM process emphasizes learning or the management objectives in a given year can be achieved via active ARM, which explicitly incorporates the evolution of model weights into the optimal decision process (i.e., dynamic programming; Williams 1996). Using active ARM, it may be beneficial in certain years to explore differences among models at the potential cost of meeting the management objective. When highly different models produce similar predictions over the range of currently observed conditions, discriminating among the model set may require probing the system in such a way that decisions are outside the range of what is normally done and may cause a population, at least temporally, to be outside the range of acceptable states (i.e., population objective). This type of management intervention may be controversial and thus unpalatable to many managers and stakeholders. As such, for sandhill crane ARM, we chose to follow a passive process where we learn about the system over time, but only as a by-product of the iterative decision process, thus emphasizing the importance of meeting the management objectives in all years over learning through model discrimination.

The process of how one chooses to measure the discrepancy between model predictions and observed values has a significant influence on how model weights sequentially evolve. We found models weights to be radically different among Prob, Laplace, and 1/MSE across all scenarios except for scenario 6 between Prob and Laplace. Using the conventional approach to model updating in ARM via Prob led to all model weight accumulating with the predictive model with the largest variance when the population size was observed with error. In contrast, model weights using Laplace were more evenly distributed among the model set because Laplace only evaluates the accuracy of predictions and the model predicted variances were more variable than the models' expected predictions. Future research is needed to better understand specific aspects of how the model updating affects the decision process when models prediction variances are highly different. More specifically, is it desirable using Prob to highly penalize models that are highly accurate and precise but do not include the observed value within the majority of their probability density (Figure 5.4).

In most ARM programs, the model set is composed of a small set of hypothesized process-driven models (Johnson et al., 1997; Nichols et al., 2015). Therefore, learning within the ARM process is specifically focused on better understanding the fundamental components of the ecological process, which should ideally provide robust predictions of the system, even when observations range outside of typical conditions. We chose a slightly different approach in selecting our model set; we included population models that were motivated by underlying dynamics of sandhill cranes, as well as purely functional models, such as the autoregressive time-series model (Model 1) and the moving three year estimator (Model 6). As such, the process of learning in our ARM framework needs to be interpreted differently.

Our model sets recognize that in some or all years, relatively simple crane population models may poorly represent the true dynamics, either because of monitoring uncertainties or because the dynamics that are governing population change are poorly captured (e.g., Model 3 is density-independent, while Generating Model is density-dependent). In some years, when the population size is far from the carrying capacity, Model 3 may produce reasonable population predictions, but as the population size approaches and exceeds carrying capacity, it will be unlikely to provide reasonable predictions. In these years, the time-series model may provide better predictions. Therefore, our ‘learning’ through iterative model weighting is not purposively aimed at increasing our understanding of system dynamics and discriminating among hypotheses about the true dynamics, but is aimed at identifying the most useful predictive model(s) in the set for a given set of circumstances. Our goal for learning is to simply provide the best predictions to make harvest decisions that will meet our management objectives. Ideally, we would most benefit if we could identify a model that captures the fundamental aspects of the true system processes, but we acknowledge that due to either structural uncertainty or partial observability, simple process-driven models that we are able to parameterize (due to limited data) may predict poorly in some or all years, such that purely functional models may be especially useful. A potential risk of using a variety of model types in a model set is that all models may do poorly when faced with highly different observations than what is typical. This is when process-driven models are especially useful.

In our simulation, we found that the only scenario where the Generating Model accumulated all the model weight was when when the population size and stage structure were annually observed without error. It is satisfying to know that if we were to characterize the true population process of a species as a possible hypothesis and observe the necessary components that we could quickly identify it as the best ecological model through model weight updating (≥ 0.9 model weight in less than ten years for Prob and Laplace). However, more importantly, we do not need to either have perfectly observed data nor hypothesize the true population process to make harvest decisions to meet our management objective. Despite the wide array of conditions (e.g., produced by changing carrying capacity and effects of density-dependence) that can not be captured by most models, highly different model sets without the Generating Model or Model 5 and even some single models performed well enough with or without perfect observations of the true population size to lead to high annual probabilities of meeting our management objective. As such, highly degenerate models (compared to the true population process) can be useful in a wide array of conditions.

One of the more surprising findings in our simulation was that we were able to meet our population objective with a probability of 1.0 using the Generating Model and optimal population-level harvest decisions, rather than optimal stage-specific harvest decisions (Hauser et al., 2006). Even without the Generating Model, population-level optimal decisions did not necessarily cause the population objective to be compromised. In fact, even when the current stage structure was unknown, assumed, and certainly not correct, we were able to meet our population objective when we simply observed the population size without error. Several factors likely contributed to this findings. The primary reason may be because the stage structure did not vary considerably, even when harvested. The difference between the initial unharvested stage structure and all simulated stage structures of the true population across all scenario, as measured by Keyfitz's Delta (Keyfitz 1968; measure of discrepancy between two vectors, where a value of 0 indicates no difference between vectors) was always less than 0.10. This was at least partly because the initial stage structure was skewed towards most individuals being in the terminal class and because harvest was in proportion to the availability of individuals in each stage.

To better understand how the stage structure influences meeting our population objective using optimal population-level harvest decisions, rather than stage-specific optimal harvest decisions, we explored a variety of stage structures in a simulation using Model 3. An optimal harvest strategy was found using this model and a fixed stage structure. We then simulated a single time step from the population model using the optimal state-dependent harvest decision but assuming one of a complete set of permutations of each stage at increments of 0.05. For each simulation, we measured the probability of meeting the RMP objective in the subsequent year and Keyfitz's Delta. We found that as Keyfitz's Delta increased, the average probability of meeting the population objective decreased. The probability of meeting the RMP objective was always ≥ 0.99 when Keyfitz's Delta was < 0.2.

5.5.3. Conclusion. Ultimately, the decision to move from the current RMP decision process to an ARM process will depend on whether managers decide the benefits of the ARM process outweigh the cost of its increased complexity, compared to the simplicity but increased risks of the current process. We found the RMP crane decision process performed adequately overall and did especially well during the years of the highest potential growth. A major limitation of the RMP decision process and likely more generally to many reactive management strategies based on prescriptive functions, is that future adjustments of the decisions process to accommodate new obstacles (e.g., changes in the timing of management decisions; U.S. Fish and Wildlife Service 2013) will be challenging to be done in a logical way. By using a coherent and logical approach to population prediction and decision making, such as ARM, there is a foundational basis to implement future changes as needed. However, as of yet, despite the lack of motivating theory and reactive nature of the RMP crane decision process, the RMP objective has been met in every year since 1997, except for one. The lack of a current problem is a strong motivation for the status quo. Looking forward to future possible population scenarios, there is some risk that a stable or slowly growing RMP without harvest could be depressed due to harvest to the lower bound of the population objective or even near the lower bound of allowable harvest (15,000). The RMP is far from threatened with extirpation from harvest under the current decision framework, only a moderate risk of not meeting the current population objective. Crane managers will need to consider the potential consequences of the two decision processes and decide whether the trade-offs in logical complexity and increased expected performance in meeting objectives outweighs limited functional simplicity that has been shown to perform adequately, so far.

As sandhill cranes increase in distribution and abundance (especially in the Eastern Population), there may be increasing interest by managers and hunters to increase harvest in already hunted populations and/or being harvesting in new populations or areas (e.g., Tennessee and Kentucky; Kruse and Dubovsky 2015). As such, it may behoove crane managers from all migratory flyways to begin developing a general outline of an adaptive management process for cranes that could be then adapted to specific monitoring programs and population objectives for each population. The coherency of management frameworks across all crane populations may allow for faster learning about crane dynamics and robust harvest decision making, as well as increased efficiency in ARM implementation. As demonstrated in this study, we expect the ARM process to reduce risk of not meeting our management objective and if monitoring uncertainties can be reduced, we may gain a deeper understanding of sandhill crane population dynamics.

Table 5.1. Simulation scenarios used to evaluate the potential for learning and meeting management objectives within an adapative resource management framework.

Scenario Number	Management Strategy[a]	Learning[b]	Monitoring[c]	Stage Structure[d]	Models
1	ARM	1/MSE or Laplace or Prob	Imperfect	Assumed	1-6, Truth
2	ARM	1/MSE or Laplace or Prob	Perfect	Assumed	1-4,6
3	ARM	1/MSE or Laplace or Prob	Perfect	Assumed	1-6, Truth
4	ARM	1/MSE or Laplace or Prob	Imperfect	Assumed	1-4,6
5	ARM	1/MSE or Laplace or Prob	Imperfect	Assumed	2-4, 6
6	ARM	1/MSE or Laplace or Prob	Perfect	Known	1-6, Truth
7	ARM	1/MSE or Laplace or Prob	Perfect	Known	Truth
8	RMP	NA	Imperfect	NA	NA
9	RMP	NA	Perfect	NA	NA

[a] Either an adaptive resource management (ARM) framework is used to make harvest decisions or a reactive strategy using the Rocky Mountain Population (RMP) of sandhill cranes current strategy.

[b] In the ARM framework, model weights are updated based on one of three methods.

[c] Population size is either observed without error (Perfect) or symmetric noise around the true population (Imperfect).

[d] Stage structure is either known perfectly in each year (Known) or is assumed to be an old stage structure prior to harvest and constant through time (Assumed).

Table 5.2. The expected probability of meeting the RMP objective and annual harvest for nine scenarios that vary by decision framework, model set, and monitoring uncertainties.

Scenario	Expected Prob. of Objective (min-max)[a]			Expected Annual Harvest (Min-Max)		
	1/MSE[b]	Laplace[b]	Prob[b]	1/MSE	Laplace	Prob
1	0.86 (0.65-1.00)	0.90 (0.74-1.00)	0.85 (0.43-1.00)	676 (236-1337)	664 (212-1302)	731 (195-1418)
2	1.00 (0.98-1.00)	1.00 (0.97-1.00)	1.00 (0.98-1.00)	815 (275-1355)	713 (200-1414)	651 (290-1390)
3	1.00 (0.99-1.00)	1.00 (0.99-1.00)	1.00 (1.00-1.00)	789 (282-1346)	804 (333-1320)	793 (321-1363)
4	0.85 (0.64-1.00)	0.88 (0.73-1.00)	0.88 (0.45-1.00)	700 (244-1385)	677 (209-1362)	728 (196-1409)
5	0.79 (0.51-1.00)	0.86 (0.64-1.00)	0.74 (0.51-1.00)	650 (244-1599)	629 (205-1573)	635 (220-1573)
6	1.00 (1.00-1.00)	1.00 (1.00-1.00)	1.00 (1.00-1.00)	777 (248-1379)	820 (371-1310)	818 (385-1345)
7[c]		1.00 (1.00-1.00)			811 (391-1363)	
8[c]		0.72 (0.01-1.00)			974 (615-1294)	
9[c]		0.77 (0.03-1.00)			981 (654-1301)	

[a] The RMP objective is to maintain a population between 17,000 and 21,000.

[b] Model probabilities evolve over time according to three different types of updating.

[c] Scenarios 7-9 do not involve model updating and thus values are irregardless of 1/MSE, Laplace, or Prob.

Table 5.3. The expected value of perfect information (EVPI) and partial perfect information (EVPXI) related to harvest management decisions for the Rocky Mountain Population (RMP) of sandhill cranes.

Value of Information	Resolved[a] Uncertainty	Unresolved[a] Uncertainty	Model Set[b]	Meeting Pop. Obj.[c]			Allowable Harvest[c]		
				1/MSE	Laplace	Prob	1/MSE	Laplace	Prob
EVPI									
	Pop, SS, Models, DF	..	..		0.28[d]			-170[d]	
	Pop, SS, Models	..	M2-4, M6	0.21	0.14	0.26	161	182	175
	Pop, SS, Models	..	M1-4, M6	0.15	0.12	0.14	111	134	83
	Pop, SS, Models	..	M1-6, Truth	0.14	0.10	0.15	135	146	79
	SS, Models	..	M1-4, M6	0.00	0.00	0.00	-5	98	160
	SS, Models	..	M2-4, M6	0.00	0.00	0.00	21	7	18
	Models	..	M1-6, Truth	0.00	0.00	0.00	34	-9	-7
EVPXI									
	Pop	DF	..		0.05[d]			7.01[d]	
	Pop	SS, Models	M1-6, Truth	0.13	0.10	0.15	113	139	61
	Pop	SS, Models	M1-4,6	0.15	0.12	0.14	116	36	-77
	SS	Models	M1-6, Truth	0.00	0.00	0.00	-13	16	25
	DF	Pop, SS, Models	M1-4, M6	0.13	0.15	0.14	-274	-297	-246
	DF	Pop, SS, Models	M1-6, Truth	0.14	0.17	0.13	-298	-310	-243
	DF	Pop, SS, Models	M2-4, M6	0.07	0.14	0.02	-324	-345	-339
	DF	SS, Models	M1-4, M6	0.23	0.22	0.23	-166	-268	-331
	DF	SS, Models	M1-6, Truth	0.23	0.23	0.23	-192	-177	-189
	DF	Models	M1-6, Truth	0.23	0.23	0.23	-204	-161	-163
	Pop, DF	SS, Models.	M1-4, M6	0.28	0.26	0.28	-159	-261	-324
	Pop, DF	SS, Models.	M1-6, Truth	0.28	0.28	0.28	-1845	-170	-182
	Pop, SS, DF	Models	M1-6, Truth	0.28	0.28	0.28	-197	-154	-156

[a] Resolved or unresolved uncertainty, for monitoring total population size (Pop), the stage structure (SS), about the correct population model (Models), and the decision framework (DF).

[b] The model set indicates the scenario with unresolved uncertainty.

[c] Model updating and thus learning evolves through time according to one of three ways.

[d] These value do not depend on model updating and thus are irregardless of updating strategies.

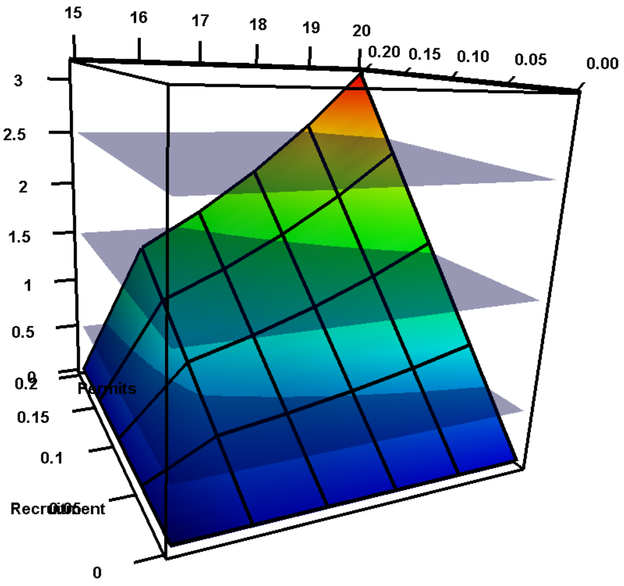


FIGURE 5.1. A three-dimensional representation of the current harvest decision framework for the Rocky Mountain Population of sandhill cranes over a range of realistic values of the population index (population, in thousands) and juvenile recruitment (Recruitment). Allowable harvest is expressed in the thousands (permits).

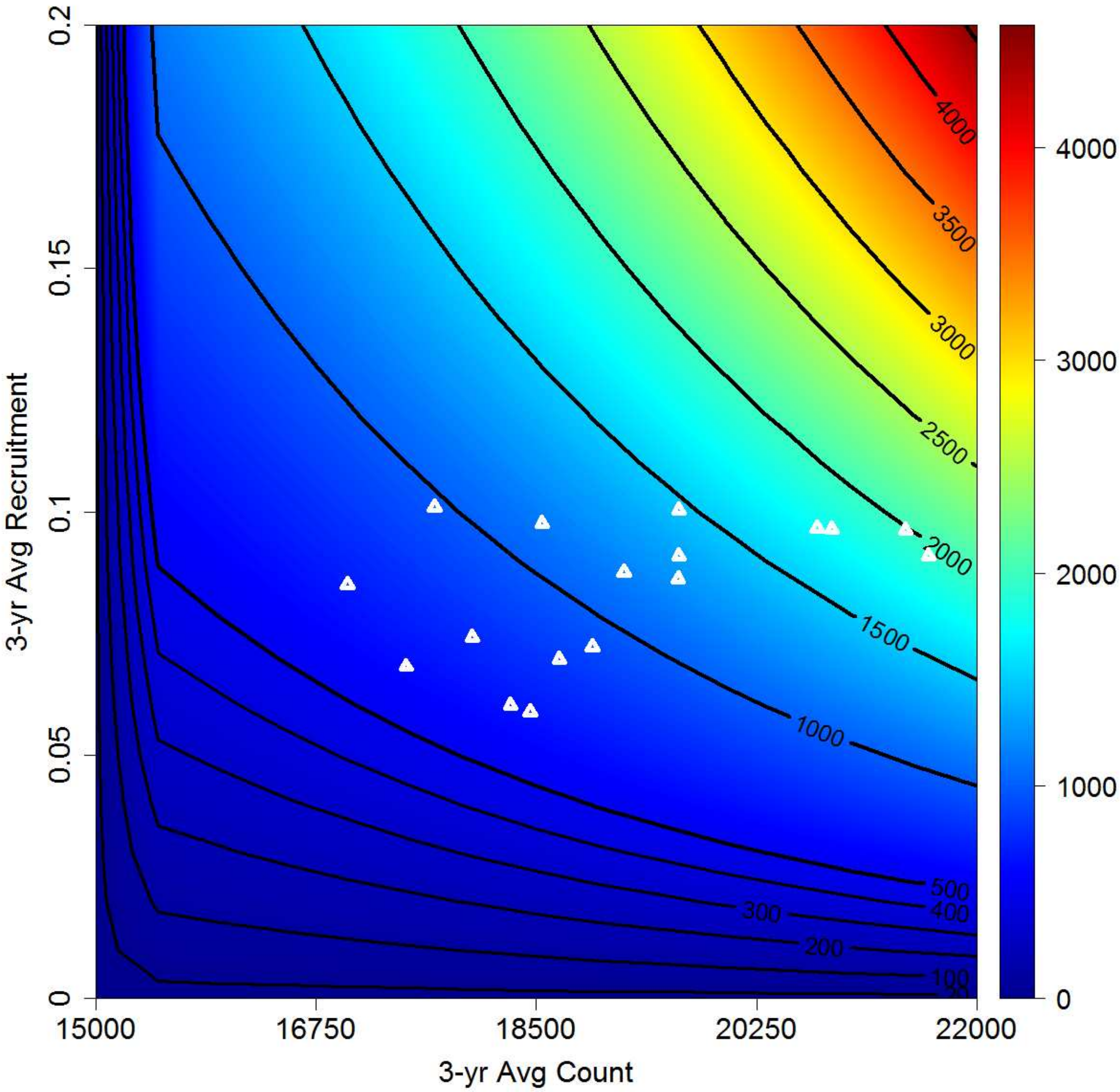


FIGURE 5.2. A representation of the current harvest decision framework for the Rocky Mountain Population of sandhill cranes over a range of realistic values, including realized allocated harvest from 1981-2014 (white triangles).

```
LOOP 1: Scenario i=1 to N.
    1) Initialize stage structured population and project 20 years using the generating model.
    LOOP 2: Simulate populations from j=1 to 1000.
        LOOP 3: Population projection from year t=20 to 100.
            1) Create model-specific transition probability array for each possible harvest
               decision.
            2) Solve optimal harvest decision based on weighted transition probability array
               and utility function.
            3) Simulate stochastic stage-structured population in year t+1 using generating
               model and optimal harvest decision.
            4) Simulate stochastic observation of the current population in year t+1.
            5) Update model weights based on new observation using Bayes theorem.
        END
    END
END
```

Figure 5.3. Descriptive process of simulating sandhill crane population dynamics, model predictions, and optimal harvest decisions in an adaptive management framework.

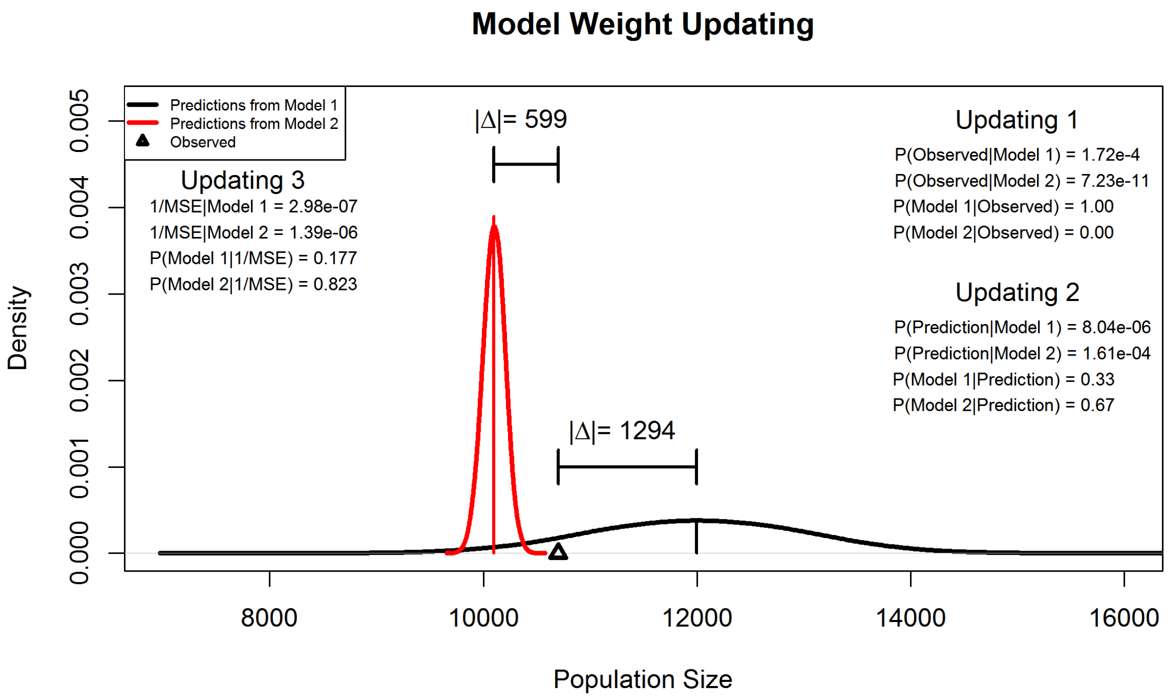


Figure 5.4. A hypothetical situation where two population models' predicted distribution are very different in terms of precision and accuracy compared to the observed true population state. Updating 1 indicates updating model weights using Bayes theorem and the probability of the new observation, given each model. Updating 2 indicates the use of the Laplace probability density to evaluate the discrepancy between the observed population and the expected prediction from each model, which is then used in Bayes theorem to update the probability of each model. For both Updating 1 and 2, equal prior probabilities for the models are used. Updating 3 uses the inverse of the MSE to calculate annual weights of each model. $|\Delta|$ indicates the absolute value of the difference between the observed value and a model's expected value.

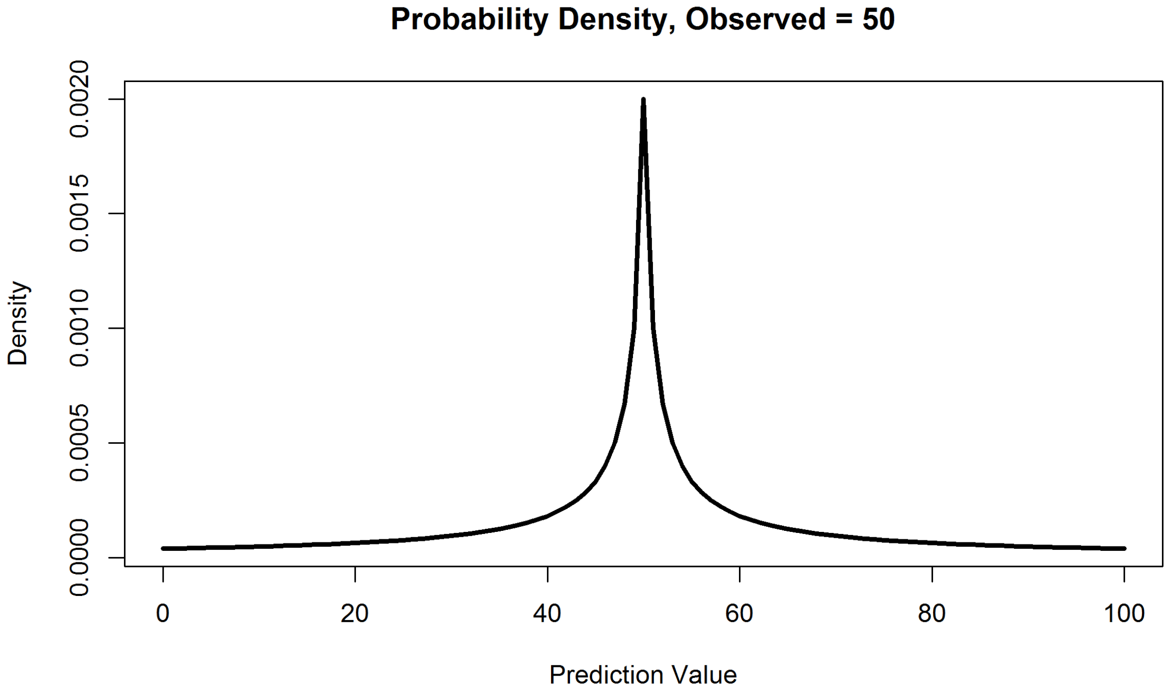
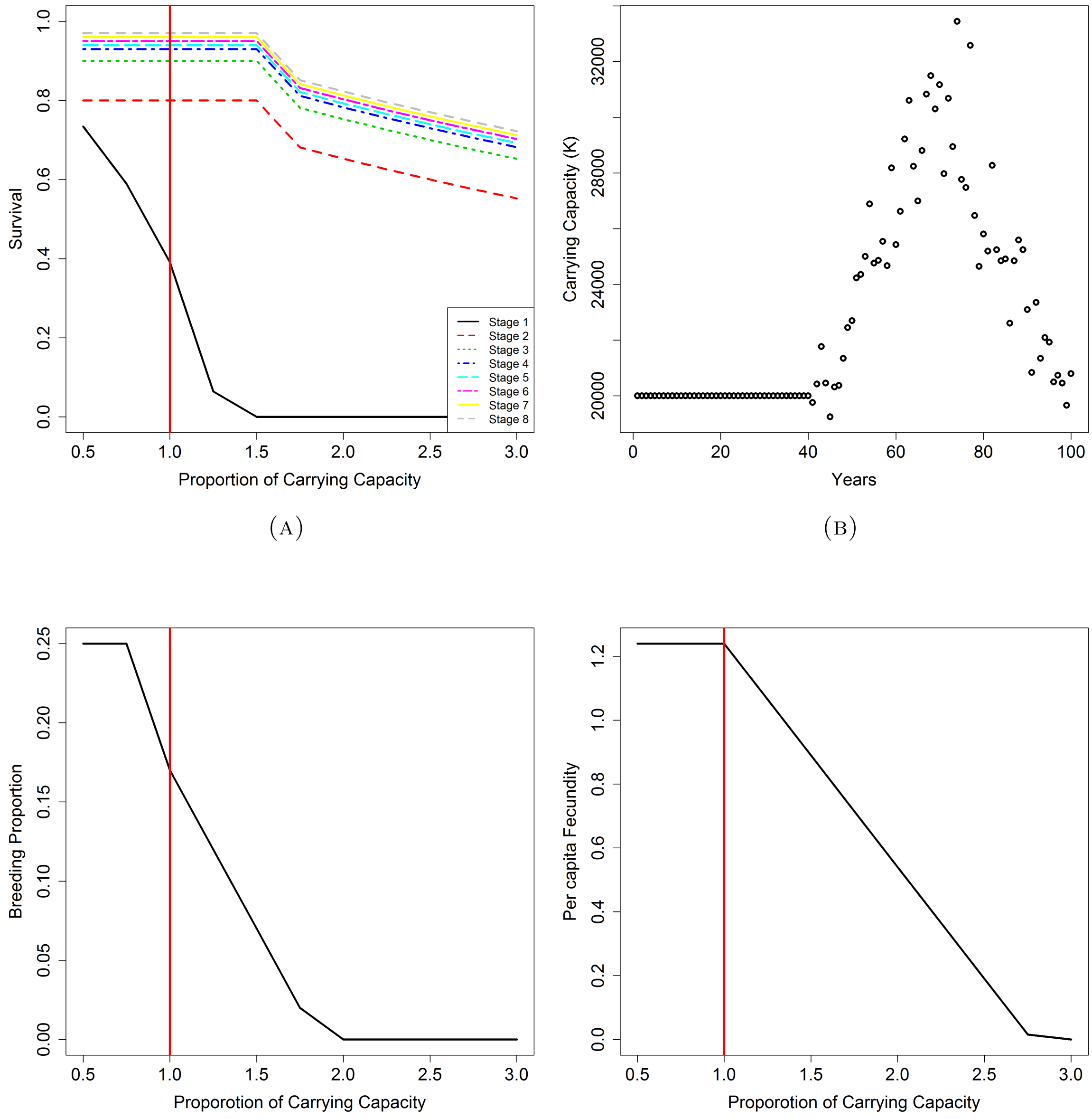


FIGURE 5.5. The Laplace probability density of predicted values from 0 to 100 when the observed value is 50.



(A) (B)

(C) (D)

FIGURE 5.6. a) Mean survival by stage under different population sizes in relation to carrying capacity. b) Carrying capacity over time., c) Proportion of breeders under different population sizes in relation to carrying capacity. d) Fecundity per capita under different population sizes in relation to carrying capacity. The vertical line at 1 indicates when the population is exactly at carrying capacity.

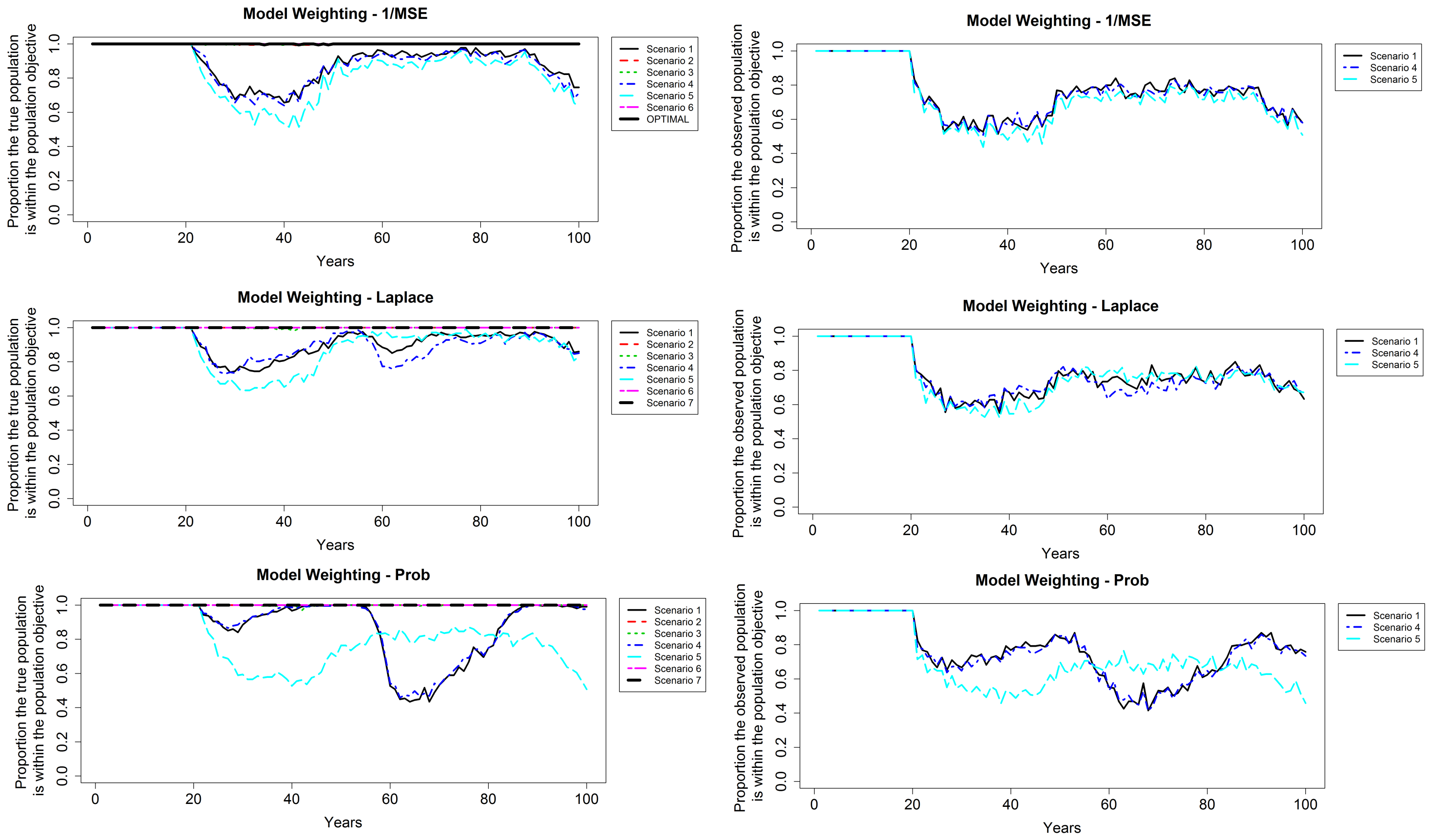


Figure 5.7. Expected annual probability of meeting the Rocky Mountain Population sandhill crane objective over time for different scenarios using an adaptive management framework for making harvest decisions.

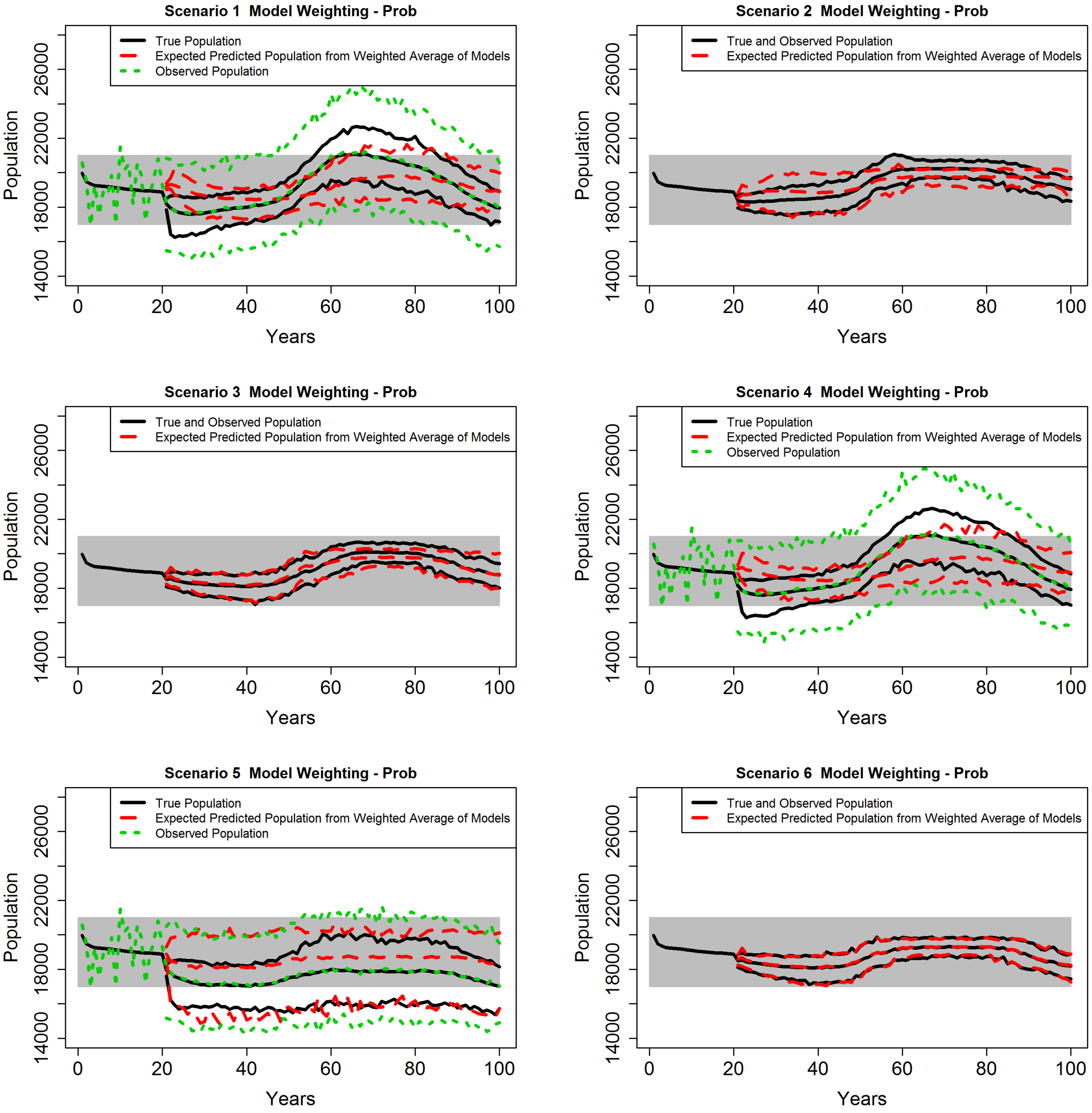


FIGURE 5.8. Population dynamics and expected population predictions from the weighted average of the model set for six adaptive resource management framework that vary in model set, whether the population is with error, and whether the stage structures is observed annually. Model updating uses Bayes theorem and evaluates new observed data (N_{t+1}) based on its probability ($P(N_{t+1}|Model)$) for each model. The population, observed population, and predicted population are presented at their means and 95% quantiles.

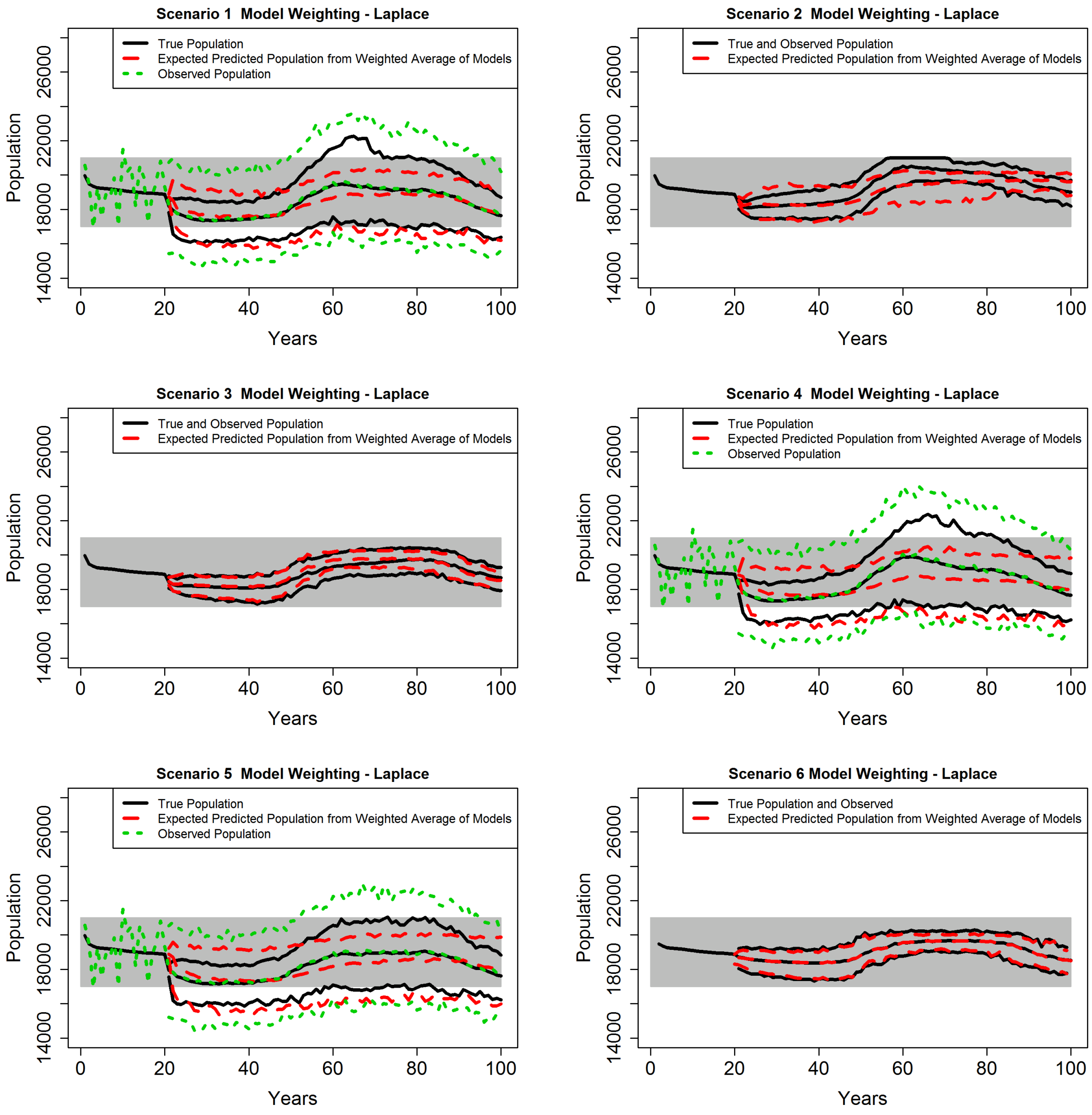


FIGURE 5.9. Population dynamics and expected population predictions from the weighted average of the model set for six adaptive resource management framework that vary in model set, whether the population is with error, and whether the stage structures is observed annually. Model updating uses Bayes theorem and evaluates new observed data based on the accuracy of each model's expected prediction using the Laplace distribution. The population, observed population, and predicted population are presented at their means and 95% quantiles.

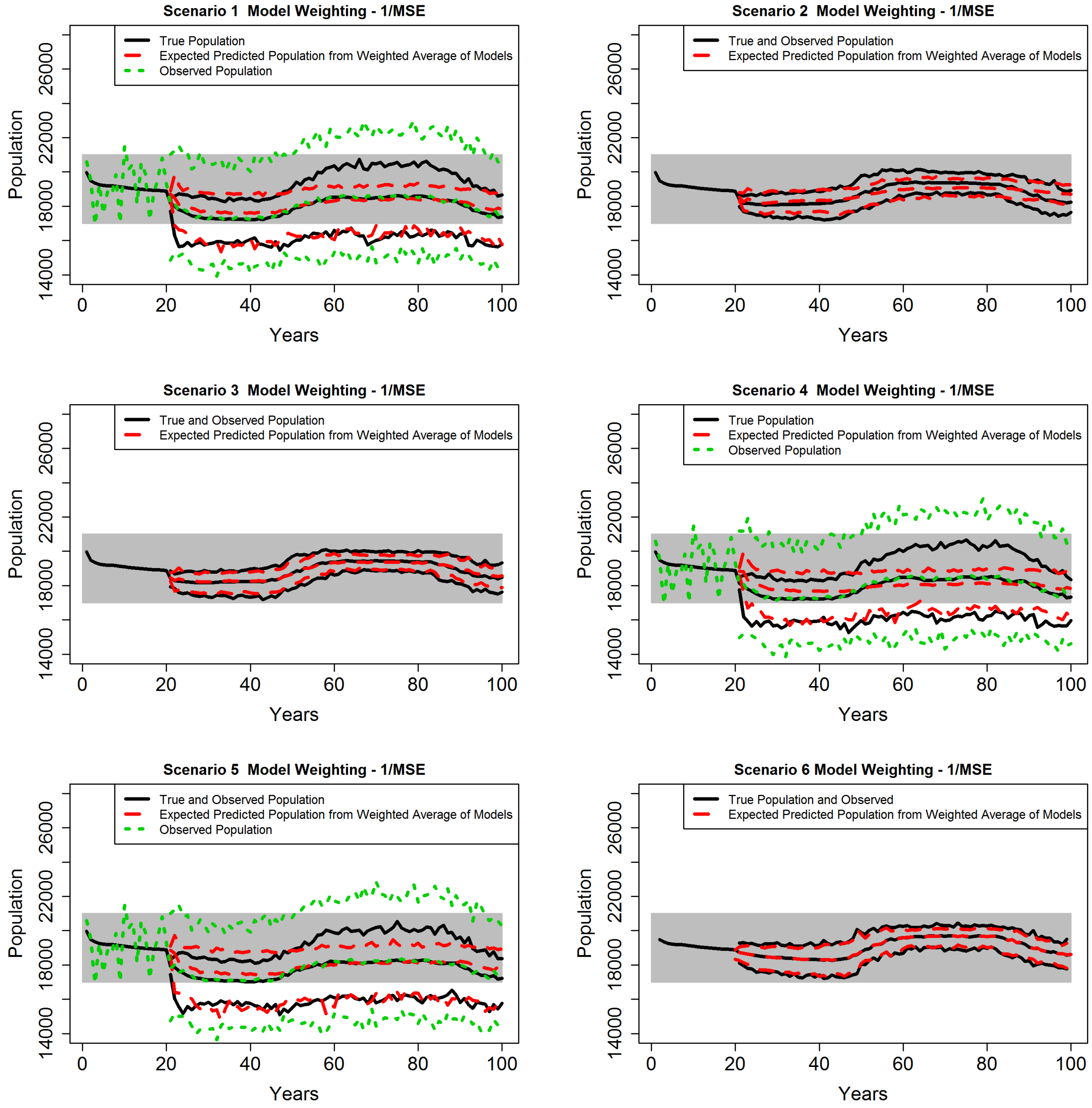


FIGURE 5.10. Population dynamics and expected population predictions from the weighted average of the model set for six adaptive resource management framework that vary in model set, whether the population is with error, and whether the stage structures is observed annually. Model updating is based on the standardization of the relative mean squared error for each model. The population, observed population, and predicted population are presented at their means and 95% quantiles.

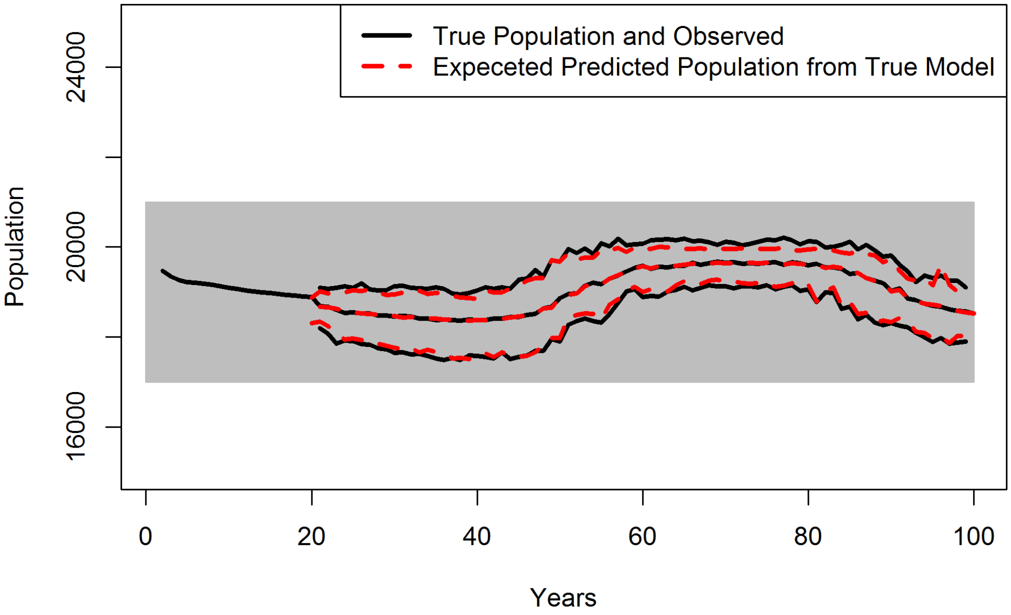


FIGURE 5.11. Population dynamics and the expected predicted population with 95% quantiles from the generating ('true') model when optimal harvest decisions are made based on the generating model, the population is monitored without error, and the annual stage-structure is known with certainty (Scenario 7). The gray area indicates the RMP population objective, such that the annual probability of meeting the objective is 1.00.

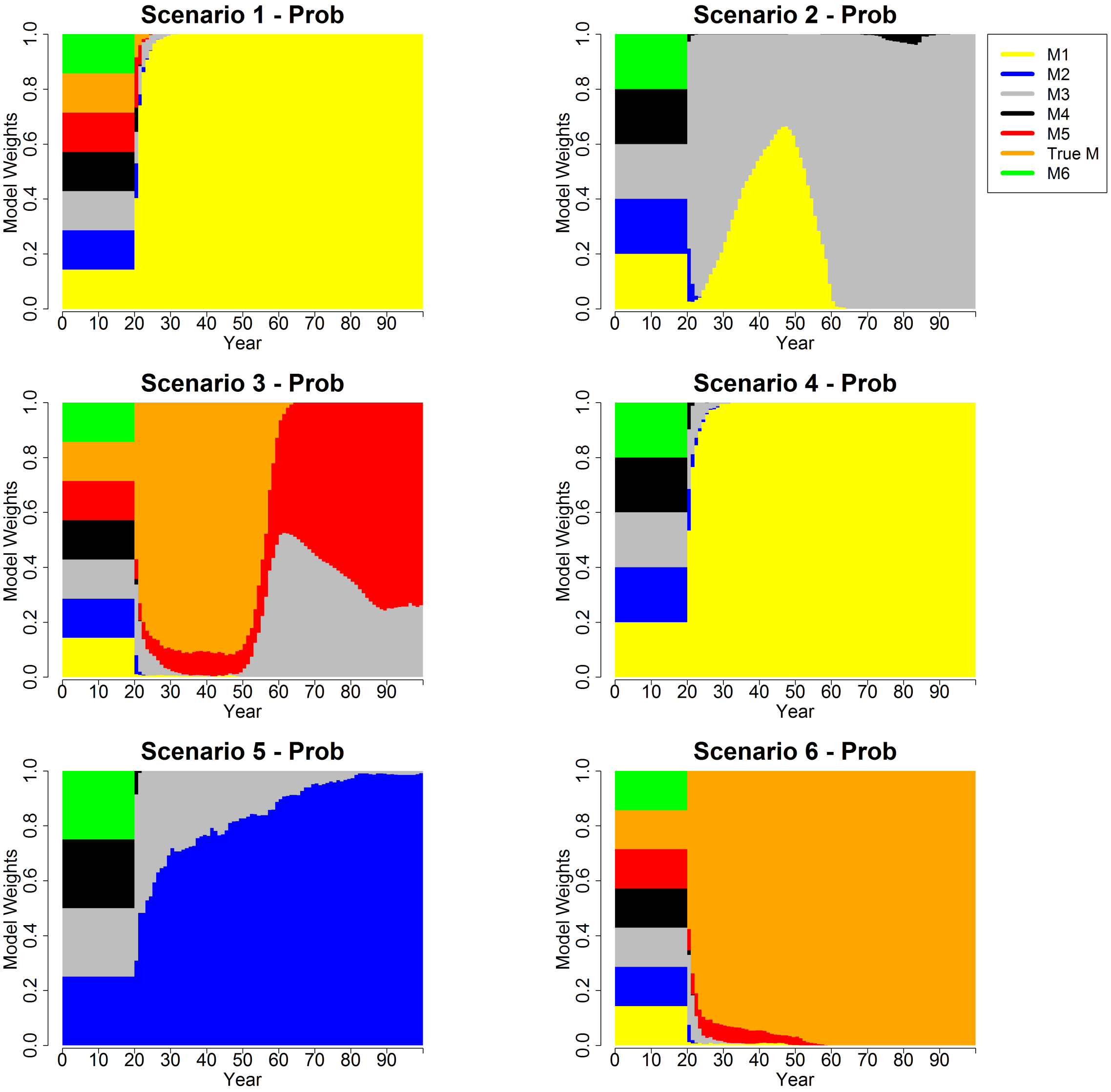


FIGURE 5.12. Model weights through time for six adaptive resource management scenarios that vary in the model set, whether the population is observed with error, and whether the stage structures is observed annually or assumed. Model updating uses Bayes theorem and evaluates new observed data (N_{t+1}) based on its probability ($P(N_{t+1}|Model)$) for each model. M1-6 indicated Models 1-6 and True M indicates the generating model.

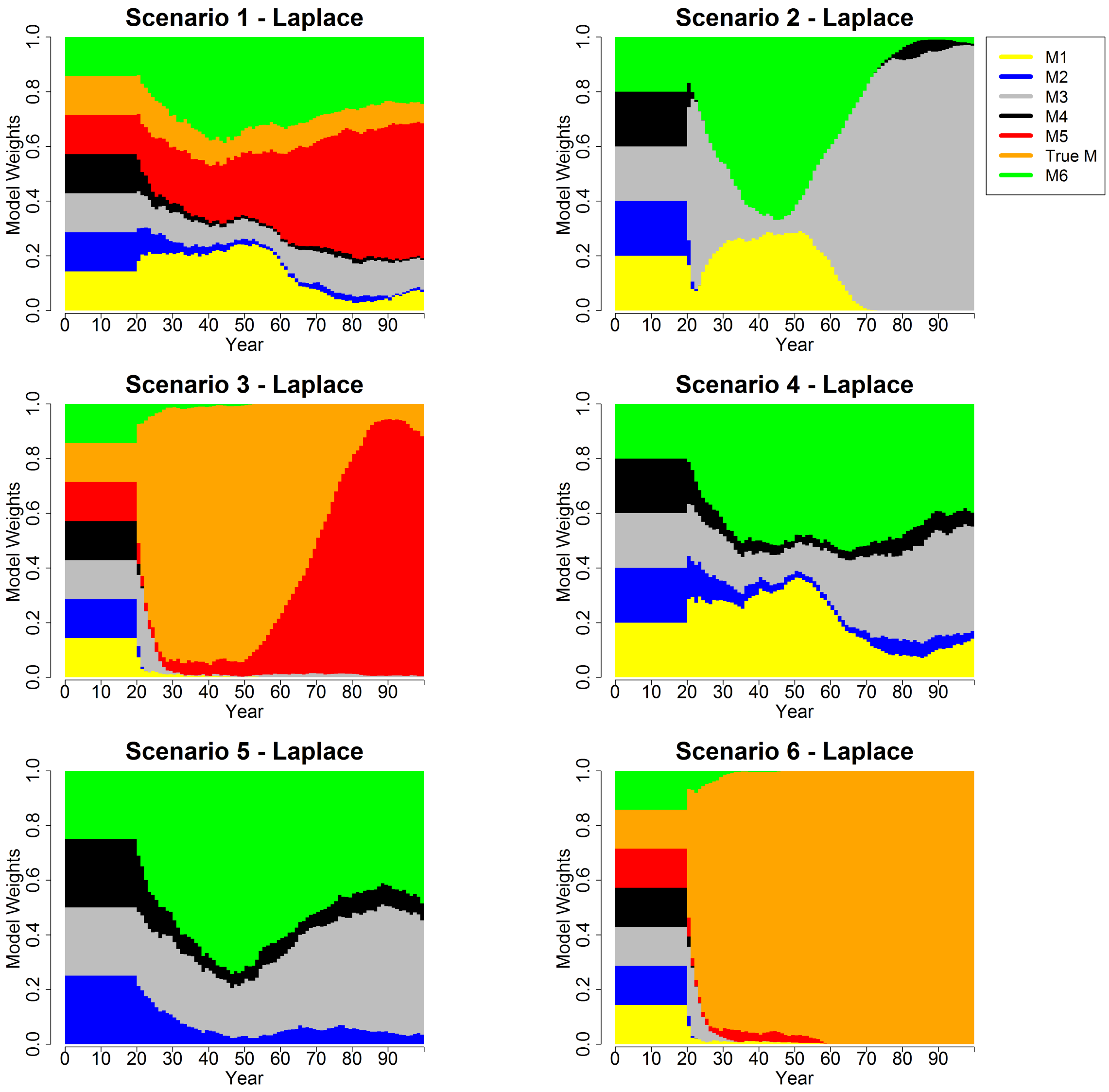


FIGURE 5.13. Model weights through time for six adaptive resource management scenarios that vary in the model set, whether the population is observed with error, and whether the stage structures is observed annually or assumed. Model updating uses Bayes theorem and evaluates new observed data based on the accuracy of each model's expected prediction using the Laplace distribution. M1-6 indicated Models 1-6 and True M indicates the generating model.

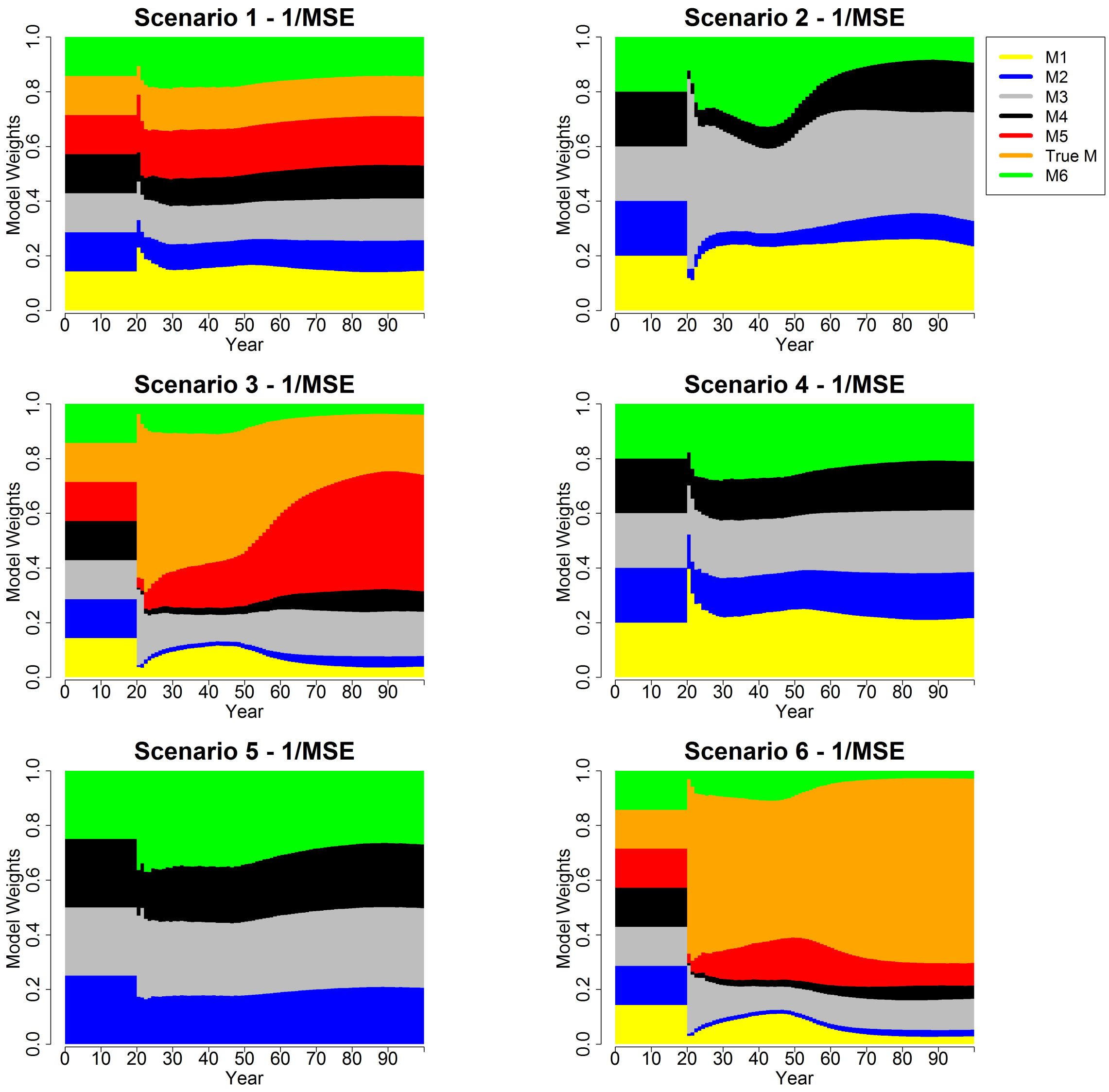


FIGURE 5.14. Model weights through time for six adaptive resource management scenarios that vary in the model set, whether the population is observed with error, and whether the stage structures is observed annually or assumed. Model updating is based on the standardization of the relative mean squared error for each model. M1-6 indicated Models 1-6 and True M indicates the generating model.

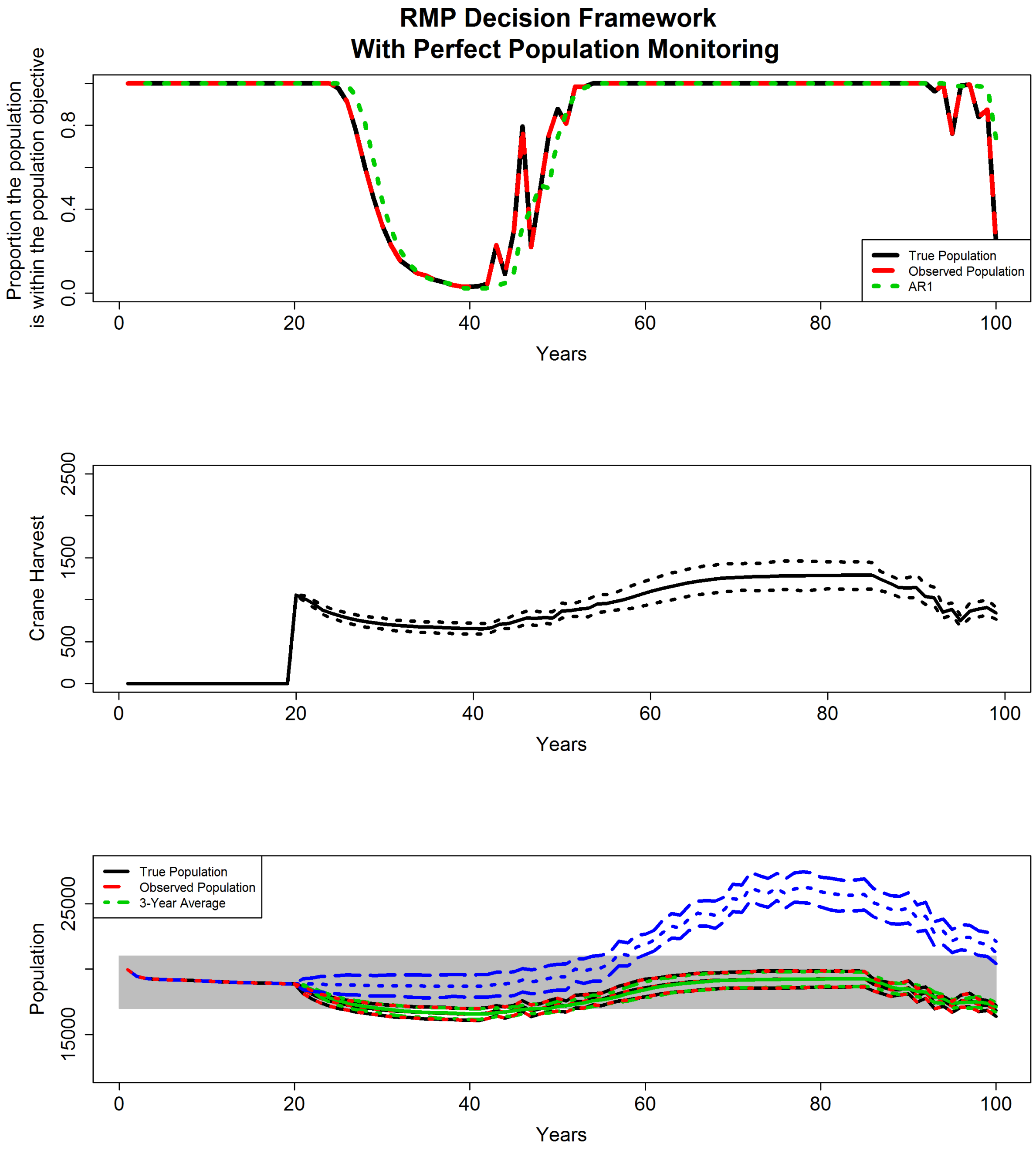


FIGURE 5.15. Annual probability of meeting the objective for the Rocky Mountain Population of sandhill cranes, total harvest, and population dynamics when the population is observed without error and harvest decisions are made using the current harvest decision framework (Scenario 9). The gray area of the third panel indicates the RMP population objective.

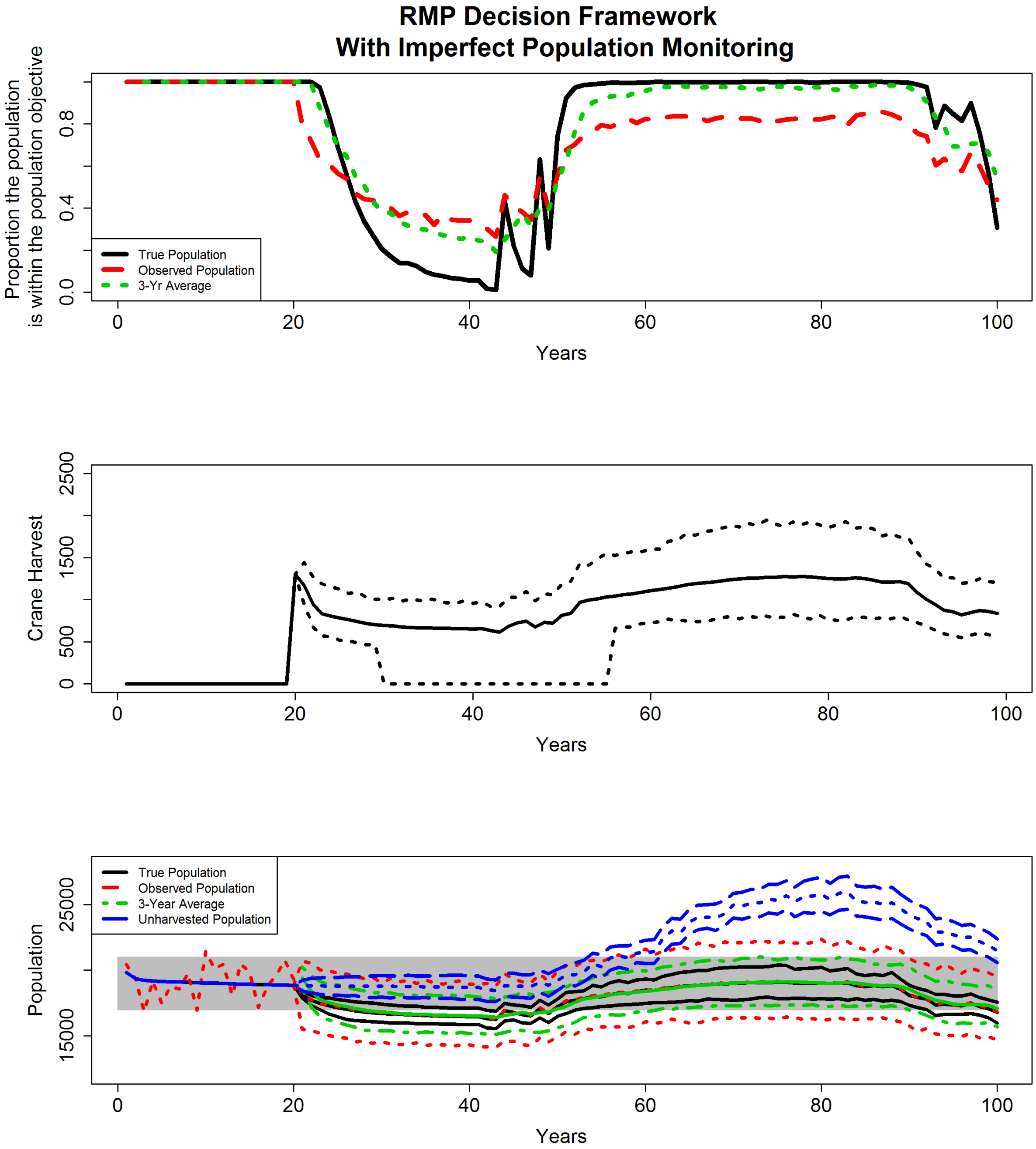


FIGURE 5.16. Annual probability of meeting the objective for the Rocky Mountain Population of sandhill cranes, total harvest, and population dynamics when the population is observed with error and harvest decisions are made using the current harvest decision framework (Scenario 8). The gray area of the third panel indicates the RMP population objective.

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APPENDIX A

Supporting Information

A.1. Chapter 2

A.1.1. Climate Regions. There are 27 NOAA climate regions throughout the Rocky Mountain Population breeding area. The climate region variation within a given year varies considerably with the standard deviation as high as 3.12 . The average range of PDSI across climate regions for a given year is -4.10 to 3.97. The variation of PDZI and PHDI across climate regions are the same or greater. See Fig. A.1 for an animation of the spatial and temporal variation in PDSI and SPEI.

A.1.2. Sandhill Crane Sampling. During the fall, juvenile and adult sandhill cranes can be distinguished by plumage; juvenile crane's upper nape, forehead and crown are feathered light gray to brown, where adults have red-orange bare papillos skin that is sparsely covered by black hairlike bristles. Juveniles also have buff-colored secondary wing coverts, whereas adults have darker gray coloring. These differences typically disappear by the following summer.

The main concern in sampling sandhill cranes to get an unbiased estimate of juvenile recruitment is to get a representative sample of all flock sizes, as juveniles are known to be a higher proportion of smaller flocks (i.e., more family groups in smaller flocks). The sampling is designed with all flock sizes to be sampled; smaller flocks are believed to not be less detectable because the San Luis Valley is generally of open terrain and even small flocks of sandhill cranes are conspicuous. An additional possibility of under-detecting juveniles is by incorrectly classifying them as adults. Juvenile cranes generally spend more time feeding and less time being vigilant compared to adults; thus without a careful visual of markings on the head, juveniles could be mistaken for an adult. This issue is minimized by the crane biologists spending enough time on each crane to accurately place them in an age class based on distinct visual markings.

A.1.3. Bayesian Model Fitting. When fitting Bayesian models, unknown parameters are required to have a prior distribution, which usually represents prior knowledge irrespective of the current/available data. In our context of selecting an optimal predictive model, we used the Normal and Laplace distributions for certain parameters ($\boldsymbol{\beta}$) to make use of the theory of ridge and LASSO (least absolute shrinkage and selection operator). We selected the hyper-parameters of the these distributions by cross-validation. As with many contexts of Bayesian model fitting, there is a question of how much information is coming from the data versus the prior when estimating parameters. We can be confident that the sandhill crane data is overwhelming the priors and informing our parameter estimates ($\alpha_0, \boldsymbol{\beta}, \sigma^2$) because the hyper-parameters for the non-regularized parameters are highly diffuse (α_0, σ^2) and trace plots of the regularized parameters ($E[\boldsymbol{\beta}]$) would be flat at zero across all values of λ, which is not the case (Fig. A.2).

A.1.4. Notes on Model Fitting using Statistical Regularization and Cross-Validation with the Log-Pointwise Predictive Density. To better translate the model fitting process used in this manuscript, we include additional information pertaining to the structure of this process. Specifically, we include extra information on picking values of λ, convergence assessment, and a diagrammatic outline of the whole process.

A.1.4.1. *Considering different values of λ.* It is usually unnecessary to examine as many values of λ as was done in the manuscript. We felt it was important for completeness for this work, but generally it is okay to examine a few values of λ that range from low (small values of λ) to high regularization (large values of λ) then use these values to determine what smaller range of λ's will likely span the optimal value. Then within this range, perform as many regularizations as one feels comfortable to make sure the optimal λ is found; meaning, that multiple values of λ provide a similar predictive accuracy and any increase or decrease in regularization clearly reduces predictive accuracy.

A.1.4.2. *Convergence Assessment.* Testing for convergence is an important part of any model fitting, including Bayesian model fitting. For our application, it was impractical to quantitatively assess convergence using statistics from multiple chains for every model fitting due to the large number of iterations that we were already doing. For each of the 100 values of λ × 2 methods (ridge, LASSO) × 4 weighting strategies, a model was fit using 500,000 MCMC samples. Instead, we opted to assess convergence on a small number of scenarios using 3 chains and calculating an $\hat{R}$ statistic (Gelman and Rubin, 1992), which indicates likely convergence when it is less than 1.1 (Gelman, 2007). Once satisfied that these scenarios, including low to high regularization, led to parameter convergence, we doubled the burn-in and MCMC iterations for fitting all scenarios. We then assessed convergence graphically for parameters using trace plots (line plots of all MCMC samples). To further ensure convergence, we strategically provided initial values for all model runs so that sampling would begin near the posterior means.

A.1.4.3. *Calculating the Log-Pointwise-Predictive Density.* The log-pointwise-predictive density (lppd) is one of many ways to consider model fit (Hobbs and Hooten, 2015; Hooten and Hobbs, 2015). It is an attractive measure because it has the statistical properties of being 'local' and 'proper', simply meaning that it is guaranteed to be an honest evaluation of predictive accuracy for the chosen model and data (Gelman, Hwang, and Vehtari, 2014). For many models, it can also be simply calculated. The basic idea is that for a set of data that is unobserved to the part of the model estimating the parameters (via cross-validation or an alternative set of data), you calculate the probability density of these values, given estimated parameters. Higher values indicate a better fit of the data to the parameters. Thus, our intended goal is to find the value of λ that achieves the maximum predictive accuracy. Conversely, if we were interested in mean-sqaured prediction error, we would be interested in finding the value of λ that leads to the minimum amount of error.

We suggest calculating the lppd during the MCMC process of fitting the model. The lppd is simply a derived parameter that could be done after the model is fit, but it is perhaps more convenient to limit the number of loops one has to execute. To calculate lppd within the MCMC, the model needs to be provided the training data for estimating the parameters and the hold-out data for calculating the lppd, given the parameters.

A.1.4.4. *Structure for Regularization, Cross-Validation, and MCMC.*

REGULARIZATION LOOP 1: Choose one value of λ from a set of potential values.

CROSS VALIDATION LOOP 2: Partition data (response variable and predictor variables) into training data and holdout data. For leave-one-out CV, remove 1 data point (response) and P number of predictor variables for that response as the holdout data and the rest as the training data.

MCMC LOOP 3: Fit the model with the training data. Calculate the point-wise predictive density using the holdout data.

END LOOP 3:

END LOOP 2:

Calculate LPPD: Take each vector of lppds for a given CV loop, divide it by the number of MCMC samples (post burn-in) then take the natural log. Add all these values together across MCMC samples for the value of lppd for a given λ. The mean of this vector is the expected lppd for a given λ. Sequentially use each value of λ to calculate the E[lppd]. **END LOOP 1:**

Plot the E[lppd] vs the log(λ). The λ with the highest E[lppd] is the optimal amount of regularization for prediction and thus the most parsimonious model.

A.2. CHAPTER 5

MODEL 2. Model 2 is a discrete logistic growth model,

$$N_{t+1} = N_t + r \times N_t \left(1 - \tfrac{N_t}{K_t}\right),$$

where K is unknown and not annually measured but is believed to be 30,000. The intrinsic growth rate (r) is defined based on juvenile recruitment (R_t), which is observed annually without error ($R = \frac{N_{juv}}{N_{juv}+N_{adults}}$) and differential survival of juveniles (S_1) and adults (S_2). N_{juv} and N_{adults} are the population size of juveniles (<1 year olds) and adults ($>$ 1 year olds), respectively. $N_{juv} = \frac{R \times N_{adults}}{1-R}$. D are adult deaths, $D = N_t(1 - S_{adults})$.

$$\begin{aligned}
N_{t+1} &= N_t + r \times N_t \left(1 - \tfrac{N_t}{K}\right) \\
r \times N_t \left(1 - \tfrac{N_t}{K}\right) &= N_{t+1} - N_t \\
r &= \frac{N_{t+1} - N_t}{N_t (1 - \frac{N_t}{K})} \\
r &= \frac{N_t + N_{juv} - D - N_t}{N_t - \frac{N_t^2}{K}} \\
r &= \frac{N_{juv} - D}{N_t - N_t^2 \times K^{-1}} \\
r &= \frac{N_{juv} \times K - D \times K}{K \times N_t - N_t^2} \\
r &= \frac{K(N_{juv} - D)}{N_t (K - N_t)}
\end{aligned}$$

Need to replace N_{juv} and D, based on R and S_{juv} and S_{adults}....

$$\begin{aligned}
R &= \frac{N_{juv} \times S_{juv}}{N_{juv} \times S_{juv} + N_{adults} \times S_{adults}} \\
\frac{1}{R} &= \frac{N_{juv} \times S_{juv} + N_{adults} \times S_{adults}}{N_{juv} \times S_{juv}} \\
\frac{N_{juv} \times S_{juv}}{R} &= N_{juv} \times S_{juv} + N_{adults} \times S_{adults} \\
N_{juv} \times S_{juv} &= R \times N_{juv} \times S_{juv} + R \times N_{adults} \times S_{adults} \\
N_{juv} &= R \times N_{juv} + \frac{R \times N_{adults} \times S_{adults}}{S_{juv}} \\
N_{juv} - R \times N_{juv} &= R \times N_{adults} \times S_{adults} \times S_{juv}^{-1} \\
N_{juv}(1 - R) &= R \times N_{adults} \times S_{adults} \times S_{juv}^{-1} \\
N_{juv} &= \frac{R \times N_{adults} \times S_{adults}}{S_{juv}(1 - R)}
\end{aligned}$$

Now replace, N_{juv} (here) into the equation for r (above),

$$\begin{aligned}
r &= \frac{\frac{K \times R \times N_t \times S_{adults}}{S_{juv}(1-R)} - K \times N_t (1 - S_{adults})}{N_t (K - N_t)} \\
r &= \frac{K \times R \times S_{adults}}{S_{juv}(1-R)(K - N_t)} - \frac{K - K \times S_{adults}}{K - N_t}
\end{aligned}$$

For each year, we observe the population (N_t) and fix K to an assumed value (30,000), fix juvenile and adult survival to an assumed value (S_{juv}, S_{adults}, respectively), and observe juvenile recruitment (R_t), we can then predict the population in the subsequent year ($\hat{N}_{t+1}$),

$$
\begin{aligned}
N_{t+1} &= N_t + \tfrac{K \times R \times S_{adults}}{S_{juv}(1-R)(K-N_t)} - \tfrac{K - K \times S_{adults}}{K - N_t} \times N_t \left(1 - \tfrac{N_t}{K}\right) \\
S_{juv} &\sim Beta(\alpha_{S_{juv}}, \beta_{S_{juv}}) \\
\alpha_{S_{juv}} &= -1 \times (\mu_{S_{juv}} \times (\sigma^2_{S_{juv}} + \mu^2_{S_{juv}} - \mu_{S_{juv}}))/\sigma^2_{S_{juv}} \\
\beta_{S_{juv}} &= ((\sigma^2_{S_{juv}} + \mu^2_{S_{juv}} - \mu_{S_{juv}}) \times (\mu_{S_{juv}} - 1))/\sigma^2_{S_{juv}} \\
\mu_{S_{juv}} &= 0.81 \\
\sigma_{S_{juv}} &= 0.06 \\
\alpha_{S_{adults}} &= -1 \times (\mu_{S_{adults}} \times (\sigma^2_{S_{adults}} + \mu^2_{S_{adults}} - \mu_{S_{adults}}))/\sigma^2_{S_{adults}} \\
\beta_{S_{adults}} &= ((\sigma^2_{S_{adults}} + \mu^2_{S_{adults}} - \mu_{adults}) \times (\mu_{S_{adults}} - 1))/\sigma^2_{S_{adults}}. \\
\mu_{S_{adults}} &= 0.956 \\
\sigma_{S_{adults}} &= 0.03
\end{aligned}
$$

Juvenile and adults survival are estimates from mark-resight and dead-recovery data (Drewien, R.C., unpublished data).

MODEL 3 AND 4. Model 3 is a density-independent stochastic stage structured population model, where harvest mortality is additive ($f(harvest_t)$), while Model 4 is the same population model but harvest is compensated up to natural mortality ($f(harvest_t)$,

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

where S_i is the survival between ages i and $i+1$, and F is the per capita fecundity. The terminal column represents the dynamics of all individuals that live beyond the finite number of stages represented by each PPM. Survival is considered to be stochastic,

$$\begin{aligned}
S_i &\sim Beta(\alpha_{S_i}, \beta_{S_i}) \\
\alpha_{S_i} &= -1 \times (\mu_{S_i} \times (\sigma^2_{S_i} + \mu^2_{S_i} - \mu_{S_i}))/\sigma^2_{S_i} \\
\beta_{S_i} &= ((\sigma^2_{S_i} + \mu^2_{S_i} - \mu_i) \times (\mu_{S_i} - 1))/\sigma^2_{S_i} \\
\mu_{S_1} &= 0.85 \\
\sigma_{S_1} &= 0.06 \\
\mu_{S_2} &= 0.95 \\
\sigma_{S_2} &= 0.02 \\
\mu_{S_{3-5}} &= 0.96 \\
\sigma_{S_{3-5}} &= 0.03
\end{aligned}$$

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 scale fecundity by partial year terminal survival. The fecundity per individual is thus calculated as, $F = PropBreeders \times \frac{brood}{2} \times S_5^{8/12}$. In order to project the population, a stage structure has to be assumed ($StageStructure$), which is also used to distribute harvest (a single annual population-level value) across each stage,

$$\hat{N}_{t+1} = PPM1 \cdot N_t \times StageStructure - f(harvest_t) \times StageStructure$$

A.2.1. Partial Controllability. To understand the relationship between Rocky Mountain Population (RMP) annual harvest allocation and the estimated annual harvest, we estimated the rate of permit allocation success by state (Wyoming, Utah, Arizona, Montana, New Mexico, Idaho) using a Bayesian Poisson regression where state was treated as a random effect. The allocated permits by state was used as an offset, while the data were the annual sandhill crane harvest from each state, as estimated by hunter surveys (Kruse and Dubovsky, 2015).

We found significant variation in the success of each state in fulfilling their annual permit allocation (Figure A.3). Most important is that Wyoming is often near their allocation and in a few years, exceeding it. In contrast, Arizona only harvests near half their annual allocation. The reasons for these differences are many, including the number of crane hunters and hunter effort, but also the number permits each state chooses to sell in each year. States are allowed to sell more permits than their annual allocated harvest, as it creates revenue for the state, allows additional hunters to participate, and recognizes that not all permitted hunters will be successful.

A.3. Tables and Figures

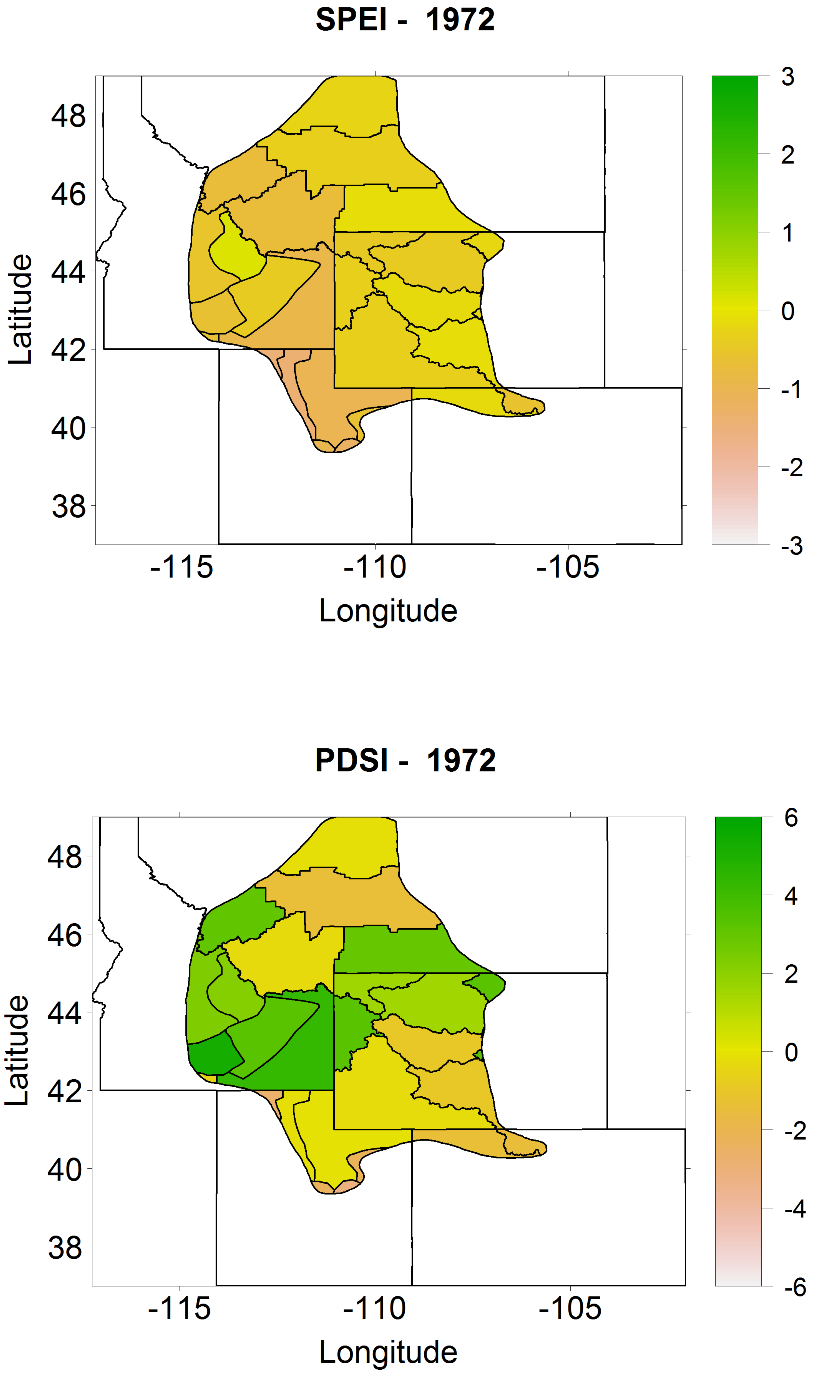

Figure A.1. Drought indices from 1972 to 2013 within the sandhill crane Rocky Mountain Population breeding area (Idaho, Montana, Wyoming, Colorado, Utah); Top: the standardized precipitation-evapotranspirtion index (SPEI). Bottom: the Palmer Drought Severity Index (PDSI).

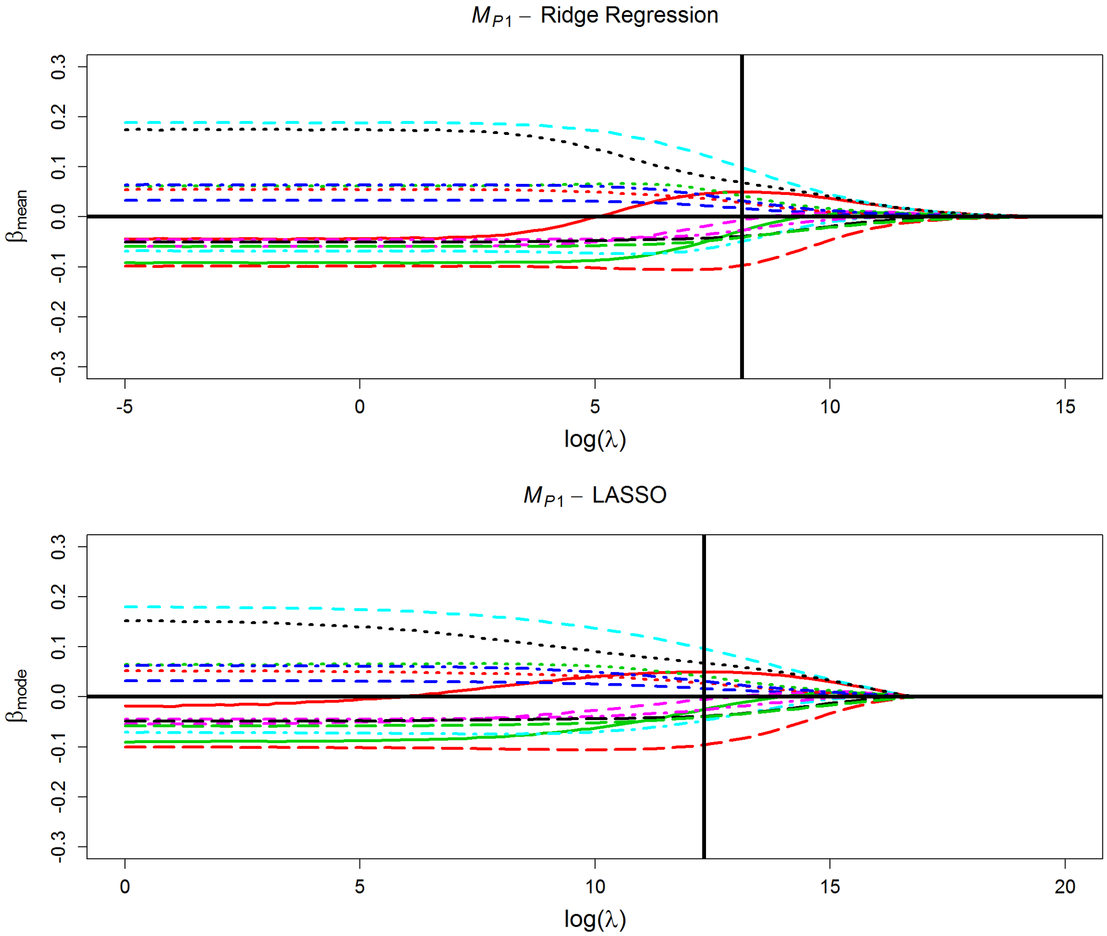

FIGURE A.2. Trace plots of the standardized regression coefficients posterior ($\mathrm{E}[\boldsymbol{\beta}]$) when using ridge regression and LASSO.

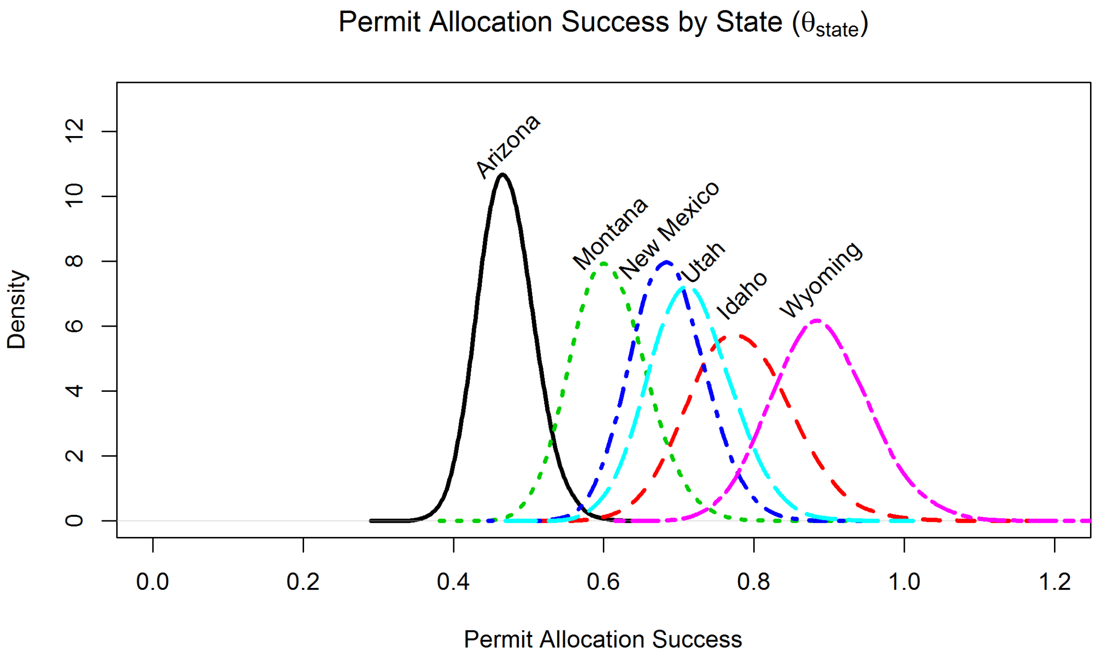

FIGURE A.3. The estimated success rate of states that harvest sandhill cranes from the Rocky Mountain Population in fulfilling their annual allocated harvest from a Bayesian Poisson regression model.

A.4. Literature Cited

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