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Andrew J. Caven
International Crane Foundation, Baraboo, WI, acaven@cranetrust.org

Hillary L. Thompson
International Crane Foundation, Baraboo, WI

David M. Baasch
Crane Trust, Wood River, NE

Barry K. Hartup
International Crane Foundation, Baraboo, WI

Amanda M. Hegg
Audubon Great Plains, Lincoln, NE

See next page for additional authors

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Authors

Andrew J. Caven, Hillary L. Thompson, David M. Baasch, Barry K. Hartup, Amanda M. Hegg, Stephanie M. Schmidt, Irvin Louque, Craig R. Allen, Carter G. Crouch, Craig A. Davis, Joel G. Jorgensen, Jane E. Austin, Bethany L. Ostrom, Richard D. Beilfuss, George W. Archibald, and Anne E. Lacy

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Biological Case Against Downlisting the Whooping Crane and for Improving Implementation under the Endangered Species Act

Andrew J. Caven[1,2,*], Hillary L. Thompson[1], David M. Baasch[2], Barry K. Hartup[1], Amanda M. Hegg[3], Stephanie M. Schmidt[1], Irvin Louque[1], Craig R. Allen[4], Carter G. Crouch[1], Craig A. Davis[5], Joel G. Jorgensen[6], Jane E. Austin[7,1], Bethany L. Ostrom[2], Richard D. Beilfuss[1], George W. Archibald[1], and Anne E. Lacy[1]

1) International Crane Foundation, Baraboo, WI, USA
2) Crane Trust, Wood River, NE, USA
3) Audubon Great Plains, Lincoln, NE, USA
4) Center for Resilience in Agricultural Working Landscapes (CRAWL), University of Nebraska-Lincoln, Lincoln, NE, USA
5) Department of Natural Resources, Ecology, and Management, Oklahoma State University, Stillwater, OK, USA
6) Nebraska Game and Parks Commission, Lincoln, NE, USA
7) Great Plains Natural Science Society, Dakota College at Bottineau, Bottineau, ND, USA

*Contact: acaven@savingcranes.org; +1-(605)-252-8007

Abstract

The Whooping Crane (*Grus americana*; WHCR) is a large, long-lived bird endemic to North America. The remnant population migrates between Aransas National Wildlife Refuge, USA, and Wood Buffalo National Park, Canada (AWBP), and has recovered from a nadir of 15-16 birds in 1941 to ~540 birds in 2022. Two ongoing reintroduction efforts in Louisiana and the Eastern Flyway together total ~150 birds. Evidence indicates the U.S. Fish and Wildlife Service (USFWS) is strongly considering downlisting the species from an endangered to a threatened status under the Endangered Species Act (ESA). We examined the current status of the WHCR through the lens of ESA threat factors, the USFWS's Species Status Assessment (SSA) framework, and other avian downlisting actions to determine if the action is biologically warranted. Our research indicates that WHCRs are facing an intensification of most threat drivers across populations and important ranges. The AWBP is still relatively small compared to other crane species and most birds of conservation concern. To date, only one avian species has been downlisted from an endangered status with an estimated population of <3,000 individuals. Representation in terms of WHCRs historic genetic, geographic, and life history variation remains limited. Also, the lack of spatial connectivity among populations, reliance of the reintroduced populations on supplementation, and continued habitat loss suggest that WHCR populations may not be resilient to large stochastic disturbances. Given that reintroduced populations are not self-sustaining, neither supplies true redundancy for the AWBP. Proposed downlisting before recovery plan population criteria have been met is objectively unwarranted

and reflects USFWS inconsistency across ESA actions. Only by incorporating basic quantitative criteria and added oversight into ESA listing decisions can we avoid an action as misguided as downlisting the Whooping Crane without consideration of its recovery plan criteria or ostensibly its population ecology.

Keywords: Endangered Species Act, ESA, Whooping Crane, *Grus americana*, Downlisting, Delisting, Recovery Criteria

Introduction

Environmental laws and regulations are critical to endangered species conservation at several political scales (national, international, etc.; Trouwborst et al. 2010, Lascelles et al. 2014, Percival et al. 2021). The determination of which species will receive enhanced protections from governmental and intergovernmental bodies based on available scientific information is fundamental to their effective implementation (Lascelles et al. 2014, Evans et al. 2016). Prioritization is often achieved by conferring a ranked status to individual species or subspecies based on their abundance, distribution, current threats, and apparent population trend(s) (USFWS 1973, Miller et al. 2007, Favaro et al. 2014). Generally, species at greater risk of extinction are provided stronger legal protections and additional funding for targeted conservation efforts (Martin-Lopez et al. 2011, Favaro et al. 2014, Evans et al. 2016). However, in many instances important species information may be lacking and guidance on status classification can be vague (Lascelles et al. 2014, Evans et al. 2016, Lind- Riehl et al. 2016). This can leave determinations open to influences beyond biology such as social, political, and financial considerations (Martin-Lopez et al. 2011, Lind- Riehl et al. 2016, Smith 2016).

The Whooping Crane (*Grus americana*; WHCR) came perilously close to extinction in the early 1940s and was first provided enhanced legal protections in 1967 by the Endangered Species Preservation Act of 1966 (USFWS 1967; CWS and USFWS 2007). The WHCR was later classified as "endangered" (i.e., in danger of extinction) under the refined Endangered Species Act (ESA) of 1973 which was intended "…to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, [and] to provide a program for the conservation of such endangered species and threatened species…." (USFWS 1973). Though the ESA is viewed as a major landmark in species conservation and environmental law, it has been criticized for vague language and inconsistent implementation (Doak et al. 2015, Wolf et al. 2015, Evans et al. 2016). Despite recent increases in WHCR abundance the species remains among the rarest birds in North America (Urbanek and Lewis 2020). Furthermore, direct and indirect threats to the species may be increasing in magnitude, number, and interrelatedness (Sandford et al. 2015, Butler et al. 2017, Caven et al. 2020a, Golden et al. 2022). Evidence suggests that the USFWS is strongly considering downlisting the WHCR from an "endangered" to a "threatened" status (Anders 2021, Kurose 2022), despite recovery benchmarks being empirically unmet (CWS and USFWS 2007, Butler et al. 2022, LDWF 2022, Thompson et al. 2022). A status change under the ESA could weaken protections for the WHCR which could negatively impact species recovery (Hartl and Owley 2021). We assess if a status change for the WHCR is biologically justifiable considering ESA guidance using the best available data and science. We also provide a critical evaluation of current ESA implementation based on insights garnered during our assessment and provide ideas to improve the consistency of ESA administration.

Whooping Crane Conservation and Natural History

The WHCR is a large wading bird endemic to North America (Urbanek and Lewis 2020). It historically ranged across much of the continent from Hudson Bay west to the Northwest Territories, Canada, at its northern extent and from Florida, USA, west to central Mexico on its southern boundary (Allen 1952, Austin et al. 2019). Historic records indicate that the greatest breeding densities likely occurred along the northern periphery of the temperate grassland biome, particularly in the Prairie Potholes region of the Great Plains (Allen 1952, Austin et al. 2019). Wintering occurred from coastal wetlands in the Mid-Atlantic (New Jersey) to playa lakes in the Mexican high plains (e.g., Guanajuato), but densities were probably highest along the Gulf Coast from southwestern Louisiana to the Rio Grande delta (Allen 1952, Austin et al. 2019). Most populations were historically migratory per existing records (Allen 1952, Austin et al. 2019). However, a couple concentrations of non-migratory WHCRs existed within the Gulf Coast region (Allen 1952, Austin et al. 2019).

Historic population estimates based on the species' former breeding range and approximate territory sizes suggest that WHCRs likely numbered >10,000 individuals prior to European settlement (CWS and USFWS 2007). This estimate is largely supported by genetic analyses (Athrey et al. *In Review*). By the late 1800s there may have been only 1,300 – 1,400 individuals remaining as a result of overhunting, human disturbance, and habitat loss and modification (Allen 1952). By the winter of 1939-1940 only two small populations remained, including a non-migratory population near White Lake, LA, numbering about 13 individuals, and 18 individuals, including 4 young, wintering at Aransas National Wildlife Refuge (NWR) in Texas (Allen 1952, CWS and USFWS 2007). It is notable that the breeding grounds for the population wintering at Aransas NWR was unknown until it was discovered in the boreal region of Canada at Wood Buffalo National Park (NP) in 1954 on the northern periphery of the species'

historic range (Allen 1952, CWS and USFWS 2007, Austin et al. 2019). The remnant non-migratory population in Louisiana steadily declined until its extirpation in 1950 (CWS and USFWS 2007). The Aransas-Wood Buffalo Population (AWBP) reached its low point in the winter of 1941-1942 at 15-16 birds. Less often recognized is that a decade later the situation remained quite tenuous with only 19 adults and 2 colts documented during the winter of 1952-1953 (CWS and USFWS 2007). After many decades of targeted habitat and species conservation efforts the AWBP was estimated to number ~540 individuals in the winter of 2021-2022 (Butler et al. 2022). Additionally, there are two ongoing reintroduction efforts with breeding grounds in Wisconsin and Louisiana that together total ≥150 WHCRs (Szyszkoski 2022, Thompson 2022, Thompson et al. 2022).

WHCRs select wetland habitat at multiple spatial scales throughout their range (Niemuth et al. 2018; Baasch et al 2019a, 2022; Barzen et al. 2019). This includes salt marsh and tidal ponds on the AWBP's Gulf Coast wintering grounds (Chavez-Ramirez 1996, CWS and USFWS 2007), wet meadows, playa lakes, and rivers during migration through the Central Flyway (Austin and Richert 2005; Pearse et al. 2017; Baasch et al. 2019a, 2019b, 2022), and shallow diatom ponds and marshes on their boreal-taiga breeding grounds within and around Wood Buffalo NP (Timoney 1999, Bergeson et al. 2001a). The reintroduced Eastern Migratory Population (EMP) and the Louisiana Non-migratory Population (LNMP) also depend heavily on wet meadow and emergent marsh habitats but likewise utilize comparable flooded agricultural habitats such as cranberry (*Vaccinium macrocarpon*) bogs [in WI] and rice (*Oryza sativa*)/crawfish (*Procambarus* spp.) aquaculture [in LA] (Pickens et al. 2017, Barzen et al. 2018a, Thompson 2018). WHCRs additionally use lowland prairies and agricultural fields including corn (*Zea mays*), alfalfa (*Medicago sativa*), wheat (*Triticum* spp.), barley (*Hordeum*

spp.), and sorghum (*Sorghum vulgare*) as foraging sites throughout their range, particularly during migration and wintering periods (Armbruster 1990, Austin and Richert 2005). Agricultural foraging sites provide significant caloric resources but their value to WHCRs is likely maximized at moderate landcover levels within a mosaic of lowland prairie and palustrine wetland landcovers that afford high-nutrient diet items and safe roosting opportunities (Niemuth et al. 2018, Caven et al. 2021, 2022a, Baasch et al. 2022).

WHCRs tend to select the most visually open landscapes available that contain shallow wetland habitats (Baasch et al. 2019b, Caven et al. 2022a). Shallow wetlands (<30 cm depth) provide protection from terrestrial predators such as bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) throughout the WHCRs annual cycle (Urbanek and Lewis 2020). This is particularly important during the molting period in the spring or summer when they can become flightless (Lacy and McElwee 2016, Barzen et al. 2019). WHCRs experience an entire molt of flight feathers every 2-3 years that renders them more susceptible to predation than species like Sandhill Cranes (*Grus* [*Antigone*] *canadensis*) that molt a few flight feathers at a time and very seldom become flightless. Wetlands provide a wide variety of highly valuable animal food sources to WHCRs including fish, anurans, snakes, mollusks, arthropods, and other invertebrates, which provide essential nutrients including protein, calcium, and phosphorus not readily available in waste grains (Chavez-Ramirez 1996, Bergeson et al. 2001a, Geluso and Harner 2013, Zimorski et al. 2013, Caven et al. 2021). WHCRs tend to be relatively sensitive to human disturbance, especially during migration, and select habitats that are farther than expected from human developments such as roads, dwellings, powerlines, and alternative energy infrastructure (Pearse et al. 2017, 2021; Baasch et al. 2019a, 2022).

WHCRs are a *K*-selected species having a relatively long lifespan (to >30 years in the wild), high adult survival (>94% annually for AWBP), and generally low productivity (fledge rate of 0.466–0.564 for AWBP; Wilson et al. 2016, Urbanek and Lewis 2020). Furthermore, WHCRs typically do not begin to breed until about 4 years of age (Wilson et al. 2016, Urbanek and Lewis 2020). WHCR population projections are highly sensitive to adult survival (Wilson et al. 2016, Traylor-Holzer 2019). Despite significant gains in recent decades, WHCR populations remain objectively small from a genetic management and species conservation perspective (Frankham et al. 2002, 2014), and they face a series of increasing threats from novel diseases (e.g., highly pathogenic avian influenza (HPAI); CMS FAO 2022, Stokstad 2022), continued habitat loss (Wright and Wimberly 2013, McIntyre et al. 2018), drought and water diversions (Caven et al. 2019a), expanding energy infrastructure (e.g., transmission lines; Smith and Dwyer 2016), continued poaching (Condon et al. 2019), predation (Pearse et al. 2019, Thompson et al. 2022), and climate change (Butler et al. 2017, Golden et al. 2022).

Potential Downlisting and the Endangered Species Act

Despite the challenges faced by objectively small WHCR populations, evidence suggests that the U.S. Fish and Wildlife Service (USFWS) has been seriously considering downlisting the WHCR from an "endangered" to a "threatened" status under ESA since the spring of 2021 (USFWS 1973, Kurose 2022). On 11 April 2022, the Center for Biological Diversity (CBD) released several documents garnered during a Freedom of Information Act (FOIA) request that indicated USFWS downlisting actions were well underway in 2021 (Kurose 2022). Relevant documents included a briefing for the Southwest Regional Director of the USFWS (Anders 2021), a news release announcing the proposed status change (Buzek 2021), and a question-and-answer document for public release (USFWS 2021a). The USFWS had also communicated this

intention to key partners verbally (Kim Smith, Chief Operations Officer, International Crane Foundation – personal communication; Wade Harrell, former Whooping Crane Recovery Coordinator, USFWS – personal communication). These actions surprised many partners in WHCR conservation as the downlisting criteria remained ostensibly unmet (Rich Beilfuss, President & Chief Executive Officer International Crane Foundation – personal communication; Brice Krohn, President & Chief Executive Officer, Crane Trust – personal communication). Downlisting criteria were outlined in a recovery plan, a formal document that determines what comprises "recovery" and outlines how that objective is to be achieved for listed species (CWS and USFWS 2007). Although the process is led by the USFWS, the recovery plan was developed with partners and went through a public comment process. Furthermore, unlike many recovery plans, the strategy for the WHCR was developed cooperatively with Canada as the species represents a shared resource co-managed by the two countries (CWS and USFWS 2007).

The ESA confers a certain set of protections (section 9 protections) to endangered species that are not automatically conveyed to threatened species, so downlisting actions can have potentially significant consequences (Hartl and Owley 2021, USFWS 2021b). Since 2019, the USFWS has been applying species- specific 4(d) rules, instead of blanket section 9 protections, to those species listed as threatened (Hartl and Owley 2021, USFWS 2021b). These 4(d) rules are often used to "streamline" or reduce regulation for projects that may produce a limited number of mortalities or harassments (i.e., "take"). This could result in energy infrastructure projects such as windfarms and transmission lines proposed within the WHCR's range receiving significantly less rigorous oversight and mitigation, which could negatively impact the species (Hartl and Owley 2021, USFWS 2021b).

The existing downlisting criteria for WHCRs are dynamic, allowing for multiple different objectives to be reached based on existing populations (CWS & USFWS 2007). Criterion "1" states that the AWBP will exceed 160 individuals, two reintroduced populations will each exceed 100 individuals, and that all populations will be "self-sustaining" for a decade prior to downlisting (CWS & USFWS 2007). Criterion 1 also specifies "a minimum of 40 productive pairs in the AWBP" and >25 breeding pairs in each of two reintroduced populations. Alternative criterion "A" suggests that "if only one additional wild self-sustaining population is reestablished" then the AWBP needs to exceed 400 individuals, including 100 productive pairs, and the reintroduced population "must remain above 120 individuals" with a minimum of 30 breeding pairs (CWS & USFWS 2007). This scenario similarly requires both populations to be "self-sustaining" for ≥10 years before downlisting. Finally, alternative criterion "B" suggests that "if establishment of second and third wild [and] self-sustaining populations is not [yet] successful," the AWBP will need to reach ≥1,000 individuals, including ≥250 breeding pairs, and be self-sustaining at that level for ≥10 years to allow for downlisting (CWS & USFWS 2007). Additionally, the "Memorandum of Understanding on Conservation of Whooping Cranes" between the U.S. and Canada includes reaching ≥1,000 individuals in the AWBP as a primary goal, which would provide more resilience for this population to catastrophic events and reach a population level where genetic diversity should be more sustainable in the long term (CWS & USFWS 2007, Pérez-Pereira et al. 2022). Research indicates that reintroduced populations are currently not self-sustaining, having high mortality rates and low recruitment rates compared to the AWBP (LDWF 2021, 2022; Thompson et al. 2022). Populations have been sustained through regular supplementation with captive-reared WHCRs (USFWS 2020a, LDWF 2021, 2022; Thompson et al. 2022). Given the lack of current sustainability in reintroduced

populations, criterion "B" should be met before downlisting proceeds, but the AWBP is still ~46% below that population objective. If the internationally agreed upon downlisting criteria have not been objectively met, what is the current justification for downlisting?

One argument made by USFWS personnel is that downlisting criteria "represent non-binding guidelines" and that downlisting actions depend upon "a contextual interpretation of the respective definitions of 'endangered' and 'threatened'" (Wade Harrell, Billy Brooks, Janess Vartanian, Whooping Crane Recovery Coordinators, personal communications). The term "'endangered species' means any species which is in danger of extinction throughout all or a significant portion of its range…" and the term "'threatened species' means any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (USFWS 1973). The ESA has been widely criticized for vague language including coarsely defined concepts that allow for a wide interpretation of biological information and therefore high variability in listing determinations (Doak et al. 2015, Lind-Riehl et al. 2016). For example, the terms "endangered" and "threatened" are based on risk assessment but include no objective guidance on what constitutes an acceptable or unacceptable risk of extinction (e.g., no time horizon for risk to occur, etc.; Woods and Morey 2008, Doak et al. 2015). Similarly, despite attempts to categorically clarify what "a significant portion" of a species' range means as a "contribution…so important that…[without it] the species would be in danger of extinction", the language gives wide latitude to USFWS personnel regarding ESA policy decisions (Carroll et al. 2010; USFWS 2011, 2014; Doak et al. 2015). The USFWS and the National Marine Fisheries Service have regularly revised guidance documents to improve implementation, but execution has arguably remained relatively subjective (NMFS 2010; USFWS 2011, 2014; Doak et al. 2015; Lind- Riehl et al. 2016).

Threat factor assessment should also be considered regarding downlisting decisions and represents a major way to evaluate species status and extinction risk. The ESA requires species to be evaluated for listing based on five threat factors: "(A) The present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; and (E) other natural or manmade factors affecting its continued existence" (USFWS 1973, Doak et al. 2015). Court rulings and subsequent interpretations thereof indicate species should only be removed from the ESA list when initial threat factors no longer pose a significant extinction risk and that recovery plans should subsequently consider all threat factors that led to listing and assess the degree to which they have been mitigated (Friedman 1995, NMFS 2010, Doak et al. 2015). Additionally, the USFWS considers the state of the extant populations in terms of number, abundance trends, and connectivity during Species Status Assessments (SSA), which represent a biological risk assessment conducted every ~5 years for listed species (USFWS 2016).

The SSA focuses on three conceptual categories to evaluate species' status that consider threat factors in addition to population factors, these evaluative frames include "representation", "resilience", and "redundancy" (USFWS 2016). *Representation* broadly refers to the current distribution of the species relative to its past reference ecological settings. Essentially, how does the species' current condition reflect their historic genetic, geographic, and life history variation (USFWS 2016). The USFWS (2016) also considers species' potential *resilience* to stochastic disturbances by virtue of its current population size, growth rates, and connectivity, as well as habitat quality. Finally, the USFWS (2016) considers the *redundancy* of extant populations,

which allows a species to withstand catastrophic events by having multiple sustainable and resilient populations throughout the species' range.

To determine if downlisting the WHCR under the ESA is warranted per the existing evaluative criteria, however equivocal, we examine the current status of the WHCR through the lens of ESA threat factors and the USFWS's SSA framework (USFWS 1973, 2016). We accomplish this by assessing the best available and most up-to-date information regarding populations and threats from published literature and primary data sources. We also examine the potential downlisting of the WHCR through the lens of other avian downlisting actions to determine if it is in line with similar cases from a population management perspective. Finally, we take a critical look at implementation of the ESA considering this metadata analysis and propose more standardized assessments for populations.

Methods

Population Trends

We revisited population trends for the AWBP, EMP, and LNMP using the most up-to-date and comprehensive data sources available (CWS and USFWS 2007, USFWS 2020a, LDWF 2021, 2022; Butler et al. 2022, Szyszkoski 2022, Thompson et al. 2022, Thompson 2022). We used ordinary least squares (OLS) linear regression models to examine trends for each population using the "stats" package in R version 4.0.2 (R Core Team 2020). We evaluated multiple functional forms (exponential, linear, and quadratic; See Rossiter 2016) of each abundance-by-year bivariate relationship as population trends are often non-linear (Clark and Luis 2020). Log-transformed parameter estimates associated with exponential models were transformed to percent change per year following Benoit (2011).

Species Relative Abundance

Having a smaller population size compared to species with similar life histories can be indicative of relative extinction risk (Pimm et al. 1993, O'Grady et al. 2006). Therefore, we examined the total abundance of wild WHCRs relative to other species of cranes in the world to better understand the species' relative resilience. We did not consider the abundance of captive populations for any crane species in this analysis. Abundance estimates came from ICF (2022), and confidence intervals were developed considering multiple species-specific sources (BLI 2022, ICF 2022, Caven et al. 2020b, Butler et al. 2022; Table 1). We examine WHCR abundance as a percentage of the number of cranes in the world and relative to other vulnerable crane species globally.

Whooping Crane Threat Assessment

We classified the major threats to WHCRs using impact categories derived from the risk assessment literature (Duijm 2015, Mamuji and Etkin 2019). Impact categories included "catastrophic" (significant irreversible population or critical habitat impacts), "critical" (significant population or critical habitat impacts), "marginal" (moderate population or critical habitat impacts), "minor" (minimal population or critical habitat impacts), and "negligible" (impacts to population or critical habitat sub-measurable in most cases) (Duijim 2015, Mamuji and Etkin 2019). Impacts were assessed at the level of threat (e.g., habitat loss) drivers (e.g., agricultural expansion) given their differential contributions to overall threat magnitude (e.g., habitat loss due to agricultural expansion vs. suburbanization). Drivers could promote one or more threats per our analysis (e.g., climate change drives both habitat loss and extreme environmental conditions). Given the challenges of quantifying the probability of risk occurrence, even categorically for some drivers (e.g., powerlines; USFWS 2019), we opted to assess the trend in risk probability. Trend categories included "increasing" (positive change in

probability of occurrence over time), "decreasing" (negative), stable (no apparent trend), and "mixed" (driver trends varied throughout portions of the population's range). For example, though it is clearly challenging to estimate the probability of risk occurrence related to powerline collisions (USFWS 2019), we have a good idea of the ultimate impact (i.e., WHCR mortalities have been documented from powerline collisions with moderate frequency; Stehn and Wassenich 2008; Yaw et al. 2020; Pearse et al. 2021). We also know that the spatial footprint of energy infrastructure including transmission lines is rapidly expanding throughout the central flyway and beyond (Smith and Dwyer 2016). Aerial collisions were therefore classified as of *marginal* but *increasing* risk to the AWBP during migration in our analyses. Threats were categorized both thematically (e.g., disease) and per ESA threat factors (A – E; USFWS 1973) for the LNMP, EMP, and AWBP of WHCRs.

Avian Populations at Downlisting

We completed a metadata analysis examining how WHCRs current population compared to other avian species that have been downlisted from "endangered" to "threatened" status as well as from "endangered" to "delisted" status given the relatively small sample size of cases. Examining these differential status changes should also provide some insight into the consistency with which population sizes are considered across listing decisions. We used the USFWS's (2022) "ECOS" (Environmental Conservation Online System) to develop a list of species that had been downlisted or delisted from an endangered status. We started with the "Reclassified Species" and the "Delisted Species" reports provided by the site (See "Listed Species Reports"). We then removed all non-avian species and then any cases related to threatened species up-listing or delisting. We also removed any records from species that were delisted because of extinction. To estimate the populations at listing and downlisting we undertook an intensive

literature review including 51 articles, reports, or notices in the Federal Register (See "Appendix A. Literature Cited"). We calculated a range of summary statistics for populations of 17 species assessed at the time of listing and downlisting/delisting under the ESA, including mean, standard deviation, standard error, 95% confidence interval, minimum, and maximum population values. Mean values for avian populations at downlisting and delisting from an endangered status were compared using a Welch's two-sample two-way t-tests for unequal variance using program R (Mangiafico 2015, R Core Team 2020).

Listing and Delisting Trends

We examined species listing and delisting trends under the ESA using Generalized Linear Models with a Poisson distribution using the "stats" package in program R (Nelder and Wedderburn 1972, R Core Team 2020) with data from the USFWS (2022). We evaluated multiple functional forms (exponential, linear, and quadratic) of each regression model as trends in listing and delisting may be non-linear (Rossiter 2016). We compared models using Aldrich-Nelson pseudo-R^2 with a Veall-Zimmermann correction, as it is a robust estimator of model fit comparable to a traditional R^2 value for OLS regression (Smith and McKenna 2013) using the "DescTools" package in R (Signorell 2022). We report the results from the top model per pseudo-R^2 values.

Results

Population Trends

The AWBP numbered 18 individuals in 1938 and did not officially surpass >40 individuals until 1964. Growth has steadily improved in recent decades and the population reached a point estimate of 543 individuals (95% C.I. = 427 – 782) in 2021. Population estimation methods were changed in 2011, incorporating uncertainty. Abundance trends in the

AWBP, across all data sources from 1938-2022, best fit an exponential growth model (B= 4.07e-02±7.70e-04, p<0.001, $R^2_{adj.}$ = 0.97). This equates to an estimated annual growth rate of 4.08–4.24% per year (±SE) (Figure 1).

The LNMP was established in 2011 with 10 individuals and currently numbers an estimated 77 individuals (as of fall 2022). The population has been regularly supplemented with reintroduced birds (R = 10–27 annually from 2010–2018; See USFWS 2020a). Trends in the LNMP best fit a linear regression model and indicate the population is growing at a rate of about 6.6 birds per year (B= 6.57±0.43, p<0.001, $R^2_{adj.}$ = 0.95) (Figure 1).

The EMP was established with 6 individuals in 2001, numbers increased steadily as a result of consistent population supplementation until 2012, when the population reached an estimated size of 107 individuals. However, for the last 10 years the population has steadily declined and was estimated at 76 individuals in the fall of 2022. Annual trends in the EMP best fit a quadratic model (B^1±SE^1= 1.88±0.28, p<0.001; B^2±SE^2= -2.08±0.28, p< 0.001; $R^2_{adj.}$ = 0.82). Separating the data at the inflection point indicates that from 2001-2011 the population increased at a rate (B) of 9.65±0.54 individuals per year (p<0.001, $R^2_{adj.}$ = 0.97) and that from 2012-2022 the population decreased at a rate (B) of -3.31±0.33 WHCRs per year (p<0.001, $R^2_{adj.}$ = 0.91) (Figure 1). Annual supplementation with captive reared birds ranged from 11–21 individuals per year from 2010–2018 but 0–5 from 2018–2022 (See Thompson et al. 2022, Thompson 2022).

Species Relative Abundance

WHCRs are the rarest of the fifteen crane species in the world by a relatively large margin (Table 1). Combining data for all extant and non-captive WHCR populations, including the EMP, LNMP, Florida Non-migratory Population (FNMP), and the AWBP, there are an

estimated 702 WHCRs persisting in the wild as of late 2022 (est. *R* = 586-941; Table 1). The next rarest crane is the Red-crowned Crane (*Grus japonensis*) with an estimated population of 4,000 individuals (est. *R* = 3,800-4,200) across East Asia, which is listed as "Vulnerable" by the IUCN (Table 1). The third rarest crane is the Siberian Crane (*Leucogeranus leucogeranus*), which numbers an estimated 5,500 (est. *R* = 4,800-6,200). It is listed as "Critically Endangered" per the IUCN in large part because of threats to habitat conditions throughout their migration route and wintering grounds, and direct poaching impacts on western populations (See Archibald et al. 2020; Table 1). WHCRs make up just 0.03% of the estimated 2.71 million cranes in the world (Gruidae spp.; 2,711,052±412,039; Table 1). Ultimately, wild WHCRs total only 17.6% of Red-crowned Crane and 12.8% of Siberian Crane populations, respectively.

Whooping Crane Threat Assessment

We noted five major threats to WHCR populations including habitat loss, environmental conditions, physical harm, disease, and pollution resulting from 19 different drivers (e.g., climate change, chemical spills, woody encroachment; Appendix B). Nearly half (47%) of the noted drivers promoted habitat loss, 37% posed a risk of direct physical harm to WHCRs, 26% were associated with the threat of disease, and 21% promoted undesirable environmental conditions that could directly or indirectly threaten WHCRs (Appendix B). An equal number of drivers posed a direct *or* an indirect threat to WHCR recovery (37% each). Additionally, 26% of drivers posed both a direct *and* indirect threat. Fifty eight percent of drivers impacted threat factor A (present or threatened destruction of habitat), 42% impacted threat factor C (disease and/or predation), 32% influenced threat factor E (other natural or manmade factors), 11% concerned threat factor D (adequacy of legal regulations), 5% of drivers contributed to threat factor B (overutilization).

Across populations and important ranges about 3% of drivers posed a catastrophic threat to WHCRs, 19% a critical threat, 30% a marginal threat, 24% a minor threat, and 25% a negligible threat. Catastrophic threats were only noted for the AWBP on their wintering grounds (n = 2; 11%) and throughout their migration corridor (n = 1; 5%; Figure 2). Drivers posed the most critical threats to the AWBP migration corridor (32%) and the LNMP (32%). Drivers presented mostly marginal threats within the EMP migration corridor and wintering grounds (53%; Figure 2). Twenty-one to 32% of drivers constituted a minor threat throughout populations and ranges, with the exception of the AWBP migration corridor, where only 5% of drivers posed a minor threat. The plurality of threat drivers comprised a negligible threat on the AWBP breeding grounds (47%) while only 5% of drivers constituted a negligible threat on the EMP wintering and migration range (Figure 2).

Sixteen of 19 drivers (84%) for the AWBP and 12 of 19 for both the EMP and LNMP (63%) posed an increasing threat (Appendix B). In aggregate, 70% constituted an increasing threat, 25% demonstrated a stable trend, 4% of drivers posed a decreasing threat to WHCRs, and about 2% showed regionally mixed trends for a population (Appendix B). Our ten-year forecasts largely indicated a continuation of current threat driver trends (Appendix B). Across populations 79% of drivers pertinent to threat factor A (present or threatened destruction of habitat) had a categorically increasing trend while 15% demonstrated a stable trend. Shootings are currently the predominant driver for threat factor B (overutilization), and recent data indicates an absolute increase in the number of shooting events per year across two-thirds (67%) of populations in recent decades (Appendix C, Table 2, Figure 4). Drivers related to threat factor C (disease and/or predation) demonstrated a predominantly increasing trend (58%), but a substantial number of these drivers demonstrated a stable trend as well (38%). Drivers related to threat factor D

(adequacy of legal regulations) demonstrated a range of trends including increasing (50%), stable (33%), and decreasing (17%). Finally, drivers associated with threat factor E (other natural or manmade factors) demonstrated an overwhelmingly increasing trend (83%). Our analysis indicates that the majority of threats facing WHCRs have not been ameliorated but continue to increase [or intensify].

Avian Populations at Downlisting

We documented 17 avian species that have been moved from a classification of endangered to threatened or directly delisted for reasons unrelated to extinction (Appendix A). Populations at listing had a mean of approximately 2,900 (μ = 2,938, σ = 4,296, *SE* = 1,042, 95% CI = 2,042, *R* = 32–15,000) for species that have since been downlisted or delisted from an endangered status. About 59% of those species assessed had higher estimated abundance in the wild when they were listed than the WHCR's current abundance. Populations at downlisting (or delisting) from an endangered status had a mean of approximately 15,600 (μ = 15,587, σ = 18,929, *SE* = 4,591, 95% CI = 8,998, *R* = 500– 83,550). Only one avian species was downlisted from an endangered status with an estimated population of <3,000 individuals. Ten species assessed here were reclassified from endangered to threatened (regardless of ultimate delisting) and 7 were delisted directly from an endangered status. Interestingly, a species' estimated population at the time of downlisting to threatened status (μ = 18,053, σ = 23,749, *SE* = 7,510, *R* = 3,252 – 83,550) and delisting directly from an endangered status (μ = 12,064, σ = 12,023, *SE* = 4,544, *R* = 500–28,230) were not statistically different via a Welch's t-test (t = 0.68, p = 0.51).

Listing and Delisting Trends

From 1967 to 2022 there were an average of 29.9±4.0 (±SE) species listed to the ESA annually (Figure 3). Listings peaked in 1994 at 128 and there were occasional years with no

species added to the list, mostly between 1968 and 1974, again in 2007, and in recent years (2020-2021). Annual listings best fit a quadratic curve over time (pseudo-R^2 = 0.69) with listings at their highest average annual rate from the mid-1980s through the 1990s. However, listings were elevated for a short period between 2010 and 2016, exceeding the annual average in 5 of 7 years (Figure 3). Nonetheless, listings were down markedly from 2017 to 2022, averaging only 3.2±1.3 per year. Delisting of species from the Endangered Species List best fit a Poisson model with a log-link function (pseudo-R^2 = 0.68) demonstrating a steady proportional increase in delistings over time with annual variation. There were only 1.6±0.3 delisting actions per year from 1967 to 2022. However, from 2016 to 2022 there were an average of 5.7±1.8 delistings per year with a maximum of 16 in 2016. In absolute terms delisting has only eclipsed listing on an annual basis on a handful of occasions beginning in 2003, but it has become more common in recent years (continual from 2020 to 2022).

Discussion

Our research indicates that WHCRs are facing an intensification of most known threat drivers and overarching threats across populations and important ranges (>70% of threat drivers pose an increasing risk; Appendix B). This may be especially true for the AWBP (Appendix B). Similarly, across populations and ranges, >51% of threat drivers pose ≥marginal (i.e., "moderate") risk to WHCR populations or their critical habitats. Concurrently, the population is still biologically small compared to other crane species and most avian [or vertebrate] species of conservation concern (Frankham et al. 2002, 2014; Appendix A; Table 1). WHCR downlisting would represent an outlier in terms of population management actions under the ESA regarding avian species (Appendix A). Additionally, the downlisting appears objectively unwarranted when evaluating ESA threat factors and their degree of amelioration, which recovery plans and

listing decisions are legally directed to consider (Friedman 1995, NMFS 2010, Doak et al. 2015). Proposed downlisting for the WHCR before recovery plan population criteria have been met and while threat drivers are ostensibly increasing highlights the inconsistency noted across listing actions per the published literature (Woods and Morey 2008, Doak et al. 2015, Lind- Riehl et al. 2016). The high variability in listing and delisting frequencies over the history of the ESA demonstrates that shifts in these rates are likely responsive to non-biological factors such as changes in agency culture and politics (Smith 2016).

Present or Threatened Destruction of Habitat

The highest proportion of drivers impacted threat factor A ("destruction of habitat"; 58%) and the vast majority of those (79%) demonstrated an increasing trend across populations and important ranges, particularly for the AWBP (100% posed an increasing threat). Habitat loss is a widespread issue, but the major drivers differ by region. For instance, agricultural expansion posed a critical and increasing threat throughout the AWBP migration corridor, but the impact was comparatively minor throughout the rest of the WHCR's range (Appendix B). Comparatively, extractive industry development posed a critical threat to habitat quality at the AWBP breeding grounds but resulted in a $\leq$marginal threat throughout the rest of the WHCR's range (Appendix B). This is largely a result of the Athabasca Oil Sands (i.e., "tar sands") mining just south of the breeding grounds, which is an area hydrologically connected to Wood Buffalo National Park (Murphy et al. 2014, Bidwell et al. 2017, Vannini and Vannini 2019, Roberts et al. 2022).

Roosting stopover habitat availability is limited and tenuous in terms of quality but is required to maintain connectivity and nutrition for the AWBP during migration (Stahlecker 1992, Pearse et al. 2020, Caven et al. 2022a). Much of the habitat that remains is wholly reliant

on coercion - intense management is required to keep remaining stopover sites in a form that resembles suitable roosting habitat (Kessler et al. 2011); many self-organizing processes have been lost therefore the future status of these habitats is uncertain (Caven et al. 2022b). Any interruption of management intervention will cause stopover habitat quality to rapidly decline in several locations (Kessler et al. 2011). McIntyre et al. (2018) found that the majority of small (≤10 ha) playas (~85%) in northern Texas have lost their ability to pond water in association with adjacent cropland increases. Similarly, Verheijen et al. (2018) documented a more than 90% decrease in the number of functioning wetlands in the Rainwater Basin ecoregion of Nebraska since European settlement. The conversion of wetlands and lowland grasslands used by WHCRs to row crop agriculture continues throughout the migration corridor with high rates (-1.0% to -5.4% annually) in the Northern Great Plains where natural herbaceous lowlands remain [for now] relatively abundant (Johnson et al. 2012, Johnston 2013, Wright and Wimberly 2013).

Climate change presents a catastrophic threat to crucial AWBP wintering habitat, while posing a critical threat to habitat throughout the rest of the AWBP's and LNMP's respective ranges (Appendix B). Forecasts indicate the EMP may be less directly impacted by wetland loss associated with climate change as the range remains within a humid climate in most projections (Appendix B; Poff et al. 2002). Törnqvist et al. (2020) demonstrated that a large proportion of coastal marshes in Louisiana, within the LNMP's range, will likely be lost to climate change. This trend is exacerbated by a massive reduction in sediment loads, necessary to sustain marshes in the Mississippi Delta as a result of extensive water control infrastructure throughout the Mississippi River Basin (Kondolf et al. 2014, Törnqvist et al. 2020). Golden et al. (2022) demonstrates that the vast majority (~95%) of areas with >50% probability of crane use on the AWBP wintering grounds could be lost as a result of a 0.9-m sea level rise. Metzger et al. (2020)

suggests that as habitat is lost analogs will be created across increasing elevational gradients inland. However, much of the created habitat will fall outside of currently protected lands. At a 1-2-m sea level rise habitat availability would be reduced by about 19-44% across protected and unprotected lands per Metzger et al. (2020) considering the more aggressive development scenario presented. However, this model does not consider changes in vegetation characteristics (e.g., Black Mangrove (*Avicennia germinans*) expansion) or declining freshwater inflows associated with climate change that could further impact habitat availability and quality (e.g., Blue Crab (*Callinectes sapidus*) abundance; Chavez-Ramirez and Wehtje 2012).

Climate change is resulting in permafrost melt at the AWBP's breeding grounds, which is altering landscape characteristics and hydrological processes and could negatively impact habitat availability and quality regionally (Cheskey et al. 2011, Holsinger et al. 2019). The melting of permafrost-supported wetlands also has the potential to release massive amounts of carbon dioxide and methane into the atmosphere creating a positive feedback loop that promotes further warming and ecosystem transition (Turetsky et al. 2020). Climate change similarly threatens wetland stopover habitat availability across the AWBP migration corridor through the Great Plains as drought periods and evaporative losses will likely increase over the coming decades while water sources such as mountain snowpack will be diminished (Chavez-Ramirez and Wehtje 2012, McIntyre et al. 2014, Fassnacht et al. 2018). The threat climate change poses to wetland habitat quality and availability is compounded by poor water management in the central and southern Great Plains (Perry et al. 2012).

Surface and groundwater overappropriation present a catastrophic threat to critical habitat availability and quality across the AWBP wintering grounds and migration corridor as instream flows into estuaries are reduced and surface water availability is diminished at vital stopover

locations (Sandford 2015, Caven et al. 2019a). This threat is comparatively minor across the rest of the species respective seasonal ranges (Atkins et al. 2017). Additional and considerable drivers of habitat loss in major portions of the WHCR's remnant and reintroduced ranges included invasive species (e.g., Kessler et al. 2011, Wheeler and Ding 2014), woody encroachment into wetlands (e.g., Giri and Long 2016, Caven et al. 2022b), suburbanization (i.e., exurban development, urban sprawl; Homer et al. 2020), and alternative energy infrastructure (e.g., Ellis et al. 2022).

Overutilization

Shootings remain the predominant driver relating to the overutilization threat factor. Shooting can either be intentional (i.e., poaching) or unintentional, which usual involves misidentification with game species during permitted hunting activities; the former is a much more common source of mortality than the latter (Condon et al. 2019). Following the federal listing and protection of WHCRs in 1967, 49 Whooping Cranes are known to have been killed as a result of 34 separate shooting incidents (Appendix C). Shootings per year have increased over the last decade in absolute terms for the AWBP (0.4 up to 0.7 per year) and the LNMP (0.3 up to 1.6 per year) while remaining stable or decreasing slightly for the EMP (0.9 down to 0.7 per year; Table 2; Appendix C). We considered shootings as a driver that poses a negligible to marginal threat throughout portions of the AWBP's range and the EMP's breeding grounds. However, shootings remain a critical threat throughout the EMP's migration corridor and wintering grounds as well as within the LNMP's range, especially considering the respective populations' relatively small sizes. The EMP and the LNMP account for about 22% of all WHCRs but accounted for 73% of documented shooting deaths during the past 10 years (Table 2, Appendix C). About 72% of WHCR deaths by gunshot in all populations were documented as

intentional killings, highlighting the importance of effective outreach and education campaigns in key portions of the species' range where shooting risks are elevated as well as strong penalties and other judicial deterrents (Condon et al. 2019).

The differentially high rate of shooting deaths across reintroduced populations may be in part due to local communities' unfamiliarity with a newly reestablishing species. However, it is also documented that costume-reared WHCRs [which only exist in reintroduced populations] are less sensitive to human use areas than wild-reared individuals (Pickens et al. 2017, Condon et al. 2019). Nonetheless, we may simply be documenting shooting incidents more readily in reintroduced populations because a greater proportion of the population is banded and they are more heavily monitored, which suggests shootings in the AWBP may be underreported (Condon et al. 2019). Across populations a plurality of mortality causes generally go undetermined and therefore the impact from particular threats is underestimated by considering raw mortality numbers (Pearse et al. 2019, Thompson et al. 2022). Shootings accounted for 10.8% of confirmed mortalities from 2001-2010 and 10.5% from 2011-2021 in the EMP (Urbanek et al. 2014, Thompson et al. 2022). In the LNMP, shootings accounted for 26.3% of mortalities with a known cause from 2011-2022 (LDWF 2021, 2022). Finally, in the AWBP, shootings accounted for 22% of mortalities with a known cause from 1967-2011 (Stehn and Haralson-Strobel 2016). Data indicates that young WHCRs are disproportionately shot, which has a compound effect on population growth as they often perish before they are recruited into the breeding population and replace themselves (Gil-Weir et al. 2012; Figure 4; Appendix C).

Disease and Predation

The second highest proportion of drivers impacted threat factor C ("disease and/or predation"; 42%). Most of these threat drivers demonstrated an increasing trend (58%) across

populations and important ranges but a fair number (38%) also demonstrated a stable trend. Diseases in WHCRs can result from a number of etiologies including viral, fungal, parasitic, and environmental toxins and may be both infectious and non-infectious (Snyder et al. 1991, Olsen et al. 2019, Hartup 2019a, Hartup and Phillips 2022). Disease impacts or transmissions can be exacerbated by a number of issues such as poor genetic diversity (King and Lively 2012, Hartup and Phillips 2022), proximity to poultry production facilities (i.e., "concentrated animal feeding operations", CAFO; Moore et al. 2021, Lee et al. 2021), dense concentrations of waterbirds (often as a consequence of habitat loss; Caven et al. 2020a, Yin et al. 2022), and environmental contaminant loads (i.e., "pollution"; Yaw et al. 2020, Hartup et al. 2021). Disease agents in WHCRs include Eastern Equine Encephalitis (Dein et al. 1986, Olsen et al. 2019), West Nile Virus (Hartup 2008, 2016), Infectious Bursal Disease (Spalding et al. 2008, Hartup 2016, Hartup 2019a), Aspergillosis (Keller and Hartup 2013, Hartup and Phillips 2022), Avian Tuberculosis (Snyder et al. 1991), Avian Cholera (Kauffeld 1987), Coccidiosis (Bertram et al. 2015, Olsen et al. 2019), lead toxicity (Yaw et al., 2020), mercury toxicity (Hartup et al. 2021), *Fusarium* spp. mycotoxin exposure (Olsen et al. 1995, 2019), and avian influenza (i.e., HPAI; CMS FAO 2022, Stokstad 2022).

Disease related mortality represented about 8 – 25% of determined mortalities from across the FNMP, the EMP, and the AWBP, but cause of mortality was undetermined in 25 – 76% of cases in those data (M.G. Spalding – personal communication, Pearce et al. 2019, Yaw et al. 2020). However, estimates of disease prevalence and resulting mortality impacts in wild avian populations are complicated by several factors that generally drive our estimates of disease-related mortality downward (Friend et al. 1999, Ryser-Degiorgis 2013). Several diseases may differentially affect young juveniles and therefore impacts may often go undetected given the

high mortality rate observed at that life stage from a myriad of other factors such as predation (King et al. 2013, Olsen et al. 2019); this may be especially true for the AWBP considering its remote breeding grounds (Hartup 2019a). Additional sources of downward bias in disease-related mortality estimates include the loss of carcasses previous to evaluation, inconclusive pathology findings due to carcass degradation prior to recovery, scavenging or predation events that disguise underlying disease, poor interpretation of subclinical disease states, and incomplete testing of carcasses (especially for toxic residue) (Friend et al. 1999, Ryser-Degiorgis 2013, Yaw et al. 2020). Considering these factors, we determined about 38% of drivers pertinent to threat factor C posed a marginal threat, while 38% posed a minor threat per our assessment. Ultimately, we felt only dense waterbird concentrations and HPAI, which compound each other, posed critical threats to WHCRs in terms of disease, particularly within the AWBP's wintering grounds and migration corridor as well as throughout the EMP's range (Appendix B).

Avian influenza (i.e., HPAI), especially the H5N1 Eurasian variant that arrived in North America in late 2021, is now an emerging threat to cranes worldwide (Stokstad 2022). Since October 2021, cranes of several species, including Demoiselle (*Anthropoides virgo*), Eurasian (*G. grus*), Hooded (*G. monacha*), White-naped (*G. vipio*), Red-crowned (*G. japonensis*), and Sandhill Cranes have experienced individual cases or outbreaks of disease in concentrated winter flocks or migrating throughout East and South Asia, the Middle East, and North America. The largest HPAI-driven mortality event to date involving Gruidae included 8,000 Eurasian Crane mortalities in the Hula Valley in Israel in December of 2021 (CMS FAO 2022). In November and December of 2022, more than 1,000 Hooded Cranes and White-naped Cranes were found dead at a major wintering area near Izumi, Japan (Yuko Haraguchi, Crane Park Izumi – personal communication; Kiyoaki Ozaki, Deputy Director General, Yamashina Institute for Ornithology –

personal communication). It is notable that supplemental grain feeding operations were ongoing at both locations which likely increased the concentration of cranes (Maeda et al. 2001, Shanni et al. 2018). WHCRs have similarly been documented in increased concentrations at automated tripod game feeders that generally dispense corn on their wintering grounds in Coastal Texas (Tiegs 2017).

Mortalities in some other waterbird species have been even greater, proportionally and in absolute terms, including about 20% of the regional population (8,000–10,000 mortalities) of Barnacle Geese (*Branta leucopsis*) in Scotland and >40% of the southeast European population (>2,400 mortalities) of Dalmatian Pelicans (*Pelecanus crispus*) (Alexandrou et al. 2022, CMS FAO 2022). The concentration of WHCRs during migration in Saskatchewan (Johns et al. 1997), at the Platte River (Baasch et al. *In Press*), and at Quivira and Salt Plains NWRs (Caven et al. 2020a), as well as on the wintering grounds in TX could potentially result in widespread transmission of HPAI and subsequent mortality in the AWBP (Ramey et al. 2021). Transmission risks are similarly high at regularly utilized stopover and wintering areas for the EMP including Goose Pond Fish and Wildlife Area, Indiana, and Wheeler National Wildlife Refuge, Alabama, especially where WHCRs cooccur with high densities of waterfowl, which can serve as a vector (Cantrell and Wang 2018, Ramey et al. 2021). The threat of HPAI needs to be closely monitored and appropriate mitigation efforts should be incorporated into site management plans for important use areas. Efforts to redistribute concentrations by providing more wetland availability through targeted restoration could provide a mechanism to limit disease transmission generally, including for HPAI (Caven et al. 2019b, Caven et al. 2020a). Additionally, efforts to limit artificial supplemental feeding could reduce disease transmission risks.

WHCRs are threatened by a diversity of predators depending on an individual's age, life stage, and/or region. Likely and confirmed predators include the Canada Lynx (*Lynx canadensis*; Butler et al. 2017), Bobcat (*L. rufus*; Cole et al. 2009), Gray Wolf (*Canis lupus*; Kuyt et al. 1981), Coyote (*C. latrans*; Thompson et al. 2022), Red Fox (*Vulpes vulpes*; Bergeson et al. 2001b), American Mink (*Mustela* [*Neovison*] *vison*; Ivey and Scheuering 1997, Boyce et al. 2005), American Black Bear (*Ursus americanus*; Kuyt et al. 1981), Raccoon (*Procyon lotor*; Urbanek 2015), American Alligator (*Alligator mississippiensis*; Thompson et al. 2022), Bald Eagle (*Haliaeetus leucocephalus*; Rabbe et al. 2019), Golden Eagle (*Aquila chrysaetos*; Ellis et a. 1999), Common Raven (*Corvus corax*; Bergeson et al. 2001b), and Great Horned Owl (*Bubo virginianus*; Stehn and Haralson-Strobel 2014). We considered the threat from predation to be stable or increasing regionally based on predator abundance trends (e.g., Laliberte and Ripple 2004, Roberts and Crimmins 2010, USFWS 2020b).

Predation was the leading cause of mortality for the AWBP, EMP, and FNMP, often comprising a majority [or at least plurality] of determined causes of death (Pearse et al. 2019, Yaw et al. 2020, Thompson et al. 2022, M.G. Spalding – personal communication). However, in the LNMP, impact trauma (e.g., collisions with powerlines, fences, and vehicles; 33%) slightly outpaced predation (30%) as the most frequently documented cause of mortality, while shootings (25%) were proportionally higher compared to other populations as well (LDWF 2022). It is possible that we overestimate the prevalence of predation as a cause of mortality because its apparent physical indicators are relatively visible on carcasses and are also challenging to distinguish from scavenging events (Friend et al. 1999, Stallknecht 2007, Ryser-Degiorgis 2013, Cristescu et al. 2022). Furthermore, underlying physical conditions such as disease can predispose cranes to depredation and often go undetected (Friend et al. 1999, Stallknecht 2007,

Ryser-Degiorgis 2013). Despite its frequency of occurrence, we generally considered predation a marginal threat throughout the AWBP's and LNMP's respective ranges as it has served as an ongoing source of background mortality for WHCR populations throughout their evolution and other novel drivers appear to pose more critical long-term threats to these populations (Frid and Dill 2002, Moseby et al. 2016; Appendix B). However, it does appear that predation is a major limiting factor for the EMP (Thompson et al. 2022). Rates of predation for all age classes appear to surpass sustainable levels; this may be especially true on the breeding grounds where a large proportion of pre-fledged chicks are lost, ostensibly to predation, within the first 20 days of life (King et al. 2013, Thompson et al. 2022).

Adequacy of Legal Regulations

Only 2 of 11 drivers pertained to threat factor D (adequacy of legal regulations). These included inadequate regulation regarding surface and groundwater appropriations as well as extractive industry development (Appendix B). Across populations and important ranges, these drivers presented an increasing threat to WHCRs in 50% of cases and a stable or decreasing trend in 50% of cases. However, trends separated strongly by population and region. Inadequate water or extractive industry regulations (i.e., "drivers") posed an increasing threat in 100% of cases pertaining to the AWBP and only in 25% of cases relating to reintroduced populations (Appendix B). A similar theme was observed considering the potential impact of drivers, as 50% comprised a catastrophic or critical threat to the AWBP while 0% of these policy-related drivers presented more than a marginal threat to reintroduced populations (Appendix B). These patterns are largely a reflection of regional trends in agricultural and extractive industry development as well as wide variation in regional laws governing such actions. For instance, oil extraction has declined in much of the EMP's range (Berg 2022), while widespread mining and poorly

regulated distribution (i.e., pipelines not designed to withstand bitumen-laden oil; Swift et al. 2011) are increasing throughout the AWBP's range, which could expose WHCRs to oil spills or open-pit oil sands excavations that contain potentially harmful pollutants (Swift et al. 2011, Murphy et al. 2014, Allred et al. 2015, Roberts et al. 2022). Similarly, surface and groundwater resources remain relatively abundant within the EMP and LNMP ranges (e.g., Atkins et al. 2017). However, throughout the Central Flyway, particularly the AWBP's wintering grounds and migratory corridor, additional surface water appropriations continue to be made despite many rivers being fully- or over-appropriated per hydrological analysis (Sandford 2015, Caven et al. 2019a). Western water laws are inadequate to meet the needs of endangered species in the era of climate change even when considering the legal protections afforded by the ESA (Benson 2004). Similarly, Jefferies (2012) contends that Canadian and American environmental regulations regarding unconventional sources of fossil fuels (e.g., Athabasca oil sands, Marcellus shale) are inadequate to safeguard freshwater resources, which are essential to both wildlife and human populations.

Other Natural or Manmade Factors

About 32% of drivers influenced threat factor E (other natural or manmade factors) and about 83% of them demonstrated an increasing trend. About 22% of these drivers posed a critical or catastrophic threat, 44% a marginal threat, and 33% a minor or negligible threat. Climate change represented the highest impact threat in this category because it not only poses an indirect threat in terms of habitat loss, as indicated in discussions regarding threat factor A, but it also alters environmental conditions which may negatively impact WHCR vital rates directly (Chavez-Ramirez and Wehtje 2012, Butler et al. 2017). Butler et al. (2017) suggests that changes in rainfall and seasonal temperatures associated with climate change, in conjunction with

variations in solar activity, may slow or reverse the AWBP's growth rate in the coming decades. Climate change also interacts with and exacerbates other natural and manmade threats. For instance, climate change will likely extend the hurricane season and make storms stronger, while concurrently generating sea level rises that will increase storm surge impacts (Walsh et al. 2016, Camelo et al. 2020). Additionally, in these contexts hurricanes have an increased potential to create coastal erosion and drive habitat losses (Camelo et al. 2020), which ultimately highlights the challenges associated with categorizing such an amorphous and pervasive threat such as climate change within standard policy frameworks. Hurricanes independently represent a substantial natural threat to WHCRs, particularly for the LNMP. Hurricane Katrina had a lasting negative impact on Mississippi Sandhill Crane (*G. c. pulla*) abundance and less intense hurricanes proved a temporary negative impact on this Sandhill Crane subspecies which maintains a small range in the Gulf Coast region (Woolley et al. 2022).

Manmade factors including extractive industry development (e.g., tar sands), alternative energy infrastructure (e.g., wind turbines), chemical spills (e.g., crude oil), and general power infrastructure (e.g., transmission lines) can pose both direct and indirect threats to WHCR populations (Swift et al. 2011, Murphy et al. 2014, Smith and Dwyer 2016, Ellis et al. 2022). Extractive industry development, particularly fossil fuel industry expansion poses a critical threat to WHCRs throughout significant portions of the species range. For instance, Athabasca oil sands development not only exposes WHCRs and other birds that stopover to harmful pollutants (Murphy et al. 2014), but the crude oil from the tar sands contains diluted bitumen which creates more friction in pipelines and increases the risks and scale of oil spills in the Great Plains (Swift et al. 2011, Murphy et al. 2014, Roberts et al. 2022). Moreover, off-shore oil extraction is

abundant along the Gulf Coast and a major spill could threaten the AWBP as well as the LNMP depending on the location of its occurrence (Burger 2017).

Within the "other natural or manmade" threat factors category, we only considered collisions with elevated infrastructure a critical threat for the LNMP, where impact trauma (much of it related to powerline collisions) currently represents a leading cause of mortality (LDWF 2022). However, this threat is projected to increase across the entire species' range and will actually be accelerated by a transition to alternative energy infrastructure in the coming decades (U.S. Department of Energy 2008, Jenkins et al. 2010, US Energy Information Administration 2015, Smith and Dwyer 2016). Collisions with anthropogenic infrastructure (e.g., powerlines) represent a significant cause of documented injury and mortality for many avian species including WHCRs and are recognized as a threat to the recovery of the species (CWS and USFWS 2007). WHCRs may be particularly vulnerable because large-bodied species with high wing loading and low maneuverability are susceptible to colliding with elevated obstacles while in flight (Smith and Dwyer 2016, Dwyer et al., 2019, Baasch et al., 2022), and species with small populations, delayed maturity, and long lifespans, can experience particularly adverse population-level effects due to interactions with energy infrastructure (CWS and USFWS 2007, Smith and Dwyer 2016, Pearse et al. 2021). Although WHCRs migrate at altitudes between 1,000 and 6,000 feet above the ground, they are vulnerable to collisions with structures during low-altitude flights at the beginning and end of migration bouts and as they traverse between roosting and foraging locations at stopover, breeding, and wintering areas in low-light conditions (USFWS 2009). Power line collisions are a documented source of mortality for 12 species of cranes (Dwyer et al. 2019). At least 46 WHCRs are documented to have died or been seriously injured by power lines since 1956; a majority of these collisions occurred in the experimental

introduced flocks (i.e., Grays Lake Population (GLP), FNMP, and EMP; Stehn and Wassenich 2008, USFWS 2019).

Most studies regarding potential interactions between WHCRs and energy infrastructure have focused on direct effects in areas where Sandhill Crane collisions are appreciable and WHCR collisions would have an elevated probability of occurrence (Brown et al. 1987, Wright et al. 2009, Hartup et al. 2010, Murphy et al. 2016, Dwyer et al. 2019, USFWS 2019, Baasch et al. 2022). While collisions are documented to occur throughout the range of both migratory and non-migratory crane populations (Stehn and Wassenich 2008, Cole et al. 2009, Hartup et al. 2010, Jenkins et al. 2010), there may be a greater collision risk where energy infrastructure intersects major flight paths or regions where flocks of birds frequently congregate (e.g., wetlands and rivers; Brown et al. 1987, Murphy et al. 2009, Smith and Dwyer 2016, Dwyer et al. 2019, Baasch et al. 2022). The biannual migration may be an especially dangerous period in terms of collision risk for the AWBP because of increased exposure to potentially novel hazards in unfamiliar areas (Brown et al. 1987, Lewis et al. 1992, CWS and USFWS 2007, Smith and Dwyer 2016, Baasch et al. 2022). However, due to its remoteness and the lower proportion of monitored individuals, collisions may be particularly underestimated in the AWBP migration corridor (Pearse et al. 2019). While the application of collision mitigation measures such as line markers (Morkill and Anderson 1991, Wright et al. 2009, Murphy et al. 2016), near-ultraviolet light (Dwyer et al. 2019, Baasch et al. 2022), and acoustic deterrents (Thady et al. 2022) on anthropogenic structures to increase their detectability to birds in flight are demonstrated to be effective, marking devices may be impractical except at significant roosting or stopover sites to prevent collisions (Hartup et al. 2010, Diamond and Hoogstad 2019). Additionally, costs and

logistics associated with purchasing, mounting, and maintaining near-ultraviolet lights to prevent nighttime collisions may be prohibitive to widespread future application (Baasch et al. 2022).

Representation

Based on our assessment of extant WHCR populations we concluded that representation in terms of WHCRs historic genetic, geographic, and life history variation remains limited. Population mean kinship is steadily increasing as retained genetic diversity is slowly decreasing in the captive population, despite both factors meeting acceptable thresholds per AZA standards (Boardman et al. 2021). Jones et al. (2010) found that alleles per locus ranged from 2-6 ($\bar{x}$ = 3.8) and mean heterozygosity ranged from 0.05-0.79 in an investigation of 14 microsatellite loci in 45 individual WHCRs (Jones et al. 2010). Jarvi et al. (2001) found that captive WHCRs have a considerably diminished number of alleles per locus and heterozygosity compared to Florida Sandhill Cranes (*G. c. pratensis*). Boardman et al. (2021) suggests that the captive WHCR population should retain 91.7% of their current genetic diversity over the next 100 years based on projections, but it is important to note that about two-thirds of WHCR genetic haplotypes were already lost following the species' near extinction and extreme population bottleneck (Glenn et al. 1999). Effective populations (N_e) of >1,000 individuals are generally needed to maintain long-term genetic fitness for vertebrate populations (Brook et al. 2006, Frankham et al. 2014, Pérez-Pereira et al. 2022). Boardman et al. (2021) estimates that N_e/N for the captive population is 0.52, indicating the effective population is about half the size of the total captive population. N_e can be estimated through genetic and/or demographic models depending on the amount of available information, however, it is generally significantly smaller than N (Wang et al. 2016). There is a strong need for a wide-reaching genetic assessment of the AWBP's effective population size, heterozygosity, and allelic richness to inform genetically sound delisting criteria.

From a population genetics management standpoint, the WHCR should likely not be downlisted until >1,000 individuals exist in the AWBP (Glenn et al. 1999, Jarvi et al. 2001, Brook et al. 2006, Frankham et al. 2014), regardless of progress in reintroduced populations, which to this point has been relatively modest (e.g., LDWF 2022, Thompson et al. 2022).

Geographic representation is also an important consideration of SSAs (USFWS 2016). As previously noted, the WHCR once had a broad geographical range and likely numbered in the tens of thousands from the Great Divide east to the Atlantic Coast and from the Northwest Territories of Canada to Central Mexico (Allen 1952, Austin et al. 2019). The AWBP apparently occupies the core of the WHCRs historic wintering range but ostensibly the most northwestern periphery of the species remnant breeding range (Allen 1952, Austin et al. 2019). The AWBP likely has a longer migration than most WHCRs historically had and probably experiences greater environmental variation throughout its range and annual cycle than historic analogs. A more typical annual cycle would have likely been breeding in the southern Prairie Potholes region of Iowa and wintering on the Chenier Plain of Louisiana (about a ~1,500 km migration as compared to the ~4,000 km journey for the AWBP; Allen 1952, Austin et al. 2019). The reintroduction of WHCRs into southwestern Louisiana at the White Lake area, which was the last location where nonmigratory WHCRs persisted, adds some geographical representation but may do more to restore important non-migratory life history variation for the species (CWS and USFWS 2007, LDWF 2022). However, this should not be considered truly additive to representation until the population is self-sustaining.

The EMP similarly has the potential to add life history and geographical representation if it becomes self-sustaining as well (Thompson et al. 2022). For instance, WHCR diet regionally appears to contain a variety of aquatic animal food items that are larger than those available to

WHCRs breeding near WBNP (Barzen et al. 2018a). The EMP breeding range exists just north of historic WHCR breeding densities in northern Iowa and the area apparently served as an occasional summering location but not necessarily breeding area prior to species extirpation (Allen 1952, Austin et al. 2019). The landscape of northern Iowa, where breeding densities may have once been highest, has ultimately been too transformed by extensive wetland drainage and subsequent loss to allow for reintroduction efforts there (Austin et al. 2019). However, Wisconsin has retained comparatively more wetland habitat, and therefore may provide some approximation of historic breeding in the region. Caven et al. (2020a) indicates that life history variation in terms of flocking behavior may be increasing along with population growth in the AWBP. Increased flock sizes during migration may represent the return of a historically more prevalent behavior when WHCR populations were comparatively abundant and widespread (Caven et al. 2020a). Despite some recent advances, WHCR populations currently represent a very limited breadth of the species' historic genetic diversity, life history variation, and geographic range. Ultimately, we must not confuse progress with success.

Resilience

SSAs consider the [demographic] resilience of the species to stochastic disturbances by virtue of population growth and connectivity as well as habitat quality and abundance (USFWS 2016). Resilience, in this sense, signifies the ability for populations to "bounce back" following a reduction. However, the term also refers to the potential emergence of an "alternative state" in which the population is unable to recover to its former level from reductions due, for example, to an altered predator regime (e.g., a predator-driven population trough; Holling 1973). Though the AWBP population is growing it is still small from a population genetics and management perspective (Brook et al. 2006, Frankham et al. 2014, Pérez-Pereira et al. 2022). Additionally, it

is objectively small considering previous policy decisions rendered under the ESA regarding avian species downlistings (Appendix A). Furthermore, there is no spatial connectivity between the AWBP and reintroduced populations at this time, which would confer additional resilience by increasing genetic diversity and allowing rescue effects (Kool et al. 2013). The population growth rate does indicate significant resilience to *common* perturbations (e.g., temporary drought) for the AWBP. Nonetheless, the AWBP remains restricted to an individual breeding and wintering range and >10% of the population has been documented together at key stopovers in the Great Plains on multiple occasions (Caven et al. 2020a, Baasch et al. *In Press*). Therefore, despite increases in abundance this single self-sustaining population remains quite vulnerable to stochastic disturbances like disease outbreaks (e.g., HPAI; CMS FAO 2022), natural disasters (e.g., drought, hurricane; Woolley et al. 2022), and industrial catastrophes (e.g., oil spill; Swift et al. 2011). The EMP has demonstrated a negative population trend since 2012 despite supplementation and is <15% of the size of the AWBP. The LNMP is of similar size to the EMP, but it has exhibited an overall positive trend in recent years, albeit with significant supplementation (LDWF 2022). Data indicate that neither reintroduced population would sustain their current abundance level without considerable supplementation (Thompson et al. 2022, LDWF 2022). From this perspective, reintroduced WCHR populations are [to date] categorically non-resilient as they are not able to sustain themselves through regularly occurring and modest perturbations, much less major stochastic events (Chevin et al. 2010, Capdevila et al. 2020, 2022). Ultimately, reintroduced WHCR populations display very little demographic resilience to environmental stressors (Capdevila et al. 2020, 2022).

Our analysis indicates there are a number of critical and potentially catastrophic threats to the continued integrity of WHCR habitat, particularly for the AWBP (Appendix B). Surface and

groundwater over- appropriation (Caven et al. 2019a), climate change (Butler et al. 2017), agricultural expansion (Wright and Wimberly 2013), invasive species (Kessler et al. 2011), woody encroachment (Giri and long 2016), extractive industry development (Roberts et al. 2022), expanding energy infrastructure (Smith and Dwyer 2016), and suburbanization (Homer et al. 2020) all threaten to reduce the availability and quality of WHCR habitat. Additionally, the problems facing WHCRs are regionally specific, interrelated, and dynamic so there is no simple solution. For instance, wetland and grassland losses resulting from row crop expansion in the Great Plains and the continued overappropriation of surface water that sustains estuaries in the Gulf Coast each threaten the availability and quality of WHCR habitat (Sandford 2015, McIntyre et al. 2018). However, both threats are also exacerbated by climate change which will likely further reduce surface water availability and therefore freshwater wetland landcover throughout the species' range (Chavez-Ramirez and Wehtje 2012, McIntyre et al. 2014, Fassnacht et al. 2018, Overpeck and Udall 2020). Moreover, climate change itself directly threatens the extent and quality of habitat by melting permafrost on the breeding grounds and promoting sea level rise on the wintering grounds (Holsinger et al. 2019, Golden et al. 2022). Ultimately, a reduction in habitat availability throughout the AWBP's migration corridor and wintering grounds likely promotes the aggregation of WHCRs where quality habitat persists, which ultimately increases the population's vulnerability to stochastic disturbances (Caven et al 2020a). Concurrently, WHCRs are faced with increasing scales and intensities of several disturbances [or threats] such as novel diseases (Stokstad 2022), extreme weather (e.g., extended droughts, unseasonable hurricanes, etc.; Overpeck and Udall 2020), and an increased density and distribution of powerlines (Smith and Dwyer 2016). As long as key wintering and migration areas lack ecological resilience it will be difficult to consider crane populations genuinely resilient as

habitat alternatives are of limited availability and quality, which would likely impact WHCR fitness and ultimately survival (Allen et al. 2011).

Interestingly, the USFWS (2020a) differs from us in their assessment of the WHCR's resilience. They suggest that based on variation in the extant populations' respective vital rates that the AWBP is "highly" resilient while the EMP and LNMP are both "moderately" resilient. However, no objective demographic indicators from comparatively healthy crane populations or similar waterbird populations were considered. Rather, the USFWS (2020a) assigned arbitrary thresholds based on the variation in the existing WHCR populations' vital rates. For instance, USFWS (2020a) defines a population needing no supplementation to persist as of "high" condition, a population in which recruitment occurs but is insufficient to sustain the population and thus supplementation occurs as of "moderate" condition, and a population in which juvenile recruitment does not occur at all as of "low" condition. What is described as "high" is only relatively so and should not be taken as an objective indicator that the population is apparently resilient (Chevin et al. 2010, Capdevila et al. 2020, 2022). Many small populations sustain themselves for a period of time with some population growth and no supplementation, yet very few population ecologists would consider such a population "highly" resilient (Pimm et al. 1993, O'Grady et al. 2006, Chevin et al. 2010, Capdevila et al. 2020, 2022).

The USFWS (2022a) demarcation of "high", "medium", and "low" growth rates similarly follows an arbitrary categorization that lacks scientific rigor. For instance, USFWS (2020a) simply applied a 90% confidence interval from a secondary data source (Butler et al. 2014) around 0% population growth (±2.3%) and contended that populations exceeding this threshold were of "high" condition, while those that fell within the bounds surrounding 0 were of "moderate" condition, and those below the confidence interval's lower bounds were of "low"

condition. In this framework, a population exhibiting a slightly negative growth rate [even with supplementation] would still be considered in "moderate" condition. In most cases, a long-term growth rate near or just below 0% would be a cause for concern (Chevin et al. 2010, Morandini and Ferrer 2017, Capdevila et al. 2020, 2022). A more robust approach would be to consider population growth rates of crane populations experiencing varying levels of success. For example, most healthy crane populations not constrained by habitat limitations have grown at a rate of >3.5% annually during their recovery from population lows in the early or mid-20th century (CWS and USFWS 2007, Prange and Ilyashenko 2019, Caven et al. 2020b, Seamans 2022). For instance, the Midcontinent and Eastern populations of Sandhill Cranes are growing at an annual rate of 3.7% and 4.4%, respectively (Caven et al. 2020b, Seamans 2022). Prange and Ilyashenko (2019) indicate that the Eurasian [Common] Crane (*Grus grus*) has grown at an even faster rate of between 5% and 8% annually in Western Europe in recent decades. A much better and more biologically sound indicator of a resilient crane population would be one that is growing at >3.5% annually without supplementation.

USFWS (2020a) determined that WHCRs did not face habitat limitations based upon a single article focused on sea level rise on the wintering grounds (Metzger et al. 2020). This article considered future human development projections, but it ignored worrying trends in vegetation characteristics and freshwater inflows at the wintering grounds which also threaten habitat (Chavez-Ramirez and Wehtje 2012). Ultimately the USFWS (2020a) omitted habitat conditions within the AWBP migration corridor and breeding grounds as well as throughout reintroduced populations' ranges in their species resilience assessment, which is short-sighted and not scientifically justifiable. Our analysis indicates that there are a multitude of interrelated threats increasing throughout important portions of the WHCR's range. Though WHCRs appear

somewhat secure based on the AWBP's current population growth rate, it is very possible that the cumulative influence of a variety of stressors (and their interactive effects) from habitat loss to climate change could push the AWBP over a tipping point and into a phase of population decline (Wardwell and Allen 2009, Butler et al. 2017, Capdevila et al. 2020, 2022; Barnard et al. 2021). On balance, considering each population's size and growth rate, level of supplementation, connectivity, habitat quality and abundance, and future threats, we cannot consider the AWBP more than "moderately" resilient at this time. Additionally, we would have to consider both the LNMP and the EMP to have categorically "low" resilience based on published definitions of demographic resilience (Capdevila et al. 2020, 2022).

Redundancy

The question of species' redundancy centers on its ability to "withstand catastrophic events" by virtue of having multiple resilient populations [or metapopulations] across its range. As we noted, the LNMP and EMP do not represent resilient populations. In fact, there has yet to be a self-sustaining WHCR population established via reintroduction efforts despite multiple attempts over the last 47 years. From 1976 to the present, there have been four reintroduced WHCR populations. All four populations have either been discontinued or remain heavily reliant on releases of captive-reared individuals. From 1976 to 1984, WHCR eggs were placed in Sandhill Crane nests at Grays Lake National Wildlife Refuge, Idaho (GLP; Drewien and Bizeau 1978). The resulting chicks were cross-fostered and taught to migrate by Sandhill Cranes. Ultimately, this reintroduction was discontinued due to high rates of mortality and a lack of reproduction in surviving WHCRs (Drewien et al. 1985, Brown et al. 1987, Doughty 1989, Drewien et al. 1989, Lewis 1990, Ellis et al. 1992). Research indicates that WHCR sexual imprinting on Sandhill Cranes early in life was the primary cause of population failure (Ellis et

al. 1992). Additionally, a non-migratory population of reintroduced costume-reared WHCRs in Florida (1992-2005) was effectively abandoned due to low survival and reproductive rates as well as significant habitat loss (Dellinger 2019).

Population growth in the EMP has been primarily limited by low levels of natural recruitment (Thompson et al. 2022). Avian-feeding black flies (*Simulium* spp.) have caused widespread nest abandonment in the EMP's core breeding area of Necedah National Wildlife Refuge (NWR; Urbanek et al. 2010, Barzen et al. 2018b). A management tool known as forced renesting was developed to address nest desertion, in which eggs were collected from first nests at Necedah NWR prior to abandonment and were brought into captivity (Fasbender et al. 2015, WCEP 2015). During 2015-16, crane pairs whose eggs were collected as a part of forced renesting were more likely to lay a second clutch of eggs compared to those who abandoned their nests naturally (Jaworski 2016). Once in captivity, collected eggs were hatched and reared using multiple techniques for release into reintroduced populations or were kept as a part of the captive breeding population (Wellington et al. 1996, Hartup 2019b, Thompson et al. 2022). Of the 167 chicks that hatched in the wild from 2006 to 2021, only 32 (19.2%) fledged (Thompson and Poitras 2021, Thompson et al. 2022). Causes of high rates of pre-fledged chick mortality are still unclear and are the focus of ongoing research (Urbanek 2015, McLean 2019, Stewart 2020).

Low levels of natural recruitment have similarly limited population growth in the LNMP. A primary driver of low reproduction in the LNMP has been high rates of embryonic death in wild eggs. During the 2021 nesting season, 61.7% of the fertile eggs produced in the wild died prior to hatch (LDWF 2021). During 2013-2021, a total of 37 chicks have hatched in the wild in LNMP, 9 of which hatched from fertile eggs produced in captivity or collected from the EMP that were swapped into nests in Louisiana that had infertile or non-viable eggs. Of these 37 wild-

hatched chicks, only 12 (32.4%) have fledged (LDWF 2021). Only one wild-hatched WHCR from the LNMP has become a reproductive adult as of 2021 (LDWF 2021). Both ongoing reintroductions represent small populations which rely heavily on captive breeding centers for propagation and rearing of juvenile WHCRs for supplementation. Forced renesting in the EMP could not be employed if captive breeding centers did not have the capacity to foster collected eggs. Similarly, there would not be fertile eggs available to swap into nests in Louisiana without captive propagation or transfer of collected eggs from the EMP to breeding centers. Moreover, captive breeding centers are facing a variety of challenges which are limiting their capacity to rear large cohort sizes of juvenile WHCRs for release into reintroduced populations (e.g., sustained funding, geriatric captive flock, difficulty in transferring cranes across international borders, human coronavirus pandemic, HPAI; WCEP 2019, WCEP 2020, Thompson et al. 2022).

We are not contending that the ongoing reintroductions are doomed to fail. Quite the opposite – we are highlighting the degree to which partners are collaborating to sustain such a labor-intensive endeavor. With each attempt at WHCR population reintroduction we learn a great amount, and arguably, we are much better at it than 50 years ago. Many endangered species reintroduction programs ultimately achieve success after decades of sustained collaborative work (Morandini and Ferrer 2017, Zhang et al. 2021). However, it is important to clearly highlight the challenges we face as they plainly demonstrate the degree to which the EMP and LNMP remain highly conservation-intervention dependent. Moreover, success is not ultimately guaranteed in either the LNMP or the EMP. With low levels of recruitment in both populations, population sizes would significantly decrease without the release of captive-reared individuals, especially considering annually variable but relatively high adult mortality rates compared to the AWBP

(LDWF 2022, Thompson et al. 2022). To conclude, given that the LNMP and the EMP have low resilience and are not self-sustaining, neither population supplies true redundancy for the AWBP of WHCRs if it were to be highly impacted.

ESA Implementation

Our analysis clearly demonstrates that populations at the time of being downlisted from an endangered to a threatened or delisted status were highly variable and inconsistent even across similar taxa. Avian populations at downlisting averaged about 15,600 individuals per our analysis with a 95% confidence interval ranging from ~6,600 – 24,600 (Appendix A). The WHCR therefore remains well below the population abundance range at which species have typically been downlisted from an endangered status. Only the Palau Ground-dove (*Gallicolumba canifrons*) was downlisted with fewer than 3,000 individuals estimated in the population. This species has a much different life history than the WHCR, as it is a non-migratory species with a small geographic range endemic to an archipelago in the western Pacific. It was delisted from endangered in 1985 with about 500 individuals estimated in the population (Baker 1951, Pratt et al. 1980, USFWS 1985). The species appears to have declined post-delisting by nearly 60% per the most recent range-wide population estimates, despite high uncertainty (213±289; VanderWerf and Dittmar 2020). Based largely on this recent survey information the species has been reclassified from "Near Threatened" to "Endangered" per the IUCN (Baptista et al. 2020). If the WHCR were to be downlisted at its current population level it would represent the second smallest avian population to be reclassified from an endangered status and the smallest avian population downlisted to a threatened status to date, as the Palau Ground-dove was delisted. It is informative that the Palau Ground-dove has fared poorly following delisting, ostensibly from a lack of active conservation and habitat protection. In fact,

the WHCR population would be smaller at downlisting than most populations when they were listed as endangered, which averaged about 2,900 with a 95% confidence interval ranging from ~900 – 5,000. Given that we only considered avian species in our analysis, we would expect more consistency across taxa regarding what constitutes an endangered, threatened, or ostensibly secure population. Smith (2016) similarly noted wide variation in what population sizes were expected to effectively confer protection from extinction for individual species across ESA listing actions.

Pérez-Pereira (2022) suggests that an N_e >1,000 generally represents a minimum viable population (MVP) that can maintain long-term genetic diversity for vertebrate species with low reproductive rates. Frankham et al. (2014) similarly determined that an $N_e \geq 1{,}000$ represents a robust minimum estimate for populations that should generally allow for the retention of evolutionary potential, whereas an $N_e \leq 100$ was associated with the development of genetic threats (e.g., inbreeding depression), specifically after ≥5 generations. Brook et al. (2006) found that the median MVP was 1,377 individuals across 1,198 species, but also determined that variation was high and not well related to estimated global extinction risk. Nonetheless, "the best available science" indicates that *effective* populations for long-lived and slow growing species generally need to be larger than 1,000 individuals to minimize long-term genetic threats. Effective population size (e.g., N_e) can be easily converted to total population size estimates using the ratio of effective to actual population size (N_e/N; Frankham et al. 2014, Pérez-Pereira 2022). N_e estimates can be produced through genetic, demographic, or integrated models and are highly influenced by a species' general mating system (e.g., random, polygyny, monogamy, etc.; Nunney 1993, Frankham et al. 2014, Wang et al. 2016). However, Frankham et al. (2014) contends that metadata analyses indicate that N_e/N often ranges between 0.1-0.2 across

populations. Nonetheless, Boardman et al. (2021) suggests that the N_e/N ratio is closer to ~0.5 in the captive WHCR population. Determining a long-term MVP for the WHCR is beyond the scope of this study, but following these basic operational rules and data outlined above would indicate that total WHCR abundance within a closed population or a series of connected metapopulations would need to between 2,000 and 10,000 individuals to ensure genetic health in perpetuity. The adoption of more standardized MVPs and growth rate estimates derived from the current scientific literature could ostensibly improve the consistency of listing decisions under the ESA from a population management perspective.

Doak et al. (2015) similarly contends that ESA implementation would be significantly improved by integrating more standardized conceptual definitions and associated quantitative guidelines into the determination of recovery criteria. For instance, what does the ESA mean by "in danger of extinction" or "a significant risk to the wellbeing" of a species? Ultimately, an "acceptable" level of risk represents a societal value judgement not clearly defined under the ESA (Doak et al. 2015, Wolf et al. 2015, Offer-Westort et al. 2020). Coarse definitions of important concepts such as "acceptable risk" are operationalized without explicit quantitative criteria which has resulted in widely varying and inconsistent determinations under the ESA in practice (Doak et al. 2015, Wolf et al. 2015, Smith 2016). For instance, Wolf et al. (2015) highlighted a range of acceptable extinction risk thresholds incorporated into vascular plant recovery plans' criteria in south Florida that varied from a 20% to a 90% probability of persistence for individual species over a 100-year period. Some efforts have been made to standardize an acceptable rate of extinction risk at a 5% chance over a 100-year period, but this threshold has not been formally enshrined in ESA policy (Wolf et al. 2015, Offer-Westort et al.

2020). Superficially, this threshold sounds reasonable, but it appears less so when considering extinction rates across time.

The current rate of extinction appears to be 100–1,000 times higher than the background rate from the fossil record (Pimm et al. 2014, Ceballos et al. 2015). Estimates of the background extinction rate range from 0.1 species extinctions per million species years (MSY) up to 2 extinctions per million species years (Barnosky et al. 2011, Pimm et al. 2014, Ceballos et al. 2015). Taking the center point of this distribution, one could infer about a 1% probability of extinction across 10,000 years as a background rate within the fossil record (Barnosky et al. 2011, Ceballos et al. 2015), which is ultimately much lower than the standard acceptable rate of extinction informally proposed for recovery criteria development (Wolf et al. 2015, Offer-Westort et al. 2020). Pimm et al. (2014) suggests that the "current" rate of extinction generally exceeds 100 per MSY, but that it varies across taxa and locations. For instance, Pimm et al. (2014) estimates the rate of mammal extinction at >240 per MSY since 1900. Similarly, Burkhead (2012) suggested the extinction rate exceeded 300 species per MSY for freshwater fishes in North America over the last century. For comparison, a 5% probability of extinction over 100 years would equate to about 500 extinctions per MSY, which generally exceeds the rate of extinction observed during the Anthropocene during the 6th major extinction in world history (Pimm et al. 2014). To set meaningful objectives, we contend that an acceptable risk of extinction should be minimally at or below the general rate of extinction observed over the last century, which would represent a ~1% probability over 100 years. However, 100 years represents a short period in evolutionary time and striving to achieve a $\leq$1% risk of extinction over $\geq$200 years would likely be a more robust approach.

Another important consideration regarding SSAs informed by population viability analyses (PVA) is that the information included within the model will ultimately drive results (Patterson and Murray 2008, Gerber and González-Suárez 2010, Wolf et al. 2015). Traylor-Holzer (2019) indicates that WHCRs have a 0% probability of extinction over the next century. Plainly, a 0% probability of extinction is a statistical impossibility, but we interpret this as an indication that the probability of extinction is exceedingly low, per this model (Beissinger and Westphal 1998). Nonetheless, this estimate of extinction probability simply does not make biological sense. Small and spatially isolated populations like the AWBP are generally more vulnerable to extinction than those connected to other self-sustaining metapopulations (Pimm et al. 1993, Dale 2001, O'Grady et al. 2006). Additionally, the WHCR's life history traits, including low recruitment, delayed reproduction, relatively long generation times, specific habitat requirements, substantial core use (i.e., "home range") area requirements, and a large physical size relative to similar taxa predispose it to an elevated extinction risk (Beissinger 2000, Dale 2001, Cardillo et al. 2005, Krüger and Radford 2008, Ripple et al. 2017). So, how is it possible that a species, with a single self-sustaining population below the abundance level necessary for long-term genetic health, with traits predisposing it to an elevated extinction risk, has an estimated probability of extinction below the ongoing rate for general biodiversity? In our valuation, Traylor-Holzer (2019) under enumerated and underestimated the existing suite of threats facing the WHCR and did not rigorously incorporate uncertainty. Several threats such as disease (an increasing threat; Stokstad 2022) and predation (a leading cause of mortality; Thompson et al. 2022) were simply omitted as stressors in the SSA and PVA "…given the uncertainty…[surrounding their] overall impact" (Traylor-Holzer 2019, USFWS 2020a). Additionally, Traylor-Holzer (2019) often provided spatially or topically incomplete coverage of

major threats that were incorporated into the PVA model. For instance, habitat was considered in a very narrow sense on the wintering grounds in terms of estimated carrying capacity per sea level rise and development scenarios provided by Metzger et al. (2020). However, the overappropriation of instream flows that sustain salt marsh and bay function as well woody encroachment from black mangrove expansion, which also threatens wintering habitat, were not explicitly considered. Similarly, wetland habitat loss within the migration corridor and impacts from melting permafrost on the breeding grounds were essentially overlooked by PVA modeling efforts. Considering the omission of these threats [and several more] it is easy to see how extinction probability would be grossly underestimated. In our calculation Traylor-Holzer (2019) considered <40% of the threat drivers we evaluated in the threat assessment conducted herein (Appendix B).

Gerber and González-Suárez (2010) highlight that PVAs often ignore risks that are hard to parameterize. Moreover, PVAs make predictions from existing relationships between threats and species demographic rates which can fundamentally change or shift in orders of magnitude over time (Beissinger and Westphal 1998, Gerber and González-Suárez 2010). Clark and Luis (2020) suggest that a relatively small fraction (29%) of time series trends remain predictable for >2 years looking forward and therefore multidecadal trends projected per PVAs are often invalid considering non-linear population trends in relation to shifting stressor conditions. Ultimately, PVAs provide a useful tool, but it is essential to recognize that PVAs inherently involve significant uncertainty, whether acknowledged or not (Beissinger and Westphal 1998, Gerber and González-Suárez 2010). Projections should be used to evaluate the relative merits of different management options such as which approach lowers the probability of extinction more (Beissinger and Westphal 1998, Gerber and González-Suárez 2010, Doak et al. 2015). Similarly,

PVAs can be used to understand the differential threats posed by various drivers and prioritize mitigation actions (Beissinger and Westphal 1998, Gerber and González-Suárez 2010, Doak et al. 2015). However, PVAs should not be reified as inevitable future outcomes on which we can base current decisions (Beissinger and Westphal 1998, Gerber and González-Suárez 2010, Clark and Luis 2020). For example, it would be inappropriate to assume downlisting is warranted based on a single forecast with limited validation or input from external and independent experts uninvolved in the model development process (Beissinger and Westphal 1998, Gerber and González-Suárez 2010). As Gerber and González-Suárez (2010) note "…our ability to make accurate predictions into the future will always be limited by our ignorance of future conditions." Additionally, every effort should be made to make models as comprehensive as possible if they are ultimately intended to objectively estimate extinction risk to inform policy decisions (Beissinger and Westphal 1998, Gerber and González-Suárez 2010).

There are a significant number of terms within the ESA or the guidance informing its execution that have received scrutiny for being too broadly defined and ultimately too subjectively applied. In addition to those already addressed, concepts including "best available science," "resilience," "representation," "redundancy," "all or a significant portion of its range," "within the foreseeable future," and "self-sustaining populations in the wild" have been widely scrutinized and debated (Woods and Morey 2008, Carroll et al. 2010, Harm Benson and Hopton 2014, Wolf et al. 2015, Lind- Riehl et al. 2016, Smith 2016, Malcom and Carter 2021, Sheikh et al. 2021). We have already demonstrated that the term "resilience" was not rigorously applied by USFWS (2020a) considering its conceptual definition in scientific literature (Wardwell and Allen 2009, Capdevila et al. 2020, 2022; Malcom and Carter 2021). Moreover, demographic resilience is clearly tied to whether a population can sustain itself [through perturbations], and

"self-sustaining" implies that a population can maintain a positive growth rate for a considerable period of time, barring a significant negative and abnormal disturbance (Capdevila et al. 2020, 2022; Sheikh et al. 2021). The current international WHCR recovery plan specifies a period of 10 years of positive or neutral population growth without supplementation for reintroduced populations to be considered "self-sustaining" (CWS and USFWS 2007). However, given that this plan ultimately serves as "guidance" and not "rule" for WHCR listing decisions, it is possible the USFWS could employ a less robust definition of "self-sustaining," which has occurred regarding other decisions. The Black-capped Vireo (*Vireo atricapilla*) was downlisted despite a recognition that sustaining or increasing populations is largely reliant upon continued habitat management (e.g., limiting woody encroachment) and Brown-headed Cowbird (*Molothrus ater*) control efforts (USFWS 2018a, 2018b). The USFWS (2018a, 2018b) admits that in the "worst case" scenario forecasted by the SSA that populations would likely decline but the USFWS contends the Black-capped Vireo would not be expected to meet the definition of "threatened" or "endangered" again for a period of at least 50 years. This downlisting action highlights the subjectivity surrounding SSAs and listing decisions. How "self-sustaining" or "resilient" does a population need to be?

As Smith (2016) notes in her review of >250 listing decisions, non-biological variables frequently exert significant influence on listing decisions. Considerations often shift per administration funding and priorities (Wyman 2012, Hartl and Owley 2021). Our data show how listing and delisting decision frequency ranged widely across years despite a relatively consistent and concerning background rate of global extinction (Ceballos et al. 2015). Delistings have not regularly met or exceeded listings until recently but have consistently done so since 2018 (Figure 3). Ultimately shifts in agency leadership, operational policy, and funding drive patterns of

policy implementation (Wyman 2012, Hartl and Owley 2021, Sheikh et al. 2021). Our examination of potential WHCR downlisting actions highlights some ways to improve the consistency, defensibility, and rigor of listing decisions across fluctuations in political administrations, agency leadership changes, and funding cycles. First, continued narrative refinement of key ESA concepts is fine, and probably beneficial. However, to really improve implementation of the act some broadly accepted minimum quantitative biological standards need to be developed to operationalize ESA language in a consistent manner (e.g., N_e >1,000; extinction probability <1% over 100 years; ≥1% growth without supplementation across 10 years; Doak et al. 2015). Incorporating and improving estimates of uncertainty in quantitative standards and policy decisions will also likely improve consistency and rigor across listing decisions (Beissinger and Westphal 1998, Gerber and González-Suárez 2010). Additionally, we strongly feel that all SSAs and PVAs for listed or candidate species should go through a rigorous peer review process, like any scientific paper published in a reputable journal. Reviewers should be recognized experts regarding particular species or closely related analogs and be familiar with the taxa's ecology and the threats facing it. Reviewers should also have demonstrated knowledge of the regions being assessed so that habitat threats are fully vetted. Finally, reviewers should have no involvement with the SSA or PVA process to make sure that their assessments are unbiased. Ultimately, we feel that these reviewers should have real power to recommend or deny an SSA or PVA based on its merits. Providing guidance on how this would be done is beyond the scope of this paper, but such an approach could be operationalized in a myriad of ways. Additionally, transparency (e.g., publicly available critiques) would be key to its success. Only with improved conceptual definitions, basic quantitative criteria, and added oversight can we

avoid a decision as misguided as downlisting or delisting the WHCR without consideration of its recovery plan criteria or ostensibly its population ecology.

Conclusions

The WHCR has come a long way from the brink of extinction but that does not mean they have arrived at security. In the end, we must not confuse progress with success. Current WHCR populations do not meet any of the downlisting objectives or criteria outlined in the 2007 recovery plan. Moving to downlist before these thresholds have been met undermines the value of recovery criteria and plans generally. Additionally, such an autonomous action by the USFWS in the face of core partner opposition considerably weakens collaborative recovery efforts for this species and potentially others per the message it sends. The failure thus far of the two experimental populations to become self-sustaining suggests that maximum care should be provided to the AWBP and that an endangered status should be retained.

Our research suggests that WHCR downlisting is also unwarranted from biological and threat assessment perspectives and would be out of alignment with past USFWS avian downlisting decisions regarding population conservation. WHCR populations are still very small (~700 individuals in the wild across 3 populations) and reintroduced populations continue to rely on supplementation. Rarity is generally considered a significant predictor of extinction risk and the WHCR is the rarest crane in the world by a substantial margin. Ultimately, if the WHCR's status were to be changed under the ESA, it would represent only the second time an avian species has been downlisted from an endangered status with a population under 3,000 individuals. In fact, the current WHCR population is smaller than most other avian species' populations assessed in our study at the time they were listed as endangered. Based on the basic

genetic information available, WHCR abundance within a closed population would likely need to reach approximately 2,000–10,000 individuals to ensure genetic health in perpetuity.

WHCRs are facing an intensification of most threat drivers across populations and seasonal ranges, which were regularly underrepresented by the USFWS-led SSA and the PVA that informed it. Habitat loss throughout the species' range is driven by a diversity of factors including agricultural expansion, suburbanization, energy development, and exotic and woody species invasion. This threat is being compounded by poor surface and ground water regulation and exacerbated by climate change. Climate change also directly threatens habitat via sea level rise on the wintering grounds and melting permafrost on the breeding grounds. Direct WHCR mortality from powerline collisions, predation, and poaching continues with a stable or increasing trend per population and range. Projections indicate that there will be significant increases in alternative energy infrastructure throughout the WHCR's range, including transmission lines to convey that power. Additionally, WHCRs continue to face threats from human derived contaminants (e.g., pollution from oil spills, tar sands, etc.), communicable diseases (e.g., HPAI), and stochastic events (e.g., hurricanes, particularly the LNMP).

Considering each WHCR population's size, growth rate, level of supplementation, connectivity, habitat quality and abundance, and future threats, we considered the AWBP "moderately" resilient and both the LNMP and the EMP to have categorically "low" resilience based on published definitions of demographic resilience. This assessment differs from that produced in the SSA, which arbitrarily defined the resilience of existing populations relative to one another rather than in regard to published definitions of resilience and quantitative criteria informed by crane population biology. To improve consistency across listing actions and recovery planning we suggest the adoption of some broadly accepted minimum quantitative

criteria at least to the Class (e.g., Aves) level. These standards should provide minimum effective population sizes (e.g., N_e >1,000) and extinction risk thresholds (<1% probability over 100 years), in addition to other information, for related taxa as broad guidelines to operationalize ESA language in a more consistent manner. Additionally, we feel that all SSA and PVA reports should be subject to a rigorous and external peer review process before being finalized. The choice to potentially downlist the WHCR can only be fully understood through the USFWS's SSA development and listing decision processes, which in our assessment often lack scientific rigor, consistency, objectivity, and transparency. Downlisting the WHCR prematurely could have negative consequences for this species and put it at greater risk of extinction. Improving ESA implementation can ensure that species in need of the law's full protections, including the WHCR, are consistently afforded them moving forward.

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Data Accessibility Statement

As a review article, the vast majority of our data is available within the manuscript itself within Appendices A, B, and C, as well as in Table 1. However, we are happy to put any additional data into a public repository upon manuscript publication.

Competing Interests Statement

The authors have no competing interests to declare.

Author Contributions

Study Conceptualization: AJC, HLT, RDB
Design: AJC
Implementation: AJC, HLT, DMB, BKH, AMH, SMS, IL
Data Collection: AJC, HLT, DMB, BKH, AMH, SMS, IL
Analysis: AJC, SMS
Manuscript Composition: AJC, HLT, DMB, BKH, AMH, SMS, IL, JEA, CGC, CAD, CRA, JGJ, BLO, RDB, GWA, AEL
Manuscript Review: AJC, HLT, DMB, BKH, AMH, SMS, IL, JEA, CGC, CAD, CRA, JGJ, BLO, RDB, GWA, AEL

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Tables, Figures, and Appendices

Table 1. Estimated abundance of cranes in the wild per species common name from the most recent (published or unpublished) and best available survey data summarized by ICF (2022) including status per the International Union for Conservation of Nature (IUCN), the best available abundance point estimates, abundance ranges, the maximum confidence interval (regarding inequilateral CIs) for abundance estimates pertaining to each species, and the estimated percentage of the worlds cranes represented by each species.

Species	IUCN	Point Estimate	Range	Max C.I.	Percentage of Cranes
Sandhill Crane	Least Concern	1,450,200	1,280,200-1,680,200	230,000[1]	53.49%
Eurasian Crane	Least Concern	790,000	687,300-892,700	102,700[2]	29.14%
Demoiselle Crane	Least Concern	195,000	170,000-220,000	25,000	7.19%
Brolga	Least Concern	75,000	50,000-100,000	25,000	2.77%
Black Crowned Crane	Vulnerable	66,500	53,000-80,000	13,500	2.45%
Grey Crowned Crane	Endangered	28,000	25,000-31,000	3,000	1.03%
Blue Crane	Vulnerable	27,500	25,000-32,850	5,350[3]	1.01%
Hooded Crane	Vulnerable	18,750	17,150-20,350	1,600[3]	0.69%
Sarus Crane	Vulnerable	17,500	15,000-20,000	2,500	0.65%
Black-necked Crane	Near Threatened	13,000	12,300-13,700	700	0.48%
White-naped Crane	Vulnerable	9,800	9,400-10,200	400[3]	0.36%
Wattled Crane	Vulnerable	9,600	8,450-10,750	1,150[3]	0.35%
Siberian Crane	Critically Endangered	5,500	4,800-6,200	700[3]	0.20%
Red-crowned Crane	Vulnerable	4,000	3,800-4,200	200	0.15%
Whooping Crane	Endangered	702	586-941	239[4,5]	0.03%
Totals	**-**	**2,711,052**	**-**	**412,039**	**100.00%**

Notes: 1) Confidence intervals adjusted from ICF (2022) per Caven et al. 2020, 2) Confidence interval estimated per median for all crane species assessed herein (0.13), 3) Confidence interval adjusted per data from BLI (2022), 4) Confidence interval per Butler et al. (2022), 5) The 134 individual Whooping Cranes in captivity are not included in the estimate here. Only birds persisting independently in the wild are included for all species assessed.

Table 2. Decadal averages of Whooping Cranes shot per year from 1982-2021 in the Aransas Wood Buffalo Population (AWBP), Florida Non-migratory Population (FNMP), Eastern Migratory Population (EMP), and Louisiana Non-migratory Population (LNMP) by decade from 1982 to 2021.

	1982-1991	1992-2001	2002-2011	2012-2021
AWBP (remnant historic)	0.3	0.0	0.4	0.7
FNMP (est. 1993)	-	0.3	0.0	0.0
EMP (est. 2001)	-	0.0	0.9	0.7
LNMP (est. 2011)	-	-	0.3	1.2
All Populations	0.3	0.3	1.6	2.6

Figure 1. Whooping Crane abundance by year per distinct population. This includes the remnant Aransas-Wood Buffalo Population (AWBP; 1938-2021), the now extirpated but remnant non-migratory population in Louisiana (LA_Wild; 1938-1949), the first reintroduced and ultimately failed Grays Lake National Wildlife Refuge Population (GLP; 1975-2001), the second and also failed reintroduction of a Florida Non-migratory Population (FNMP; 1993-2022), and the ongoing reintroduction of the Eastern Migratory Population (EMP; 2001-2022), and the reintroduced Louisiana Non-migratory Population (LNMP; 2011-2022).

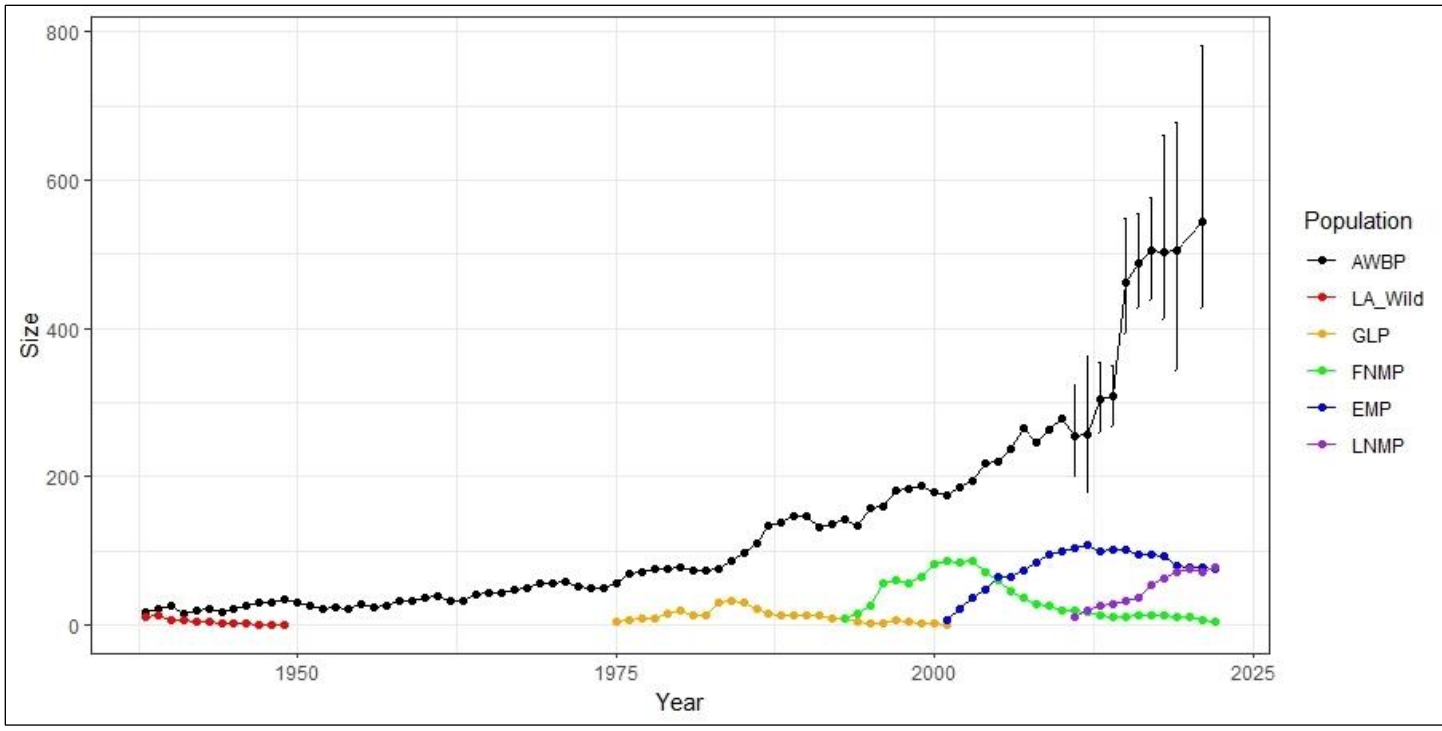


Figure 2. The percentage of threat drivers per potential impact level category by WHCR population and seasonal range including the Aransas Wood Buffalo population (AWB), Eastern Migratory Population (EMP), and Louisiana Non-migratory population (LNM).

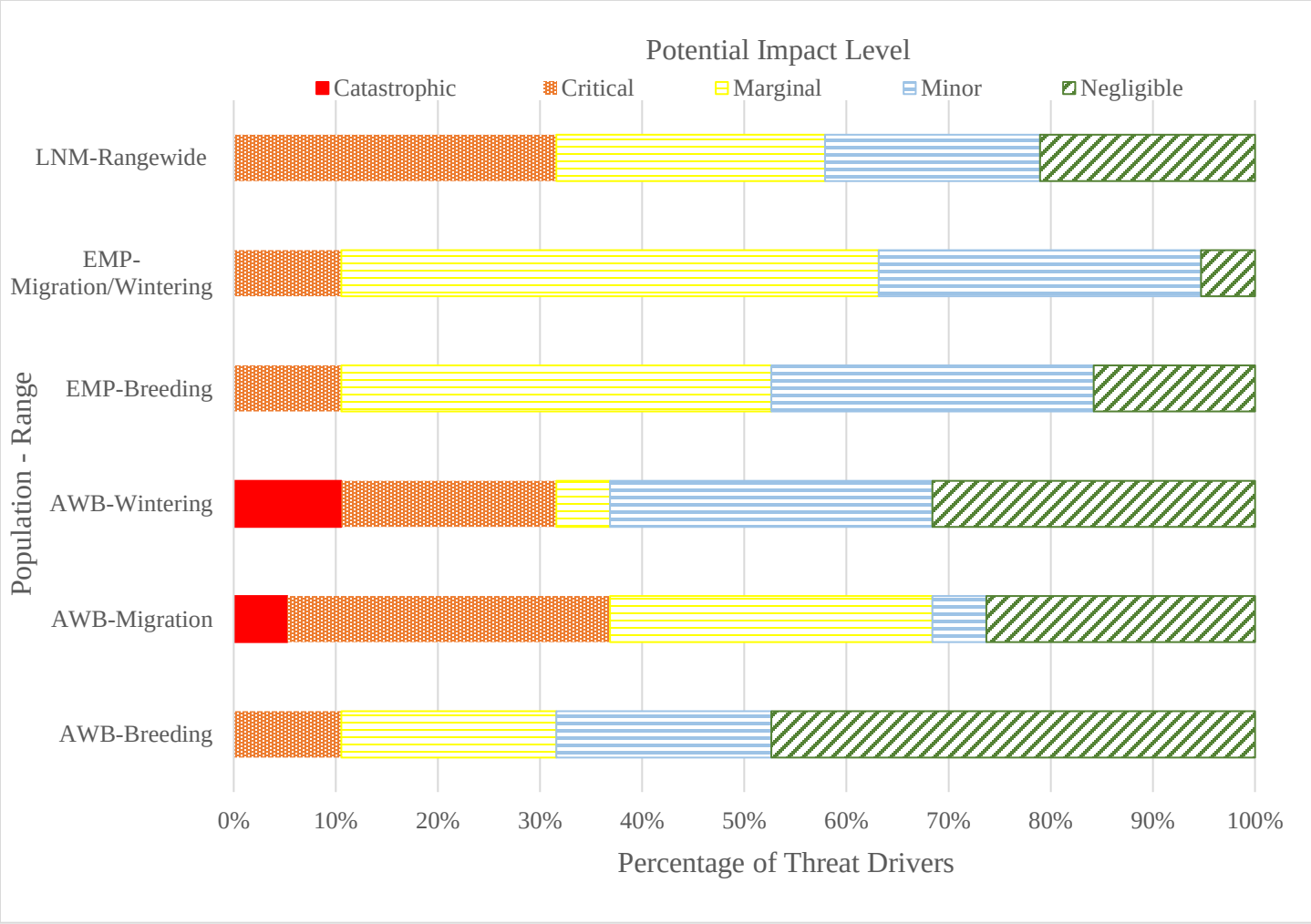

Potential Impact Level
Catastrophic
Critical
Marginal
Minor
Negligible
LNM-Rangewide
EMP-Migration/Wintering
EMP-Breeding
AWB-Wintering
AWB-Migration
AWB-Breeding
Population - Range
0%
10%
20%
30%
40%
50%
60%
70%
80%
90%
100%
Percentage of Threat Drivers

Figure 3. Listing and delisting trends from 1967 to 2002 under the Endangered Species Act (Endangered Species Preservation Act of 1966, amended 1969; Endangered Species Act of 1973) including best fit second order polynomial trendlines for listing and delisting actions per year.

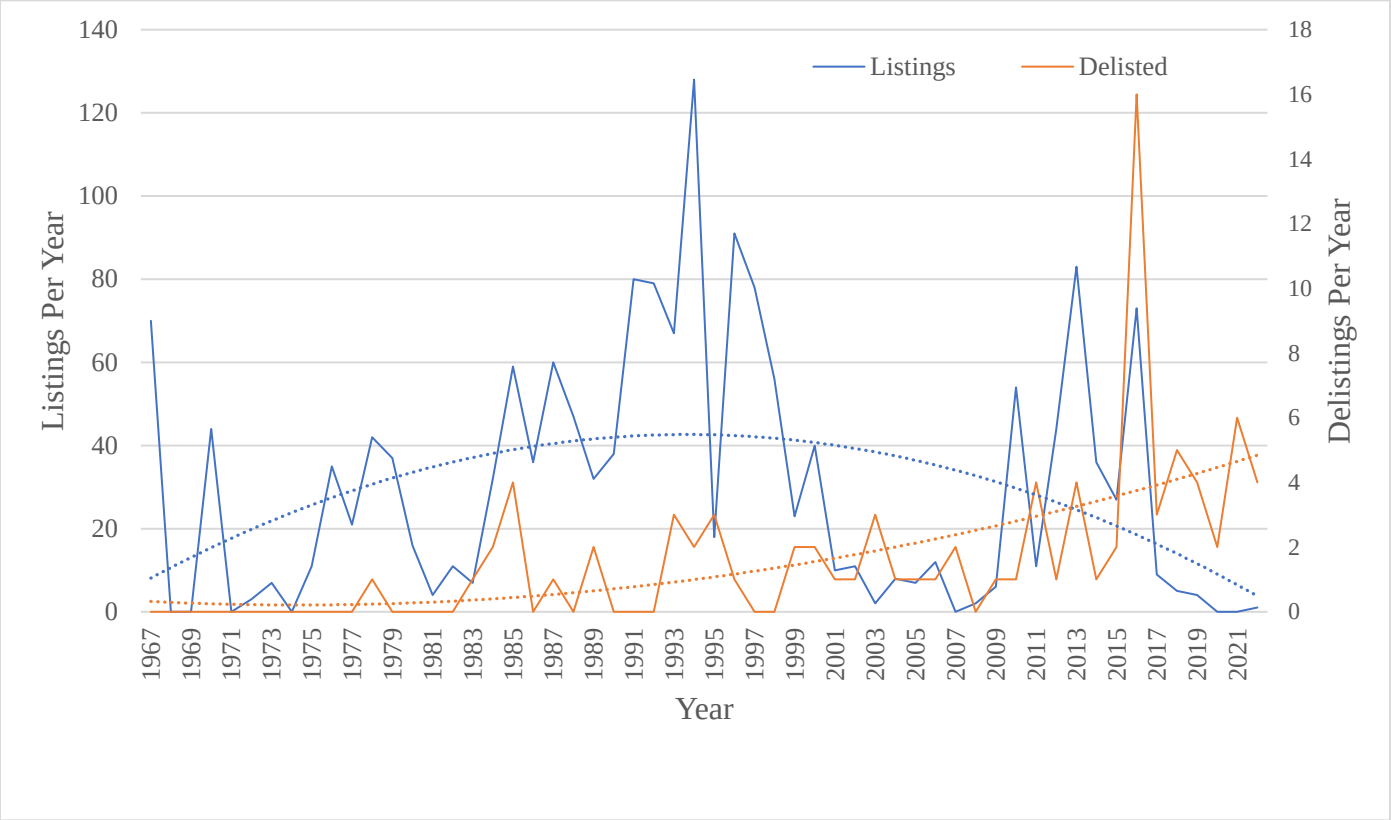
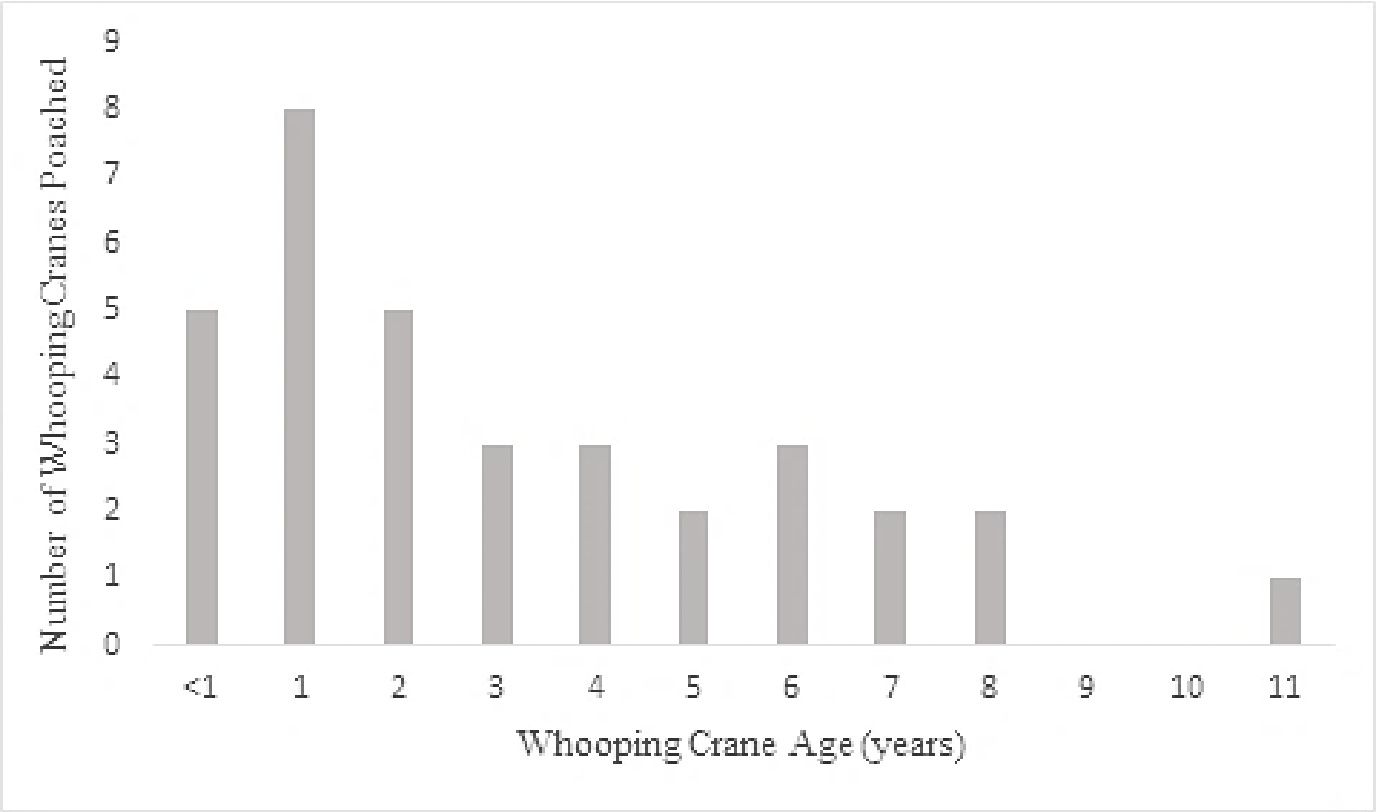


Figure 4. The known age distribution of Whooping Cranes killed by shooting in all populations from 1967 to 2022 (n=34).



Appendix A. Populations of species or distinct population segments at the time of downlisting from an "endangered" (EN) to a "threatened" (TH) or "delisted" (DE) status under the Endangered Species Preservation Act of 1967 [1969] or the Endangered Species Act of 1973 (ESA). The table includes species' common name, scientific name, downlisting status (complete or proposed), listing year, initial status under the ESA, point estimate for population at listing and downlisting [or delisting] (Unk. = unknown), range estimate for population at listing and downlisting [or delisting], the year the species status changed [or a change was proposed for ongoing cases], the initial change in status from endangered to threatened (TH) or delisted (DE), and the information sources on which abundance estimates were based.

Common Name	***Scientific Name***	**Downlisting Status**	**Year Listed**	**Initial Status**	**Est. Pop at Listing (Point)**	**Est. Pop at Listing (Range)**	**Year Changed (Proposed)**	**Changed Status**	**Est. Pop at Downlisting (Point)**	**Est. Pop at Downlisting (Range)**	**Sources**
Golden Parakeet (Conure)	*Aratinga guarouba*	Complete	1976	EN	2,750	2,500-3,000	2020	TH	10,875	6,600-13,400	Reynolds 2003; Laranjeiras 2011; Laranjeiras 2020; BLI 2022c
Aleutian Canada Goose	*Branta canadensis leucopareia*	Complete	1967	EN	1,040	990-1,090	1990	TH	6,415	5,450-7,400[1]	Bailey and Trapp 1984; USFWS 2001
Hawaiian Goose (nēnē)	*Branta (Nesochen) sandvicensis*	Complete	1967	EN	279[2]	Unk.	2019	TH	3,252[3]	Unk.	Smith 1952; USFWS 2004a, 2019a
Hawaiian Hawk ('Io)	*Buteo solitarius*	Complete	1967	EN	125	100-150	2020	DE	3,085	2,496-3,680	Griffin 1984; Gorresen et al. 2008; USFWS 2020a
American Peregrine Falcon	*Falco peregrinus anatum*	Complete	1970	EN	345	325-365	1999	DE	3,380	3,300-3,460	USFWS 1999; Pfannmuller 2017
Arctic Peregrine Falcon	*Falco peregrinus tundrius*	Complete	1970	EN	1,200[4]	1,020-1,380[1]	1984	TH	4,430[4]	3760-5,100[1]	USFWS 1984a, 1994; PIF 2020; BLI 2022b

Palau Ground Dove	*Gallicolumba canifrons*	Complete	1970	EN	268	35-500	1985	DE	500	164-1000	Baker 1951; Pratt et al. 1980; USFWS 1985; Baptista et al. 2020; VanderWerf and Dittmar 2020; BLI 2022a
Bald Eagle	*Haliaeetus leucocephalus*	Complete	1967	EN	834[5]	834-901[6]	1995	TH	8,904[5]	8,904-9,616[6]	USFWS 1995, 2020b
Tinian Monarch	*Monarcha takatsukasae*	Complete	1970	EN	15,000[7]	10,000-20,000[7]	1987	TH	83,550	39,338-127,758[8]	Pratt et al. 1979; Lepson 1998; USFWS 2004b, 2018a
Wood Stork	*Mycteria americana*	Complete	1984	EN	11,250[5]	10,000-12,500[5]	2014	TH	22,558[5]	20,000-24,000[5]	USFWS 1984b, 2007a, 2010; Kushlan and Frohring 1986; Frederick and Meyer 2008
Brown Pelican (US Gulf Coast - TX & LA)	*Pelecanus occidentalis*	Complete	1970	EN	32[9]	16-32[9]	2009	DE	28,230[9]	22,860-33,600[9]	USFWS 2007b, 2009; Selman et al. 2016
Red-cockaded Woodpecker	*Picoides borealis*	Proposed	1970	EN	6,500	3,000-10,000	2020 (ongoing)	TH	17,550	15,600-19,500[10]	Jackson 1971; USFWS 2020c
Palau Owl	*Pyrroglaux podargina*	Complete	1970	EN	5,075	150-10,000	1985	TH	10,000	Unk.	Marshall 1949; Pratt et al. 1980; USFWS 1985; Eakle 2004
Palau Fantail Flycatcher	*Rhipidura lepida*	Complete	1970	EN	Unk.	Unk.	1985	DE	27,175	21,400-32,950	Baker 1951; USFWS 1985; VanderWerf and Dittmar 2020
Kirtland's Warbler	*Setophaga kirtlandii*	Complete	1967	EN	368	334-402	2019	DE	4,490	4,180-4,800	USFWS 2019b; Bocetti et al. 2020
Interior Least Tern	*Sternula antillarum athalassos*	Complete	1985	EN	1,600	1,400-1,800	2021	DE	17,591	13,855-21,855	Lott 2006; USFWS 2013, 2021

Black-capped Vireo	Vireo atricapilla	Complete	1987	EN	350	Unk.	2013	TH	12,993	10,488-15,498[11]	Benson and Benson 1990; Farquhar and González 2005; USFWS 2018b, 2018c
Mean					2,938				15,587		
SD					4,296				18,929		
SE					1,042				4,591		
95% CI					2,042				8,998		
MIN					32				500		
MAX					15,000				83,550		

Notes: 1) Used a 15% CI for population range estimates; 2) Smith (1952) estimated the population at 30 individuals and USFWS (2004) indicated 240 persisted on Hawai'i and 39 on Maui in 1967; 3) USFWS (2019a) indicated that Hawaii had 1,104, Kauai had 1,482, Maui had 627, Molokai had 37, and Oahu had 2 Hawaiian Geese in 2017; 4) Population estimates extrapolated from +127% per decade trend per BLI 2022b, current PIF (2020) population estimates, and historic survey data (USFWS 1994); 5) Estimates = 2*breeding pairs; 6) Upper confidence limit (+8%) is based on SE confidence internals surrounding recent modern population estimates that accounted for detection probability per USFWS (2020b); 7) Minimum estimate at listing per interpretation of Pratt et al. (1979); 8) Lower CI for population at downlisting is the 1982 abundance estimate and the upper CI is the higher confidence limit for 1996 survey data reanalyzed in 2013 per USFWS (2018); 9) Estimates only include counts of breeding pairs*2 from the US Gulf Coast Region (TX & LA). The Gulf of Mexico as a whole likely supported >75,000 Brown Pelicans at delisting with the global population, excluding the Atlantic Coast distinct population segment, being 637,000 at delisting with ~400,000 of those in Peru; 10) USFWS (2020c) reports 7,800 clusters that hold family groups. We multiplied this by a factor of 2 and 2.5 to estimate population ranges; 11) Minimum number of adult males counted on surveys within the US = 5,244, assuming a 1:1 sex ratio, the minimum population = 10,488. A more advanced population estimate from Fort Hood M.I., Fort Sill M.I., Kerr WMA, Wichita Mountains NWR, and Val Verde alone included 14,418 individuals in 2013–2014. Population estimates from across the US totaled >15,498 individuals using data from 2009-2014 and advanced methods. Mexico breeding populations are not included in the abundance estimates, but they likely exceed the US population.

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Appendix B. Whooping Crane threat categorizations for the Aransas-Wood Buffalo Population (AWBP), the Eastern Migratory Population (EMP), and the Louisiana Non-migratory Population (LNMP). Categorizations consist of threat drivers, their categorization as direct (D) or indirect (I), their contribution to an overarching stressor, and categorization under the Endangered Species Act (ESA) Threat Factors. Threats are assessed per population and range including for breeding (Breed), migration (Migrate), wintering (Winter), and/or "range" (for LNMP). The potential impact of threats is classified per risk assessment categories including catastrophic (Catastr.; highest), critical, marginal (Marg.), minor, and negligible (Negl.; lowest). The trend in threat exposure [or probability of] is assessed across the period of active federally engaged conservation for each population (e.g., 1967-2022 for AWBP). Trends are also forecasted for the next 10 years per the scientific literature. Details on classifications including key notes and citations are provided on a per threat driver basis. Trend categorizations include increasing (Inc.), stable, decreasing (Dec.), and "mixed" (varied throughout the population's range).

Threat Categorizations				**AWBP**					**EMP**				**LNMP**			**Details**	
Threat	**Direct/ Indirect**	**Notable Driver(s)**	**ESA Threat Factors**	**Impact**			**Trends**		**Impact**		**Trends**		**Impact**	**Trends**		**Key Notes**	**Key Citations**
				Breed	***Migrate***	***Winter***	***1967 - 2022***	***10-Yr. Forec.***	***Breed***	***Winter/ Migrate***	***2001 - 2022***	***10-Yr. Forec.***	***Range***	***2011 - 2022***	***10-Yr. Forec.***		

Habitat Loss	I	Agricultural Expansion	A	Negl.	Critical	Minor	Inc.	Inc.	Negl.	Minor	Stable	Mixed	Negl.	Dec.	Dec.	↓ Wetland & grassland for ↑ Ag. in Great Plains. Ag. ↓ WI, ↓ LA, ≈ IN	CLUE 2013, McBride et al. 2018, Homer et al. 2020
Habitat Loss	I	Invasive Species	A	Negl.	Critical	Critical	Inc.	Inc.	Marg.	Marg.	Inc.	Inc.	Critical	Inc.	Inc.	*Phragmites australis* (migration), *Triadica sebifera*, *Avicennia germinans* (wintering)	Kessler et al. 2011, Wheeler & Ding 2014
Habitat Loss	I	Suburbaniza-tion	A	Negl.	Marg.	Critical	Inc.	Inc.	Minor	Marg.	Inc.	Inc.	Minor	Inc.	Inc.	↑ Human infrastructure, roads, across regions	Blair & Johnson 2008, Homer et al. 2020
Habitat Loss	I	Woody Encroachment	A	Marg.	Critical	Critical	Inc.	Inc.	Marg.	Minor	Inc.	Inc.	Marg.	Inc.	Inc.	↓ Flooding frequency & fire return intervals. Altered grazing regimes	Giri & long 2016, IUCN 2020, Caven et al. 2022, Keim et al. 2022
Habitat Loss, Env. Cond.	I	Surface/Ground Water Over-appropriation	A, D	Minor	Catastr.	Catastr.	Inc.	Inc.	Minor	Marg.	Inc.	Stable	Minor	Stable	Stable	↓ Instream flows & estuary inflows	Sandford 2015, Atkins et al. 2017, Caven et al. 2019
Habitat Loss, Env. Cond., Physical Harm	I/D	Extractive Industries Development	A, D, E	Critical	Marg.	Marg.	Inc.	Inc.	Negl.	Minor	Dec.	Stable	Marg.	Stable	Stable	↑ Tar sands, mining, oil & natural gas extraction including development footprints	Allred et al. 2015, Holcomb et al. 2015, Berg 2022, Roberts et al. 2022

Habitat Loss, Env. Cond.	I/D	Climate Change	A, E	Critical	Critical	Catastr.	Inc.	Inc.	Marg.	Marg.	Inc.	Inc.	Critical	Inc.	Inc.	↓ Surface water, ↓ permafrost, ↓ snowpack, ↑ sea-level rise	McIntyre et al. 2014, Butler et al. 2017, Fassnacht et al. 2018, Holsinger et al. 2019, Törnqvist et al. 2020, Golden et al. 2022
Habitat Loss, Physical Harm	I/D	Alternative Energy Infrastructure	A, E	Negl.	Marg.	Marg.	Inc.	Inc.	Minor	Marg.	Inc.	Inc.	Negl.	Inc.	Inc.	↑ Wind & solar farms & associated infrastructure	Lopez et al. 2012, Ott et al. 2021, Ellis et al. 2022
Physical Harm	D	Shootings	B	Negl.	Marg.	Marg.	Inc.	Inc.	Marg.	Critical	Stable	Stable	Critical	Inc.	Inc.	↑ With population growth. Several likely undetected	Condon et al. 2019, LDWF 2021, 2022; Thompson et al. 2022
Disease	D	Highly Pathogenic Avian Influenza	C	Marg.	Critical	Critical	Inc.	Inc.	Critical	Critical	Inc.	Inc.	Marg.	Inc.	Inc.	Capacity to cause high mortality where birds are concentrated	Ramey et al. 2021, CMS FAO 2022, Stokstad 2022
Disease	D	Other Diseases	C	Minor	Minor	Minor	Stable	Stable	Minor	Minor	Stable	Stable	Minor	Stable	Stable	Eastern Equine Encephalitis, West Nile Virus, Infectious Bursal Disease, Aspergillosis, Avian Tuberculosis, Avian Cholera, Coccidiosis	Snyder et al. 1991, Hansen et al. 2008, Bertram et al. 2015, Hartup 2019, Hartup & Phillips 2022, Olsen et al. 2019, Yaw et al. 2020
Disease	I	Waterbird Concentrations	C	Negl.	Critical	Marg.	Inc.	Inc.	Marg.	Marg.	Inc.	Inc.	Negl.	Inc.	Inc.	↓ Wetland = ↑ waterbird densities.	Blanchong et al. 2006, Caven et al. 2020, Yin et al. 2022

Physical Harm	D	Predators	C	Marg.	Minor	Marg.	Inc.	Inc.	Critical	Marg.	Stable	Stable	Marg.	Stable	Stable	*Lynx canadensis*, *L. rufus*, *Canis lupus*, *C. latrans*, *Vulpes vulpes*, *Mustela vison*, *Ursus americanus*, *Alligator mississippiensis*, *Haliaeetus leucocephalus*, *Aquila chrysaetos*, *Corvus corax*	Bergeson et al. 2001, Roberts & Crimmins 2010, Butler et al. 2017, Pearse et al. 2019, Rabbe et al. 2019, LDWF 2021, 2022; Yaw et al. 2020, Thompson et al. 2022
Physical Harm, Disease	I	Limited Genetic Diversity	C	Minor	Minor	Minor	Stable	Stable	Marg.	Marg.	Inc.	Inc.	Marg.	Inc.	Inc.	Critical uncertainties remain & genetic diversity may be slowly declining	Glenn et al. 1999, Jones et al. 2010, Boardman et al. 2021
Pollution	D	Toxins (e.g., lead, mercury, *Fusarium* spp.)	C	Minor	Minor	Minor	Mixed	Mixed	Minor	Minor	Stable	Stable	Minor	Stable	Stable	≈ Overall heavy metal contaminant inputs but ↑ in agrochemical & petroleum-based product contamination. Uncertain impacts on WHCRs.	Benbrook 2012, Hartup et al. 2021, Korosi et al. 2018, Pattee & Pain 2003, Yaw et al. 2020
Disease, Habitat Loss	D/I	Poultry CAFOs	C, A	Negl.	Marg.	Marg.	Inc.	Inc.	Minor	Marg.	Inc.	Inc.	Negl.	Stable	Stable	↑ Concentration near major stopovers	Lee et al. 2021, Moore et al. 2021
Pollution	D	Chemical/Oil Spills	C, E, A	Marg.	Marg.	Critical	Inc.	Inc.	Marg.	Minor	Inc.	Inc.	Critical	Inc.	Inc.	↑ Diluted bitumen in tar sands pipelines raising risks & impacts of spills	Swift et al. 2011, Murphy et al. 2014, Bidwell et al. 2017, Burger 2017

Physical Harm	D	Aerial Collisions (Powerlines, Towers)	E	Negl.	Marg.	Minor	Inc.	Inc.	Marg.	Marg.	Inc.	Inc.	Critical	Inc.	Inc.	↑ Infrastructure to support energy development	Jenkins et al. 2010, Smith & Dwyer 2016, Baasch et al. 2022b; LDWF 2021, 2022
Physical Harm, Env. Cond.	D/I	Hurricanes	E, A	Negl.	Negl.	Marg.	Inc.	Inc.	Negl.	Negl.	Stable	Inc.	Critical	Inc.	Inc.	Direct exposure likely in LA, potential in TX with climate change. Potential catalyst for coastal erosion	Traylor-Holzer 2019, LDWF 2021, 2022; Woolley et al. 2022

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Appendix C. Thirty-four fatal shooting incidents of 49 Whooping Cranes documented across the Aransas Wood Buffalo Population (AWBP), Florida Non-migratory Population (FNMP), Eastern Migratory Population (EMP), and Louisiana Non-Migratory Population (LNMP) from 1967-2022 by month and year of occurrence, province or state (Location), the number of Whooping Cranes poached, as well as the poached birds' sex and age.

Month and Year	Population	Location	Number of Whooping Cranes Poached	Sex	Age (Years)
Dec. 2021	AWBP	Oklahoma	4	-	-
Nov. 2019	LNMP	Louisiana	1	Male	11
April 2019	EMP	Ontario	1	Female	1
Nov. 2018	LNMP	Louisiana	1	Male	2
July 2018	LNMP	Louisiana	1	Male	7
Dec. 2017	LNMP	Louisiana	1	Female	5
Jan. 2017	EMP	Indiana	1	Female	5

May 2016	LNMP	Louisiana	2	Male, Female	1, 1
Jan. 2016	LNMP	Texas	2	Male, Female	2, 2
Nov. 2014	LNMP	Louisiana	1	Female	1
Feb. 2014	LNMP	Louisiana	2	Female, Male	3, 4
Dec. 2013	EMP	Indiana	1	Female	4
Nov. 2013	EMP	Kentucky	2	Female, Male	4, 6
July 2013	EMP	Wisconsin	1	Female	2
April 2013	LNMP	Louisiana	1	Female	3
Jan. 2013	AWBP	Texas	1	-	-
April 2012	AWBP	South Dakota	1	Male	-
Jan. 2012	EMP	Indiana	1	Male	3
Jan. 2012	AWBP	Texas	1	-	<1
Dec. 2011	EMP	Indiana	1	Male	6
Oct. 2011	LNMP	Louisiana	3	Male, Female, Female	1, 1, 1
Jan. 2011	EMP	Alabama	2	Female, Male	<1, 6
Dec. 2010	EMP	Georgia	3	Male, Male, Female	<1, <1, <1
Nov. 2009	EMP	Indiana	1	Female	7
Dec. 2004	EMP	Alabama	1	Female	2
Nov. 2004	AWBP	Kansas	3	-	-
July 2004	EMP	Michigan	1	Male	1
Nov. 2003	AWBP	Texas	1	-	-
Nov. 2000	FNMP	Florida	2	Male, Male	8, 8
May 1999	FNMP	Florida	1	-	-
April 1991	AWBP	Texas	1	-	-
April 1990	AWBP	Saskatchewan	1	-	-
Jan. 1989	AWBP	Texas	1	Female	-
1968	AWBP	Texas	1	-	-