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CHAPTER

6

Mortality in Aransas-Wood Buffalo Whooping Cranes: Timing, Location, and Causes

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INTRODUCTION

The Aransas-Wood Buffalo Population (AWBP) of Whooping Cranes (*Grus americana*) has experienced a population growth rate of approximately 4% for multiple decades (Butler et al., 2014a; Miller et al., 1974). Population growth for long-lived species of birds is generally highly sensitive to variation in adult mortality rates (Sæther and Bakke, 2000). A population model for endangered Red-crowned Cranes (*Grus japonensis*) in Japan conforms to this pattern, where growth rate is most sensitive to adult mortality (Masatomi et al., 2007). Earlier analyses observed that the AWBP growth rate increased in the mid-1950s and that this increase was likely caused by reduced annual mortality rates, even while the population experienced slightly decreasing natality (Binkley and Miller, 1988; Miller et al., 1974). A more contemporary analysis of the AWBP determined that approximately 50% of variation in annual population growth could be explained by variation in annual mortality (Butler et al., 2014a). Therefore, as a vital rate, mortality is critical to the maintained growth of the AWBP.

Understanding where, when, and why animals die can be of use for setting priorities among multiple management, conservation, or reintroduction practices. The Whooping Crane recovery plan lists numerous threats that relate to mortality and includes identification of mortality

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factors, and reducing mortality rate specifically, as important recovery actions (Canadian Wildlife Service and U.S. Fish and Wildlife Service, 2005). Using information primarily from winter aerial surveys, Lewis et al. (1992) estimated 19% of mortality occurred during winter. Because few deaths had been documented during the breeding or summer season, Lewis et al. (1992) speculated that 60–80% of annual mortality occurred during migration and the small remainder occurred during breeding. Migration in Whooping Cranes specifically and migratory birds in general has been thought to be especially dangerous because of exposure to potential hazards encountered in unfamiliar areas (Lewis et al., 1992; Newton, 2008). Causes of mortality have been determined for a limited number of deaths and, in certain instances, causes have related to man-made structures or human activities (e.g., collision with power lines, gunshot; Stehn and Haralson-Strobel, 2014). Therefore, the notion that most mortality has occurred during migration has motivated recovery objectives and actions (Canadian Wildlife Service and U.S. Fish and Wildlife Service, 2005).

Current information on causes, timing, and location of mortality of AWBP Whooping Cranes has known biases and limitations. Specifically, few mortality events estimated from winter surveys have been confirmed with carcass recovery; thus, knowledge of where or why birds die is sparse. Furthermore, certain areas within the AWBP annual range are remote, whereas other areas are more densely populated and much more likely to yield discovery of a Whooping Crane carcass. Thus, recovered of carcasses may not be a representative sample of all deaths. The use of birds marked with satellite telemetry can provide less biased mortality information. We review what is known about patterns of mortality in Whooping Cranes, provide updates based on a sample of birds marked with transmitters, and compare our results with those presented previously. This review provides insights for management of this population and for comparison with reintroduction efforts underway and in the future.

METHODS

During 2009–14, we captured 68 individual Whooping Cranes. The AWBP was estimated to have between 264 and 314 individuals during these years (Butler et al., 2014a, 2014b; U.S. Fish and Wildlife Service, 2015). At sites in and adjacent to Wood Buffalo National Park, we marked 31 prefledged juvenile cranes during August 2010 (9), August 2011 (12), and July and August 2012 (10). At sites along the Texas Gulf coast in the primary wintering areas, including the Aransas National Wildlife Refuge Complex, the Lamar Peninsula, and Welder Flats (Smith et al., Chapter 13, this volume), we captured 35 subadult or adult cranes during December 2009 (1), January 2011 (1), November–December 2011 (11), November 2012–January 2013 (11), and January–February 2014 (11). Finally, we captured two fledged juvenile cranes along the Texas Gulf coast, one during December 2009 and the other during January 2013. Capture teams consisted of persons with experience handling endangered cranes, including a licensed veterinarian. We captured prefledged juvenile cranes before they were capable of flight (approximately 40–60 days old) at breeding sites by locating family groups via helicopter and positioning personnel nearby for ground pursuit and hand capture (as described in Kuyt, 1979). We captured cranes in Texas using leg snares, which enclosed on the bird's lower tarsus (Folk et al., 2005). We placed the band and transmitter on the tibiotarsus of captured birds. Transmitters were platform transmitting terminals with global position system capabilities (North Star Science and Technology LLC, Baltimore, MD and Geotrak, Inc., Apex, NC) mounted on a two-piece leg band (Haggie Engraving, Crumpton, MD). Transmitters had solar panels integrated on three exposed surfaces and were expected to provide a 3–5-year life span. The transmitter and leg band weighed approximately 75 g, which was approximately 1% of body mass of adult Whooping Cranes. Survival of 651 Sandhill Cranes (*Grus canadensis*) fitted with similar-sized transmitters also mounted on leg bands had similar survival rates compared with cranes fitted only with metal U.S. Geological Survey bands, suggesting low potential for markers to negatively influence survival (Pearse et al., 2012). Transmitters were programmed to collect four or five GPS locations daily at equal time intervals and to attempt upload of location data to the Argos satellite system every 56 h (Service Argos, 2008). Capture and marking was conducted under Federal Fish and Wildlife Permit TE048806, Texas research permit SPR-1112-1042, Aransas National Wildlife Refuge special use permit, Canadian Wildlife Service Scientific Permit NWT-SCI-10-04, Parks Canada Agency Research and Collection Permit WB-2010-4998, and Northwest Territories Wildlife Research Permits WL004807, WL004821, and WL500051. Procedures were approved by the Animal Care and Use Committee at Northern Prairie Wildlife Research Center and Environment Canada's Animal Care Committee.

To summarize and compare with previously published reports, we identified four age classes of cranes: prefledged juveniles, fledged juveniles, subadults, and adults. Cranes were considered prefledged juveniles from hatching until they displayed the ability to fly by leaving their natal area. We marked prefledged juveniles exclusively at Wood Buffalo National Park. We captured all other age classes while they were on their wintering grounds. Fledged juveniles had the ability to fly and were less than 1 year old. We assigned birds to the subadult category (between 1 and 2 years of age) based on the presence of brown contour feathers. All birds with completely white body plumage were considered adults (2 years or older).

We determined mortality events primarily based on carcass and transmitter recovery. Generally, we were able to determine death initially by lack of movement in transmitter locations, but transmitter failures introduced uncertainty in some instances (Hays et al., 2007). Thus, we included two types of mortality events in summaries (Table 6.1). We identified mortalities as confirmed with a known location only upon recovery of a carcass with transmitter or identifying bands. For two cranes only, mortality was suspected based on circumstantial evidence rather than carcass recovery. An example of such evidence was a sudden cessation of data acquisition from a transmitter along with no additional sightings of that bird, generally for years after the suspected mortality. We present summaries including and excluding those two suspected mortalities. Furthermore, we summarize with and without deaths that occurred <14 days after capture, a time period that we used to represent transmitter acclimation (Withey et al., 2001).

We assigned date of death based on interpretation of movements and motion sensor information from transmitters. We categorized mortality by season in the annual cycle of cranes: summer, spring migration, winter, and fall migration. Seasons were assigned based on time of year and migration behavioral patterns of individual cranes. Cranes were identified as wintering if they remained at a southern terminus for more than three weeks. Beginning of spring migration was identified by northerly movements from wintering areas. The summer period was defined as the northern terminus of yearly locations, and fall migration began with southerly movements from summering areas (Krapu et al., 2011; Pearse et al., 2015). We assessed the relative influence of deaths during each season using cause-specific mortality analyses. We used a nonparametric cumulative incidence function estimator to estimate mortality rates during different times of the year under a competing risks framework (Heisey and Patterson, 2006). We used this method because it accounts for multiple mortality factors and accounts for different numbers of individuals at risk throughout

TABLE 6.1 Confirmed and Suspected Deaths, 2010–15, of Whooping Cranes of the AWBP Marked with Satellite Telemetry Devices

Marking			Mortality					
Bird ID	**Date**	**Age**[a]	**Type**	**Date**	**Age**[a]	**Season**[b]	**State/Province/ Territory**	**Cause**[c]
C01	01/08/11	A	Confirmed	06/12/11	A	S	NWT[d]	Unknown
B01	08/04/10	Pre-FJ	Confirmed	08/05/11	SA	S	NWT	Undetermined
B09	08/03/10	Pre-FJ	Confirmed	10/05/11	SA	S	NWT	Undetermined
C19	08/02/11	Pre-FJ	Confirmed	11/08/11	FJ	FM	Kansas	Unknown
C20	08/03/11	Pre-FJ	Confirmed	11/30/11	FJ	W	Texas	Potential bacterial infection
C18	08/02/11	Pre-FJ	Confirmed	01/06/12	FJ	W	Texas	Undetermined
C14	08/02/11	Pre-FJ	Confirmed	02/09/12	FJ	W	Texas	Undetermined
C17	08/02/11	Pre-FJ	Confirmed	06/07/12	SA	S	NWT	Undetermined
D27	08/01/12	Pre-FJ	Confirmed	08/04/12	Pre-FJ	S	NWT	Predation
D22	07/31/12	Pre-FJ	Confirmed	08/14/12	Pre-FJ	S	NWT	Undetermined
C16	08/03/11	Pre-FJ	Confirmed	08/18/12	SA	S	Alberta	Undetermined
A01	12/10/09	FJ	Confirmed	04/08/13	A	SM	South Dakota	Predation
D26	08/01/12	Pre-FJ	Confirmed	12/17/13	SA	W	Texas	Injury (see text)
D40	12/12/12	A	Confirmed	12/31/13	A	W	Texas	Undetermined
E50	02/02/14	SA	Confirmed	02/03/14	SA	W	Texas	Unknown
E54	02/03/14	SA	Confirmed	02/04/14	SA	W	Texas	Unknown
D41	01/08/13	FJ	Confirmed	03/30/15	SA	W	Texas	Undetermined
B02	08/03/10	Pre-FJ	Suspected	08/13/10	Pre-FJ	S	NWT	NA
D29	08/01/12	Pre-FJ	Suspected	11/23/12	FJ	FM	Nebraska	NA

[a] *A = Adult; SA = subadult; FJ = fledged juvenile; Pre-FJ = prefledged juvenile.*
[b] *S = Summer; W = winter; SM = spring migration; FM = fall migration.*
[c] *Cause was assigned as "Undetermined" if necropsy was inconclusive as to cause of death. Cause was assigned as "Unknown" if no necropsy was attempted.*
[d] *NWT = Northwest Territories, Canada.*

the year. We performed analyses using the *wild1* package in R (Sargeant, 2011). Finally, we estimated daily survival rates for each season by determining number of days cranes were monitored and at risk each season (Pollock et al., 1989).

Locations of mortality events were reported as latitude and longitude in the World Geodetic System, 1984 datum. We also reported locations by state, province, or territory and county or rural municipality. In instances where deaths were suspected, location of mortality refers to the last known location of the bird before cessation of data transmission; we suspected death occurred within the vicinity of the location but lacked definitive evidence.

We report cause of mortality based on assignments made from information developed from necropsies conducted by the Canadian Cooperative Wildlife Health Centre, U.S. Geological Survey Wildlife Health Laboratory, or U.S. Fish and Wildlife Service National Wildlife Forensics Laboratory. Necropsies were not available for all birds, or not practical when remains were in poor condition or incomplete (e.g., bones and feathers only). In other instances, a necropsy was carried out, but a definitive cause of death could not be assigned because of the deteriorated state of remains. We classified cause of mortality as *undetermined* when a necropsy was conducted and cause of mortality could not be diagnosed. The term *unknown* was assigned as a cause when a necropsy was not performed. Finally, we assigned *not applicable (NA)* to suspected mortalities when a carcass was not available for necropsy.

RESULTS

Among 68 Whooping Cranes marked with transmitters, we confirmed deaths of 17 by recovering remains between 12 June 2011 and 30 March 2015 using location information provided by satellite transmitters. Birds confirmed or suspected dead were marked as adults (2), subadults (2), fledged juveniles (2), and prefledged juveniles (11). At death, three birds were adults, seven subadults, four fledged juveniles, and two prefledged juveniles. Median time between estimated time of death and carcass recovery was 16 days (mean = 40 days; minimum = 1 day; maximum = 291 days).

We suspected mortality but could not confirm it in two instances. Bird B02 was marked as a prefledged juvenile and its transmitter ceased functioning 10 days after marking, suggesting a potential mortality event or transmitter malfunction. We received one additional GPS location from the transmitter on 20 February 2011 (192 days after last signal) 300 meters from its last location in Wood Buffalo National Park. To our knowledge, the bird had not been observed and reported since marking in 2010. The other suspected mortality was Bird D29, which showed unusual movements before the date of suspected death. This fledged juvenile was in its first fall migration and making typical southerly movements until reaching northern Oklahoma. After one night in Oklahoma, the bird flew north to central Kansas, where it had spent time previously. After three nights in Kansas, the bird moved farther north into south-central Nebraska. We collected six days of data in this location and then received no further information. This lengthy reverse migration of approximately 450 km was unique in our project thus far. Furthermore, the U.S. Fish and Wildlife Service received public reports of a single juvenile Whooping Crane in central Kansas at the same time and place as Bird D29 (R. Laubhan, U.S. Fish and Wildlife Service, personal communication). Because juvenile birds are typically accompanied by parents during fall and winter (Urbanek and Lewis, 2015), we suspect this juvenile may have been separated from its parents during migration. Similar to the other suspected mortality, Bird D29 has not been observed again since its suspected death in 2013.

Mortalities occurred in all seasons and over a wide time frame within summer and winter. During summer, the first mortality occurred on 7 June and the last occurred on 5 October (Table 6.1). In winter, deaths occurred between 30 November and 30 March. Both mortalities during fall migration occurred in November (8th and 23rd) and the single mortality during spring migration occurred on 8 April. We summarized mortality timing by season using various subsets of data. Including all confirmed and suspected deaths, eight mortalities occurred during summer, eight during winter, and three during migration (fall and spring combined). Estimated annual mortality related to factors occurring during winter was greatest and similar to summer (Table 6.2). Based on cause-specific rates, deaths occurring during winter accounted for 43% of annual mortality; 41% of deaths occurred during summer, and 16% during migrations. Including only events confirmed and those occurring after an acclimation period, six mortalities occurred during summer, six during winter, and two during spring and fall migrations. Cause-specific mortality rates for summer and winter were greatest and similar (Table 6.2). Mortality during winter accounted for 44% of annual mortality; 42% of deaths occurred during summer, and 14% during migrations. For fledged juvenile birds or older birds, we recorded five deaths during summer, six deaths during winter, and two deaths during migrations. Mortality during winter was greatest and accounted for 47% of overall annual mortality; 38% of deaths occurred during summer, and 15% during migration (Table 6.2).

We monitored 68 Whooping Cranes for a total of 34,948 days during winter (41%), summer (40%), and migration (19%). Daily survival during migration (S = 0.99954; 90% CI = 0.99910–0.99998) was slightly greater than during summer (S = 0.99943; 90% CI = 0.99910–0.99976) or winter (S = 0.99944; 90% CI = 0.99912–0.99977), yet 90% confidence intervals overlapped, suggesting differences in point estimates may have been due to chance alone.

Confirmed mortalities during migration occurred in South Dakota and Kansas, and we suspected one death in Nebraska (Fig. 6.1A). All deaths in the summer period occurred within

TABLE 6.2 Estimates of Annual Mortality (m) and Numbers of Deaths (n), 2010–15, for Whooping Cranes of the AWBP Marked with Satellite Telemetry Devices

Data subset	Season	n	m	SE	90% CI	% of overall
All	Summer	8	0.060	0.021	0.026, 0.094	41
	Winter	8	0.064	0.022	0.028, 0.100	43
	Migration	3	0.023	0.013	0.001, 0.045	16
	Overall	19	0.147	0.031	0.096, 0.199	
Restricted[a]	Summer	6	0.047	0.019	0.016, 0.079	42
	Winter	6	0.049	0.019	0.017, 0.081	44
	Migration	2	0.016	0.011	0.000, 0.035	14
	Overall	14	0.112	0.028	0.066, 0.159	
Postfledged birds only	Summer	5	0.040	0.018	0.011, 0.069	38
	Winter	6	0.049	0.020	0.017, 0.081	47
	Migration	2	0.016	0.011	0.000, 0.035	15
	Overall	13	0.106	0.028	0.060, 0.151	

[a] *Includes mortality events confirmed with carcass recovery and those occurring 14 days post marking to account for potential biases from capture and marking.*

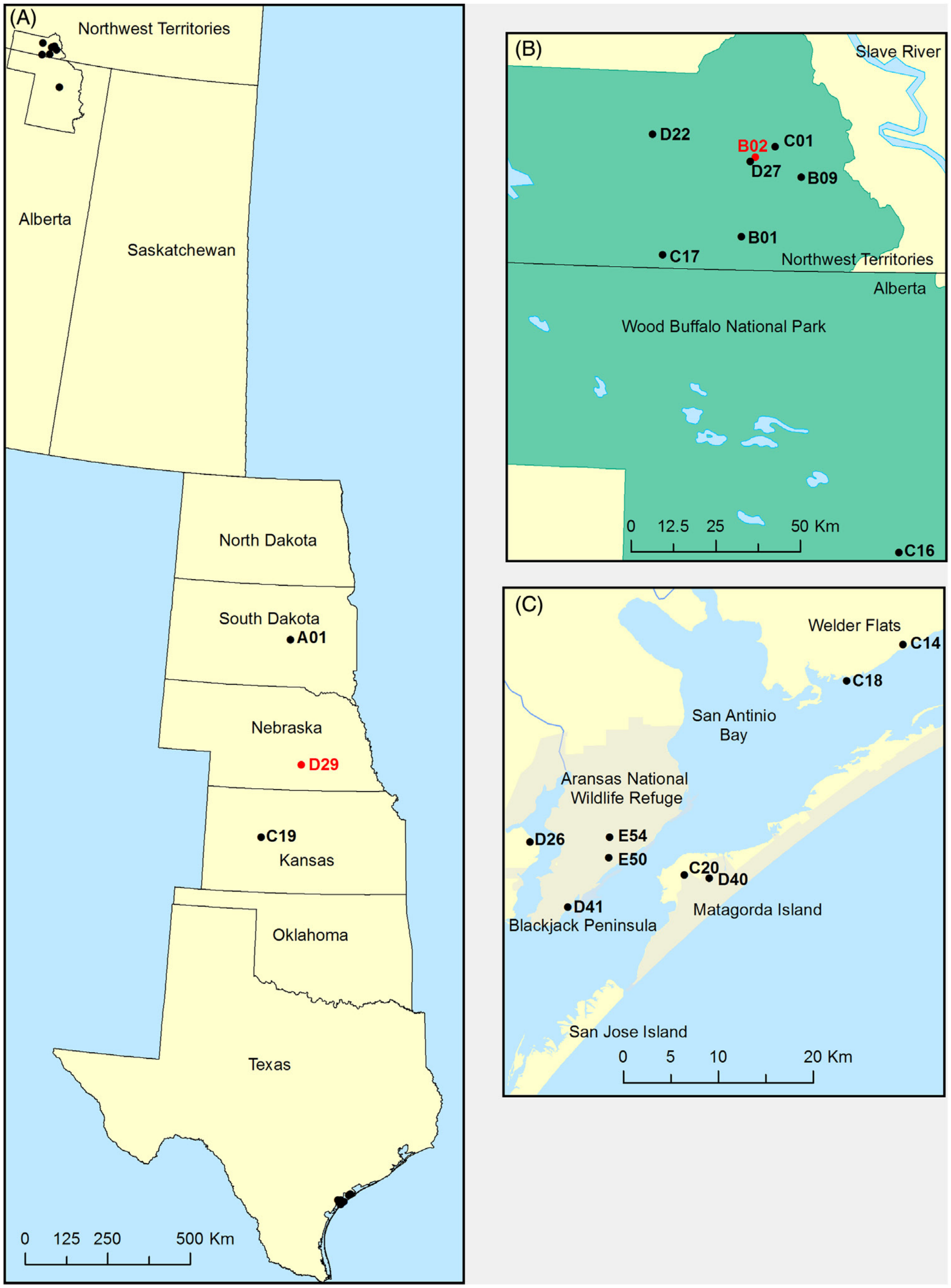

FIGURE 6.1 Locations of confirmed (black) and suspected (red) deaths of Whooping Cranes of the Aransas-Wood Buffalo Population (AWBP) marked with satellite transmitters, 2010–15 in the migration corridor (A), at Wood Buffalo National Park, Canada (B), and at the Texas Gulf Coast at and near Aransas National Wildlife Refuge (C).

Wood Buffalo National Park, and all but one within an approximately 30 km radius within the main nesting area (Johns et al., 2005; Fig. 6.1B). Finally, mortality during winter was distributed among traditional wintering locations such as the Blackjack Peninsula (three), Matagorda Island (two), and Welder Flats (two; Fig. 6.1C). Bird D26 was captured on the Lamar Peninsula and died in captivity at the San Antonio Zoo (see later).

Predation and disease were known causes of mortality for Whooping Cranes in our study (Table 6.1). For most confirmed mortalities ($n = 13$), cause of death could not be determined because of the advanced state of scavenging and/or decomposition. Cause of death was more likely determined where carcasses were recovered somewhat more quickly (median of 9 days postmortality) compared to the overall median recovery time of 16 days.

We included Bird D26 as a mortality event, although this bird was captured, removed from the remnant population, and perished in captivity. Approximately 2 months prior to capture, Bird D26 was observed at the wintering grounds near the ultimate capture site with a severed lower left leg. The cause of this injury was not known. At the request of the U.S. Fish and Wildlife Service, the bird was captured on 17 December 2013 and transported to the San Antonio Zoo for further assessment and treatment. The bird perished in captivity approximately 6 weeks after capture. We included this incident as a winter mortality because, based on the physical condition of the bird at capture and extent of the injury, our team believed it would not have survived the entirety of the winter.

We confirmed an additional mortality of a radio-marked bird that has not been included in Table 6.1. Remains of an adult Whooping Crane from our study were found without aid of transmitter location data on San Jose Island in June 2015 by a member of the public (Fig. 6.1B). The last transmission we received was within approximately 2 km of where the remains were found in early October 2014 but, at that time, we did not have sufficient information to determine whether the bird had died or the transmitter had malfunctioned. Based on location data, we could not determine timing of death. Thus, this mortality was confirmed by observation alone, similar to those reported in Lewis et al. (1992) and Stehn and Haralson-Strobel (2014) rather than via transmitter information. Because this mortality was identified solely from recovery of carcass without determining death from location data, we did not include it in summaries above.

DISCUSSION

Timing of Mortality

Previously available information on seasonal mortality of AWBP Whooping Cranes has come from three main sources. Information from the many years of winter aerial survey provided insights primarily regarding winter mortality (Strobel and Butler, Chapter 5, this volume). The proportion of mortality occurring from 1950 to 1987 during winter at Aransas NWR was estimated to be approximately 19% (Lewis et al., 1992) and 20% after an update (1950–2010; Stehn and Haralson-Strobel, 2014). Also using data from 1950–2010, Butler et al. (2014a) estimated 17% of annual mortality occurred during winter under average precipitation conditions and 43% under extreme drought conditions. Winter surveys also have been used to infer mortality at other times of the year. Based on few reported deaths during summer, researchers have speculated that 60–80% of deaths likely occurred during migration and only a small percentage of annual mortality occurred during summer (Lewis et al., 1992; Stehn and Haralson-Strobel, 2014).

A second source of information comes from a previous radio-telemetry study. Kuyt (1992) reported fates of 15 Whooping Cranes, all marked as prefledged juveniles during summers 1981–83. This work confirmed or suspected deaths of 12 cranes; 6 (50%) before fledging at Wood Buffalo National Park, 4 (33%) during winter, and 2 (17%) during migration. Finally, the third source of data on mortality comes from 48 carcasses recovered. The greatest percentage of carcasses was found in areas where birds migrate (55%). Forty percent of carcasses were found on wintering areas and only 5% in areas typically used during summer (Stehn and Haralson-Strobel, 2014). Authors noted that recoveries at Wood Buffalo National Park were likely underrepresented because of the inaccessibility of the area to people who could potentially discover carcasses.

Because all mortalities could not be confirmed and some occurred soon after capture and marking, we provided multiple estimates of seasonal mortality based on various subsets of deaths, which resulted in consistent seasonal distributions of deaths. Winter tied for or had the greatest percentage of deaths in all summarizations (43–47%). Mortalities during summer were equal to winter or ranked second (38–42%), and migration consistently had the lowest percentage (14–16%). Whooping Cranes from the AWBP generally spend approximately 2 months in migration (17%) and 5 months each at summer and winter locations (41.5%; Urbanek and Lewis, 2015). The birds we monitored were at risk for similar percentage of time each season. Furthermore, daily survival rates were comparable among seasons, implying that daily risk of mortality was relatively equal among seasons during our study.

Some similarity and numerous differences existed in timing of Whooping Crane mortality between our results and those reported previously. Similar to the past telemetry study, we documented mortality of prefledged juvenile cranes before they left the breeding area and began fall migration, which is common in other bird species as well (Bergenson et al., 2001; Grüebler et al., 2014; Johnson et al., 1992; Kuyt, 1992). In contrast with previous studies, our results were markedly different from past information related to the AWBP and support the notion that mortality of subadult and adult Whooping Cranes during summer may have been underestimated and underappreciated. We documented more than double the number of mortality events on fledged birds than ever reported on summering grounds (two adults recovered; Stehn and Haralson-Strobel, 2014). Four subadults died in their second summer season, which corresponded with the cessation of parental attendance (Urbanek and Lewis, 2015). This timing suggested that initial independence from parents may be an especially risky time for young Whooping Cranes. Numerous deaths have been reported during summer in the Eastern Migratory Population of Whooping Cranes (53%, 9 of 17), with birds of all available age classes dying (Cole et al., 2009).

Migration has been identified as a time when 60–80% of AWBP Whooping Crane deaths occur (Lewis et al., 1992; Stehn and Haralson-Strobel, 2014). Our findings do not support these assertions and indicate that migration contributed the least proportionally to annual mortality while also representing the smallest proportion of the annual cycle. Migration posed a nearly equal rather than greater risk to Whooping Cranes as compared with other times of the year, because daily survival rates were similar among seasons. Mortality during migration has been difficult to study in birds, given their high mobility (Newton, 2008). Some studies have inferred the potential of high mortality during migration, as has been done with Whooping Cranes, when researchers were forced to combine multiple life events (e.g., breeding and migration) in survival estimates (Clausen et al., 2001; Madsen et al., 2002). High rates of mortality during migration have been observed more directly in other studies where season-specific estimates could be ascertained, providing evidence of the hazardous nature of migration (Klaassen et al., 2014; Lok et al., 2015; Oppel et al., 2015; Owen and Black, 1989; Sillett and Holmes, 2002). Yet this pattern is not universal, and numerous studies of many species have found migration of similar or less risk to birds than other times of the year [Pacific Brant (*Branta bernicla nigricans*), Ward et al., 1997; Greater Snow Goose (*Chen caerulescens atlantica*), Gauthier et al., 2001; Emperor Goose (*Chen canagica*), Hupp et al., 2008; Red Knot (*Calidris canutus*), Leyrer et al., 2013; Trumpeter Swan (*Cygnus buccinators*), Varner and Eichholz, 2012; Barn Swallow (*Hirundo rustica*), Grüebler et al., 2014; Sandhill Crane, Fronczak et al., 2015]. Relative seasonal mortality apparently varies between species and situations, suggesting our collective understanding of the risks faced by migratory birds during migration and throughout the rest of the year is incomplete and requires continued study.

Juvenile birds can experience lower survival rates than adults during their first fall migration (Owen and Black, 1989). Both mortality events during fall migration that we confirmed or suspected were juvenile birds. In Egyptian vultures (*Neophron percnopterus*), juveniles using a migration route over the Mediterranean Sea died at a much greater rate than those using an alternative overland route, and the authors suspected that lack of experienced birds in the population may have contributed to the deaths (Oppel et al., 2015). As Whooping Crane adults generally attend juveniles during their fall migration (Johns et al., 2005), risky situations where juveniles would be required to migrate alone would be rare. Accordingly, a suspected death we reported during fall migration may have been related to separation of the juvenile from its attending parents.

We found double the percentage of mortality during winter compared to previous estimates based on winter surveys. We suspect this discrepancy may be related to methodological aspects of aerial surveys, as well as winter weather and habitat conditions during our study. Determination of mortality via aerial survey of unmarked birds relies upon numerous assumptions, though Butler et al. (2014a) observed that violations would generally overestimate rather than underestimate the contribution of winter to annual mortality. Deaths occurring before many of the birds have arrived or after spring migration has begun (i.e., periods of turnover) or outside of when or where aerial surveys were conducted would potentially be missed entirely and misclassified. Such deaths that had occurred during winter but missed would be included the following year as losses occurring during migration or summer. We documented one death during winter at Aransas National Wildlife Refuge on 30 November 2011 as fall migration was ending and another death during winter on 30 March 2015, which occurred after the beginning of spring migration. If these two deaths had been incorrectly attributed to a season other than winter, the percentage of deaths during winter would have decreased to 29% (4 out of 14 confirmed and after acclimation period). It is unclear how winter surveys could consistently and reliably identify deaths that occurred during periods when birds were still arriving at or leaving the wintering grounds (Butler et al., 2014b).

The time period of our study coincided with consistent drought conditions on the wintering grounds. During our study, winter 2011–12 was classified as extreme drought, winter 2012–13 as severe drought, winter 2013–14 as moderate drought, and winter 2014–15 as mild drought (Palmer, 1965; National Climatic Data Center, 2007). Butler et al. (2014a) reported that drought conditions influenced winter mortality and extreme drought conditions could increase percentage of mortality occurring during winter up to 43%. Linkages between environmental conditions and annual or seasonal survival have been observed in other migratory birds. Kéry et al. (2006) found that pink-footed geese (*Anser brachyrhynchus*) survived at a greater rate during years when their wintering grounds were warmer and wetter. Poor habitat conditions influenced winter survival for oystercatchers (*Haematopus ostralegus*) in Europe (Duriez et al., 2012). Continued mortality monitoring of Whooping Cranes in times with less extreme drought or without drought would be useful to determine if poor environmental conditions were the primary cause of the higher incidences of winter mortality observed.

Our study was conducted over a limited time period and included few mortality events and as such may not be fully representative of AWBP mortality. Survival rate of the AWBP varies annually (Nedelman et al., 1987) as does season-specific mortality (Butler et al., 2014a). Our study was conducted in years of sustained drought conditions at wintering areas, which likely influenced results. These shortcomings will be somewhat overcome by adding more data as our project concludes, which we can use to update results and estimate season-specific mortality rates. In addition, our sample of mortality events was dominated by birds marked as juveniles and subsequently dying as young birds. Young Whooping Cranes have a greater mortality rate than older birds (Gil-Weir et al., 2012; Link et al., 2003; Nedelman et al., 1987), and they may die in different places, at different times, and from different causes. Given the high survival rate of adult Whooping Cranes, transmitters lasting greater than 5 years would be required to gather an unbiased and adequate sample of deaths from these long-lived birds.

Cause-Specific Mortality

Frequent known causes of mortality in Whooping Cranes include predation, collisions with power lines, gunshot, other trauma, and disease (Cole et al., 2009; Stehn and Haralson-Strobel, 2014). Predation and disease were the only known causes of mortality in our study. We were not able to add to existing knowledge of the causes of mortality in this population, as most recovered carcasses were degraded to a state where cause could not be determined. Power line collisions have been identified as an important cause of mortality for the AWBP and reintroduced populations of Whooping Cranes (Cole et al., 2009; Hartup et al., 2010; Stehn and Wassenich, 2008). We did not observe direct evidence from necropsy reports or indirect evidence based on location of remains near power lines to suggest mortalities in our sample resulted from power line strikes.

Stehn and Haralson-Strobel (2014) did not assign a cause to 24% of AWBP mortalities, and Cole et al. (2009) could not determine cause of death for 35% of a sample of Eastern Migratory Population of Whooping Cranes. We classified a high rate of confirmed mortalities to unknown or undetermined causes (76%). Our protocols for defining cause relied primarily on necropsy reports and used circumstantial evidence sparingly. Many of the remains were degraded because of scavenging and decomposition; hence, cause of death could not be determined. The carcasses for which cause of death was determined may present a biased picture of mortality overall (Bumann and Stauffer, 2002; Faanes, 1987; Flint et al., 2010). Our experience underscores the difficult task of determining cause-specific mortality for a wide-ranging migratory species or whenever circumstances prevent prompt collections of fresh carcasses. If determining cause-specific mortality is a primary objective of future studies, then using different monitoring devices that transmit more frequently may be necessary to identify deaths and collect carcasses more quickly.

SUMMARY AND OUTLOOK

The AWBP has experienced positive exponential growth for decades (Butler et al., 2014a; Miller et al., 1974). Increasing annual survival through management actions would result in an increased rate of population growth, potentially allowing the population to reach recovery status more quickly (Butler et al., 2013), as long as an adequate quality and quantity of habitat will exist to support a larger future population. For a migratory bird, knowing when deaths occur in the annual cycle provides insight to effectively implement conservation actions (Klaassen et al., 2014). We provided evidence that past assessments of timing of mortality may have been based on weak assumptions, suggesting some modifications to perceptions about risks and threats. Mortality of fledged Whooping Cranes at Wood Buffalo National Park occurred at a much higher rate than had been reported previously in the AWBP. This mortality occurred in remote areas where causes, although unknown in many cases, were likely related to natural phenomena (e.g., predation), which are unlikely to be modified without intensive and costly management. Conversely, migration may be less risky than previously assumed, with birds at a similar rather than an elevated risk as compared to summer or winter. Managers should expect only modest influence on annual survival rates from efforts to reduce mortality during migration, as a low percentage of deaths occurred during this time and cranes migrate for the shortest time period annually. Finally, our results supported earlier conclusions that mortality during winter can be a large component of annual deaths during times of drought. The primary wintering grounds of the AWBP are a condensed area where the birds remain for many months each year; thus, management efforts to increase survival during winter may be more effective than those conducted at summering grounds or more feasible than in the migration corridor. Such efforts may be effective at increasing annual survival if conducted in years of high winter mortality and less so when conditions are naturally more favorable. Conservation and management activities attempting to abate winter mortality, especially those related to drought conditions, will need to be identified and tested to determine risks, efficacy, and cost effectiveness. Because we documented few deaths of adult birds, more information of their mortality, especially that of actively breeding birds, would be useful to update our results. Future work could be directed at investigating potential patterns in seasonal survival, which may be cyclic especially during summer, as in the nature of other predator–prey relationships in northern latitudes and at times of average to good winter habitat conditions.

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