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A RETROSPECTIVE OF WHOOPING CRANES IN CAPTIVITY

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Abstract: Early records of captive whooping cranes (*Grus americana*) were compiled from historical files kept at the Aransas National Wildlife Refuge and other literature. Additional early records of captive whooping cranes in Europe were discovered. Annual numbers and location for all captive whooping cranes were tabulated. Starting in 1949, initial attempts at breeding the species in captivity were conducted opportunistically with a few injured birds captured from the wild. A captive breeding flock was started in 1966 at the Patuxent Wildlife Research Center in Laurel, Maryland, from second eggs collected in Canada from the only remaining wild flock. In 1989, the flock at Patuxent was split to guard against a catastrophic event from affecting the entire captive population. Currently, breeding occurs at 5 locations. The captive flocks are a safeguard of genetic material against catastrophic loss in the 266 birds currently in the Aransas-Wood Buffalo population. Captive production is also used to attempt to reintroduce additional flocks into the wild.

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Key words: breeding, captive propagation, *Grus americana*, whooping crane.

The whooping crane (*Grus americana*) is one of the most widely known endangered species in North America. All whooping cranes alive today were derived from only 15 wild individuals present Aransas National Wildlife Refuge (NWR), Texas, in the winter of 1941-42. Early haphazard attempts at propagation from 1949 to 1965 involved a few injured birds obtained opportunistically from the wild. An official whooping crane captive breeding program was initiated in 1966 at the Patuxent Wildlife Research Center (PWRC), Laurel, Maryland, with eggs and 1 injured wild-caught bird taken from Wood Buffalo National Park (WBNP) in the Northwest Territories of Canada (Lewis 1995). To guard against catastrophic loss at a single location, the captive flock was split among additional breeding facilities starting in 1989. One or 2 whooping cranes have also been placed for display purposes at 5 other institutions in the United States and 1 in Canada. As of October 2008, the world's captive whooping crane population consisted of 152 birds at 10 institutions. All whooping cranes are currently under joint stewardship of Canada and the United States through a memorandum of understanding that serves as an excellent example of international cooperation to save a species.

Captive propagation is often needed for organisms whose future cannot be ensured by conventional methods of legal protection and habitat management (Doughty 1989). The goals of the captive flocks are to protect the genetic material of the species in times of high risk and support reintroduction programs to establish additional flocks in the wild. Captive propagation also allows for the comprehensive investigation of key physiological or behavioral traits that can provide clues for the better management of wild populations and can contribute to education by enabling the public to view and become knowledgeable about those species in greatest jeopardy (Carpenter and Derrickson 1982).

This paper provides a retrospective on whooping cranes in captivity, ongoing breeding programs, and use of captive offspring. This paper also compiles all known records of captive whooping cranes prior to 1936, and provides the first ever annual numerical record and location of all whooping cranes in captivity.

METHODS

Literature research was done to validate the existence of captive whooping cranes documented in Allen (1952). Referenced documents in Allen (1952) were reviewed and additional leads from literature were pursued. Electronic mail was sent to a variety of sources in the eastern United States and Europe. During this process, additional historical records of captive whooping cranes were discovered.

The whooping crane studbook (Jones and Lacy 2007) was used to validate the captive population held since the start of the propagation program. Any bird living on 31 December of a given year was counted as being captive for that year. This was consistent with the methodology used for population tables in the recovery

plan for the whooping crane (CWS and USFWS 2007).

RESULTS

Early Records of Whooping Cranes in Captivity

Few whooping cranes were in early zoological collections (Pratt 1996), and information about them is limited (Doughty 1989). Validated records of captive whooping cranes and previously undocumented captive birds are given in Tables 1 and 2.

Allen's monograph of the whooping crane (1952) was the first known compilation of captive cranes. Additional records of captive cranes were found in Blaauw (1897) and Loisel (1912) and were not readily available to Allen. Blaauw (1897) documented the existence of 4 cranes in Europe prior to 1900. They were all purchased from the same bird dealer in Antwerp, Belgium. Whooping cranes were crated and transported by sailing ships to Europe. Archival records from the Amsterdam Zoo, now known as ARTIS, show that there were at least 5 whooping cranes in their collection starting in 1865 (R. Vleck, ARTIS, personal communication). Both Lord Lilford and the Duchess of Bedford were documented to have had whooping cranes in their avian collections in England (Allen 1952). In preparing this manuscript, 10 whooping cranes were validated in Europe prior to any captive breeding attempts. Seven had never been cited previously in whooping crane literature.

There were at least 13 whooping cranes in captivity in the U.S. and at least 3 in Mexico prior to 1936. Several of these birds were kept at private estates in the early 19th century, copying the manner of European estates of the time. One was a pet found by farm children in the upper Midwest (Allen 1952). Prior to the New Orleans Zoo receiving a crane in 1946, the only U.S. zoos to have had whooping cranes were the National Zoo in Washington, D.C., starting in 1897 and the Bronx Zoo in New York City in 1913. John James Audubon reported keeping a pet juvenile whooping crane in Boston that gradually turned from grayish-brown to white (Audubon 1835). However, Audubon hypothesized in that same account that sandhill and whooping cranes were the same species, so it is not clear whether his pet was a whooping crane.

Early Breeding Attempts

Due to limited knowledge of physiology and breeding requirements, early attempts at captive breeding of whooping cranes were fraught with mishaps caused by both humans and nature. These early propagation efforts that involved 4 birds are well

Table 1. Captive whooping cranes in Europe.

Number of birds	Location	Dates	Captured	Death	Years in captivity	References	Validation
1	Lilford Collection, County of Northampton, England	1892	Purchased as adult	1931	39	Allen1952	Moody 1931
5[a]	Amsterdam Zoo (aka Artis Zoo), Holland	1851 1851 1864 1868 1868		1852 1855 1865 1871	1 4 1 3	Moody 1931 Astley 1907 Blaauw1897	Vlek, ARTIS, Amsterdam, personal communication.
2	Woburn Park Collection, Woburn, England	1866				Allen 1952 Bedford 1907	Mitchell, 2007, Woburn Abby, Woburn, U.K., personal communication.
2[a]	Zoological Society of London, England					Blaauw1897	Palmer, 2008, Zoological Society of London, London, U.K., personal communication.

[a] Denotes birds previously not documented in the whooping crane literature, 1952-2008.

Table 2. Captive whooping cranes in North America prior to 1966.

Number of birds	Location	Dates	Captured	Death	Years in captivity	References	Validation
3[a]	Washington National Zoo, Washington, D.C.	1897	T12, R24, Sec. 18, west of 6th principal meridian of Kansas	1910	13[b]	Allen 1952 Loisel 1912	S. Hallager, 2007, Washington National Zoo, personal communication.
		1905[c]					
		1914	Hutchinson, Kansas[d]	1923	At least 9		
1	Bronx Zoo, New York	1913[e]		1929	16[e]	Allen 1952 McNulty 1966	Sheppard, Bronx Zoo, personal communication.
1	South Dakota Farm	1885	South Dakota	1888	3	Oliver 1948	
1	J. J. Audubon Home, Boston, Mass.		Florida			Audubon 1835	
1	Magwood, Charleston, S.C.					Audubon 1835	[f]
2[a]	C. W. Marsh Collection, DeKalb, Ill.	1890s	Minnesota	[g]	[g]		Marsh 1910
2+[h]	Hacienda el Molino, LaBarca, Jalisco, Mexico	1894				Allen 1952	[f]
1	Hacienda de Buena Vista, near Jalisco, Mexico	1903				Allen 1952	[f]
1	G.D. Tilley, Darien, Conn.					Allen 1952	Phillips 1912
1	The Grand Prairie, Dunklin Co., Missouri	1864				Widman 1907 as cited by Allen 1952	[f]
1	Scioto River, Ohio	1902				Henninger 1902 as cited by Allen 1952	[f]
1	Manhattan, Riley Co., Kansas	1884				Blachly (sic) 1884 as cited by Allen 1952	[f]

[a] Denotes birds previously not documented in the whooping crane literature.

[b] Smithsonian inventory record indicated bird hatched in 1896.

[c] Smithsonian inventory record indicated bird returned to owner, Dr. C. French, on 17 February 1906.

[d] Konrad C. Beck managed Riverside Park in Hutchinson, Kansas, starting in 1902. Beck had contacts with trappers and hunters around the world and was reported to have supplied animals to the Bronx Zoo (NYC), Lincoln Park Zoo (Chicago), and the Zoological Gardens (Hamburg, Germany). Riverside Park is reported to have had 1,000 birds in residence in special lagoons built for that purpose (Decker 2002).

[e] Inventory card shows bird "on hand" January 1, 1926. Acquisition date is unclear as McNulty (1966) writes that Dr. William Hornaday wrote of having a specimen in 1913. The inventory card could reflect this particular bird or a second one added to collection after loss of bird written about by Dr. Hornaday.

[f] The authors have not been able to validate these citations in Allen (1952).

[g] Marsh (1910) writes of 1 chick being killed by wild turkeys in his collection. Second chick, he writes survived to adulthood until shot after escaping.

[h] Allen (1952) records this as several birds; for purposes of this paper the author have chosen to use 2+.

chronicled (McNulty 1966, Doughty 1989, CWS and USFWS 2007). Three of these were injured birds captured from the Aransas-Wood Buffalo population (AWBP) (McNulty 1966, Maroldo 1980). The first whooping crane used for breeding in the U.S. was named Pete (studbook no. 1000), a crane captured from the AWBP in June 1936 and held near Gothenburg, Nebraska, for 11 years. In 1947, he was taken by the Bureau of Sport Fisheries and Wildlife to the Audubon Zoo in New Orleans, Louisiana, and paired with Josephine (studbook no. 1001), an injured nonmigratory whooping crane captured in Louisiana in 1941 (McNulty 1966, Pratt 1996). Josephine had remained solitary for her first 8 years in captivity (Pratt 1996) and became the last survivor of the non-migratory, southwestern Louisiana population. In 1948, Josephine and Pete were taken to a large salt marsh enclosure at Aransas NWR where they nested unsuccessfully in 1949. Pete died shortly thereafter. Josephine was re-paired with Crip (studbook no. 1002), an injured flightless wild bird at Aransas NWR. In 1950, the pair hatched 1 chick named Rusty (studbook no. 1003) at Aransas NWR, but a predator killed it a few days after hatching. Rusty was the first whooping crane chick hatched in captivity. After nesting unsuccessfully in 1951, Crip and Josephine were transferred to the Audubon Zoo. Chicks subsequently produced by Josephine and Crip, along with 1 adult crane transferred from the San Antonio Zoo, San Antonio, Texas, raised the number of whooping cranes in New Orleans to a peak of 7 birds in 1964 (McNulty 1966). Josephine died in 1965 after having lived in captivity for 25 years. She produced 13 chicks with Crip, 4 of which lived for more than a decade but left no survivors; the genetic material of the Louisiana non-migratory flock was lost.

In the mid-1950s, with only 3 whooping cranes in captivity, ownership and custody of the birds was being hotly debated (McNulty 1966). From 1951 to 1963, the San Antonio Zoo (Lauver 1992) and Audubon Zoo were the only locations holding captive whooping cranes. The number and location of all captive whooping cranes utilized for propagation from 1936 to 2007 are shown in Table 3. The names, pairings, and fledged offspring of the 4 original captive cranes are provided in Fig. 1. Offspring from these early attempts at captive breeding exist today in captive flocks and reintroduced flocks.

Events Leading To Establishment of a Captive Breeding Flock

As the Louisiana wild flock dwindled in the 1940s to a single captive bird in 1951, the migratory flock wintering in Texas during that same time period fluctuated between 15 and 34 birds. To guard against extinction of the AWBP, plans for propagating whooping cranes surfaced in the 1950s among Canadian wildlife experts in Saskatchewan (Lynch 1956, Doughty 1989). Captive propagation was formally proposed in June 1956 at the Twentieth Federal-Provincial Wildlife Conference held in Vancouver, Canada (Pratt 1996). At the meeting, biologist John Lynch from Louisiana recommended capturing young cranes to serve as a nucleus of breeders producing offspring in captivity to release back into the wild. This proposal, although passed by the participants, was very controversial and opposed by the National Audubon Society (McNulty 1966). Later in 1956, the 11th Congress of the International Union of Zoo Directors directed that a letter be sent to the U.S. Fish and Wildlife Service (USFWS) proposing that zoos be designated as possible breeding sites for whooping cranes as soon as possible (Dunlap 1991, Pratt 1996).

Starting in about 1959, the Bureau of Sport Fisheries and Wildlife began to accept the husbandry concepts espoused by aviculturists (Pratt 1996). By 1962, the policy of the Bureau intended to take full advantage of the aviculture talent available in zoological parks and private aviaries for the propagation of whooping cranes (Pratt 1996). Aviculturists hoped to eventually re-establish the species by releasing captive-bred individuals directly in the wild or by transferring eggs or young to be reared by foster parents (Doughty 1989).

The actual implementation of a captive breeding program fell initially to Bureau of Sport Fisheries and Wildlife biologist Ray Erickson (Doughty 1989). Based on an analysis of the Aransas NWR winter population counts from 1938 to 1960, Erickson (1961, U.S. Fish and Wildlife Service, unpublished administrative report) reiterated Lynch's proposal to bolster the wild population through captive propagation and the release of captive-produced stock. However, he cautioned that before stock was obtained from the wild, safe and effective procedures should be developed using sandhill cranes (*G. canadensis*) as research surrogates (Erickson 1975).

Experimentation bringing sandhill cranes into captivity began in 1961-1962. Immature sandhill cranes,

Table 3. Number and location of whooping cranes at captive breeding centers, 1936-2007. This table does not include display birds except as noted.

Year	ANWR[a]	SSC[b]	ICF[c]	DWCC[d]	MVNWR[e]	NE[f,g]	PWRC[h]	SAZOO[i]	Grand total
1936						1			1
1937						1			1
1938						1			1
1939						1			1
1940						1			1
1941		1				1			2
1942		1				1			2
1943		1				1			2
1944		1				1			2
1945		1				1			2
1946		1				1			2
1947		2							2
1948	2								2
1949	2								2
1950	2								2
1951		2							2
1952		2							2
1953		2							2
1954		2							2
1955		2							2
1956		2						1	3
1957		4						1	5
1958		5						1	6
1959		5						1	6
1960		5						1	6
1961		6						1	7
1962		6						1	7
1963		6						1	7
1964		7			1				8
1965		6			1				7
1966		5					1	1	7
1967		4					6	2	12
1968		4					11	2	17
1969		4					16	2	22
1970		3					13	2	18
1971		3					16	1	20
1972		3					16	1	20
1973		3					16	1	20
1974		2					20	1	23
1975		2					20	1	23
1976		1	2				19	2	24
1977			3				19	2	24
1978			2				21	2	25
1979			2				22	2	26
1980			2				20	2	24
1981			1				20	2	23
1982			1				27	2	30
1983			1				36	2	39
1984			1				32	2	35
1985			1				38	1	40
1986			1				38	1	40
1987			1				41	1	43
1988			1				46	1	48
1989			21				32	1	54

Table 3. Continued.

Year	ANWR[a]	SSC[b]	ICF[c]	DWCC[d]	MVNWR[e]	NE[f,g]	PWRC[h]	SAZOO[i]	Grand total
1990			29				35	1	65
1991			27				40	2	69
1992			37	4[j]			49	2	92
1993			29	14[j]			56	3	102
1994			31	14[j]			57	4	106
1995			35	16[j]			70	4	125
1996			34	15[j]			62	4	115
1997			30	18[j]			58	4	110
1998		2[j]	30	21[j]			67	4	124
1999		2[j]	29	21[j]			71	6	129
2000		4[j]	27	18[j]			72	6	127
2001		5[j]	32	17[j]			67	7	128
2002		7[j]	35	16[j]			55	10	123
2003		9[j]	31	17[j]			57	6	120
2004		10[j]	34	17[j]			53	5	119
2005		9[j]	38	20[j]			54	6	127
2006		9[j]	37	22[j]			59	9	136
2007		10[j]	35	22[j]			63	8	140[k]

[a] Aransas National Wildlife Refuge, Austwell, Texas.
[b] From 1941 to 1976 captive breeding was performed at the Audubon Zoo, New Orleans, Louisiana. The captive breeding flock is currently housed at the Audubon Species Survival Center, New Orleans, Louisiana.
[c] International Crane Foundation, Baraboo, Wisconsin.
[d] Devonian Wildlife Conservation Center, Calgary, Alberta, Canada.
[e] Monte Vista National Wildlife Refuge, Alamosa, Colorado.
[f] Gothenburg Sanctuary, Brady, Nebraska.
[g] While not a breeding facility, Gothenburg Sanctuary housed a bird used subsequently in captive breeding.
[h] Patuxent Wildlife Research Center, Laurel, Maryland.
[i] San Antonio Zoo, San Antonio, Texas.
[j] This number reflects cranes utilized for breeding and up to 2 cranes for display.
[k] This number reflects a total of 4 cranes utilized for display purposes.

eggs and downy chicks were taken from the wild in Oregon, Idaho, Florida, Mississippi, and Wisconsin and housed in temporary facilities at Monte Vista NWR, Colorado (CWS and USFWS 2007). This research indicated that there were many problems associated with capturing and retaining juvenile sandhill cranes (Doughty 1989). Experiments showed that egg collecting was the safest and most convenient method of obtaining and transporting wild stock to reduce the dangers of shipping cranes long distance, and also lessening the risk of introducing parasites and diseases into a captive flock (McNulty 1966, Doughty 1989). Erickson and colleagues hypothesized that taking 1 egg from a wild clutch would not compromise the productivity of the wild population (Doughty 1989). Research done on sandhill cranes indicated that nest desertion was negligible and population productivity was relatively unaffected when single eggs were removed from 2-egg clutches, since cranes normally lay 2 eggs, but rarely fledge 2 chicks. Observations on the Canadian breeding grounds (Novakowski 1966) confirmed that whooping cranes also generally followed this pattern.

Establishment of the First Whooping Crane Captive Breeding Facility

In 1966, U.S. Senator Karl Mundt sponsored a supplemental appropriation to establish the Endangered Wildlife Research Program and develop permanent whooping crane propagation facilities at PWRC (CWS and USFWS 2007). One reason for locating the crane propagation facility in Maryland was that the U.S. Department of Agriculture operated a specialized breeding center for domestic birds in nearby Beltsville. Experts used to rearing such birds were able to offer suggestions about food, incubation schedules, treatment of diseases, and provide equipment for breeding cranes and other endangered birds in captivity (Doughty 1989).

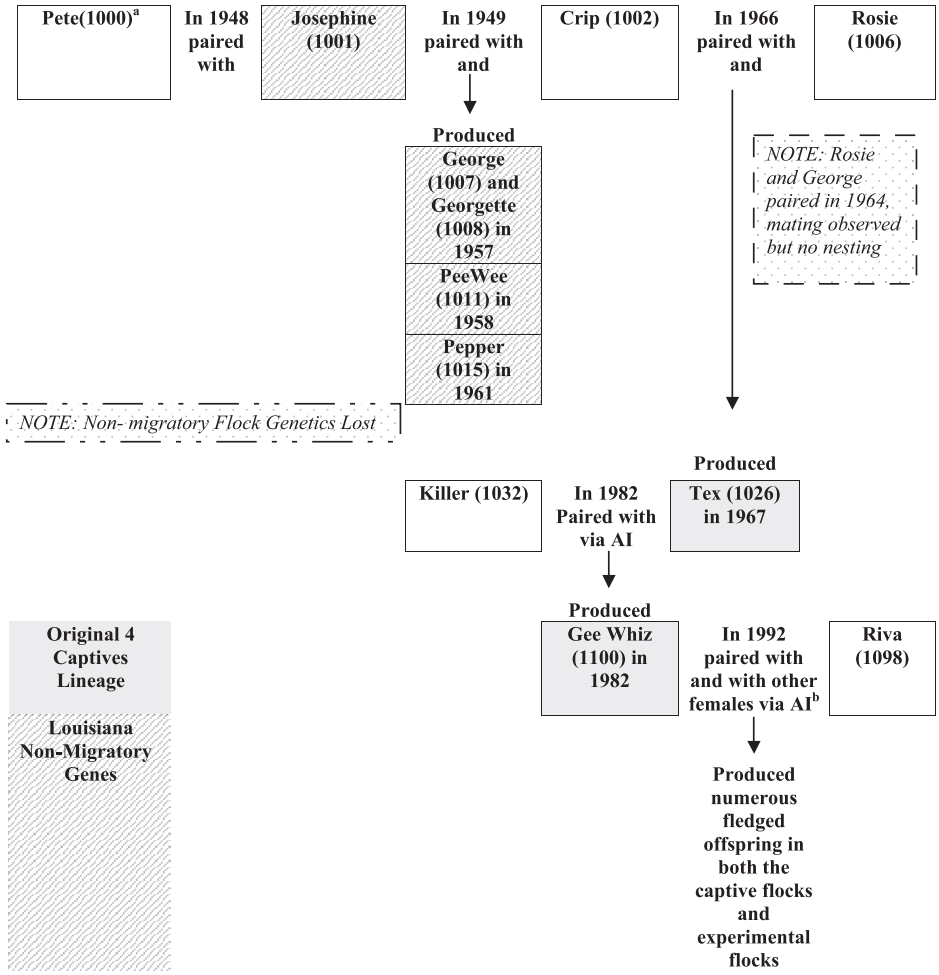

Figure 1. Breeding chart of the 4 original captive whooping cranes showing fledged offspring. Number in parentheses[a] is the studbook number of the whooping crane. AI[b] indicates artificial insemination."

PWRC is currently part of the U. S. Geological Survey's Biological Resources Division and funded by federal appropriations.

A single whooping crane with an injured wing captured as a juvenile in WBNP in 1964 (Novakowski 1965) was transported to the Monte Vista NWR in Colorado. In spring 1966, this male crane (named Canus, studbook no. 1019) was the first whooping crane transferred to PWRC along with sandhill cranes.

Use of Wild Eggs from WBNP to Build the Captive Flock

The Canadian Wildlife Service (CWS) and USFWS agreed in 1964 to obtain eggs from Canada and take them to a propagation center to establish a captive flock (Pratt 1996). In all but 4 years between 1967 and 1998, eggs were taken from wild nests in WBNP and used to build the captive flocks (n = 206) and support reintroductions (n = 230) (CWS and USFWS 2007). Egg collections and subsequent propagation efforts have been described by Kepler (1976), Kuyt (1976), and Ellis et al. (1996). Egg transfers in the 1990s were designed to increase the size and genetic diversity of the captive flock (CWS and USFWS 2007). Chicks raised from these eggs currently form the nucleus of the captive breeding flocks.

The removal of 1 egg from wild nests in WBNP was the key methodology used in establishing a captive flock. Although the total number of cranes (wild plus captive) was dramatically increased by taking 1 egg from a clutch

of 2 and rearing it in captivity (Erickson 1975), the effect of egg removal on the growth rate and overall fitness of the wild flock has been hotly debated by crane researchers and has not yet been determined. Erickson (1976), Kuyt (1976, 1981*a*, 1981*b*) and Boyce et al. (2005) noted that egg removals had not adversely affected the productivity of the wild population. Cannon et al. (2001) noted that the total number of chicks reaching Aransas NWR was less when eggs were collected compared to when no eggs were removed since some pairs arrive at the refuge with 2 chicks.

Captive Propagation at Patuxent

The size of the captive flock at PWRC (Fig. 2) increased as eggs were collected from the wild in WBNP and shipped to PWRC where they were hatched. CWS and the USFWS obtained 50 eggs from nests in WBNP from 1967 to 1974 to establish a breeding population at the PWRC. At the end of 1974, 19 whooping cranes were at PWRC. Egg transfers from WBNP to PWRC were resumed in 1982-1989 and 1991-1996, and totaled 128 eggs, with 114 retained in captivity and 14 used for the Florida reintroduction (CWS and USFWS 2007).

The first breeding at PWRC occurred in 1975, when 1 whooping crane female laid 3 eggs (Derrickson and Carpenter 1982) and hatched 1 chick (Doughty 1989). In 1976, the first chicks from captive-produced eggs at PWRC successfully fledged (CWS and USFWS 2007). From 1975 through 2005, the PWRC flock produced 967 eggs of which 503 were fertile (52%). Through 2005, from these 503 fertile eggs, PWRC fledged 350 birds (70%) (CWS and USFWS 2007). With most of the eggs being used to support reintroductions, the size of the captive flock at PWRC grew slowly and totaled 63 birds in December 2007.

Decision to Divide the Captive Flock

In the 1980s, the captive flock at PWRC suffered 2 major setbacks. In 1984, 7 whooping cranes died from eastern equine encephalitis (EEE), of which 5 were females. The sex ratio in the surviving adult captive population was 10 males to 4 females. Whooping cranes appear especially susceptible to EEE since no sandhill crane mortality occurred (Carpenter et al. 1987). In 1987, a mycotoxin in commercially prepared crane feed poisoned about 240 of the 300 captive cranes at the

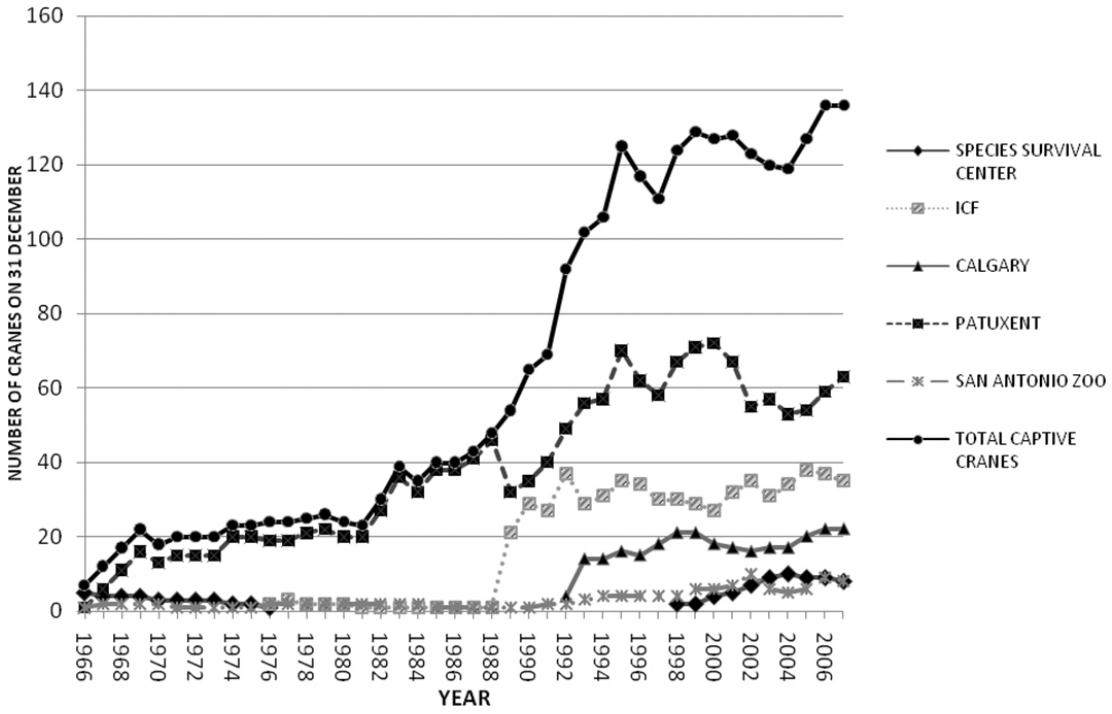

Figure 2. Number of cranes at propagation centers, 1966-2007.

center. Fifteen cranes died (5% of the flock), including 3 whooping cranes. Laboratories found a trichothecene in the feed that may have been the toxic agent (Valente 1992).

In 1989, the then separate Canadian and United States recovery teams decided to split the captive flock to reduce the threat of catastrophic events decimating the flock at PWRC. Since the whooping crane has always been a species shared by 2 nations, the teams wanted 1 of the new breeding centers to be located in Canada. Birds from PWRC were sent to the International Crane Foundation (ICF) in Baraboo, Wisconsin (n = 22), San Antonio Zoo (n = 2), and the Calgary Zoo in Calgary, Alberta (n = 13) (J. Chandler, PWRC, personal communication). Eggs from WBNP were also taken to the new captive centers and used to build the captive flock (ICF, n = 36; Calgary Zoo, n = 6). Starting in 1998, birds from breeding centers were shipped to the Audubon Freeport-McMoran Species Survival Center (SSC) in New Orleans, Louisiana (n = 10).

Display Facilities

Starting in the 1930s and through the mid-1970s, whooping cranes on public display were located only in Gothenburg, Nebraska (1936-1946) (Gothenburg Times 1936), Audubon Zoo (1941-1947, 1951-1975), Aransas NWR (1948-1950), and San Antonio Zoo (1956-1963, 1966-1975). In 1976 and 1977, the remaining whooping cranes at the Audubon Zoo were moved to initiate the captive breeding program at ICF. In November 2001, a whooping crane shipped to New Orleans marked the historic return of the species to the Audubon Zoo. A new whooping crane exhibit was dedicated in September 2004 with a pair on display featured prominently near the zoo entrance.

In recent years whooping cranes with health problems or genetically over-represented are designated by the joint international Whooping Crane Recovery Team (WCRT) as "display" birds and through an application process are placed at suitable zoos. There are currently 8 facilities with whooping cranes on public display: Audubon Zoo, Calgary Zoo, ICF, Milwaukee County Zoo, San Antonio Zoo, and at 3 facilities in Florida (Homosassa Springs Wildlife State Park, Jacksonville Zoo, and the Lowry Park Zoo in Tampa). No whooping cranes are currently located outside of North America.

Captive Propagation of Whooping Cranes

Biologists through many years of research developed techniques for successfully breeding whooping cranes in captivity (Ellis et al. 1996). Whooping cranes are a difficult species to breed, much more so than sandhill cranes (Erickson 1975). Although some propagation techniques developed for sandhill cranes can be applied to whooping cranes, the latter have required certain procedural modifications (Doughty 1989). Most mortality has occurred within 1 month of hatching as a result of bacterial infections, coccidiosis, congenital abnormalities, and leg disorders resulting from rapid growth (Kepler 1978). All mortalities in the captive flock at PWRC have been summarized from 1967 to 1981 (Carpenter and Derrickson 1982) and from 1982 to 1995 (Olsen et al. 1997). A similar summary has recently been published for ICF (Hartup et al. 2010).

Breeding pair numbers and egg fertility have been the primary factors limiting annual production in captivity (Gee and Temple 1978). Successful natural copulations were not observed until 1991 (Nicolich et al. 2001). Natural fertility, which reduces the risk of injury due to handling, is good in some pairs but overall productivity is increased by using artificial insemination (CWS and USFWS 2007). Production has been increased substantially by removing initial clutches and recycling the females to lay multiple clutches. Captive birds have in almost all cases first bred at an older age than their wild counterparts (CWS and USFWS 2007). Although a few birds in captivity have bred as early as 4-5 years of age, most captive females have not laid until they were 7-10 years old. Possible factors responsible for delayed reproduction in the captive flock include improper photoperiod, rainfall, rearing conditions, dominance relationships, age of separation of potential pairs from a bachelor flock, sexual incompatibility, inadequate pen size, lack of access to ponds, and stress associated with handling and disturbance (Kepler 1976, 1978; Derrickson and Carpenter 1982; Ellis et al. 1996; Mirande et al. 1996). Although most reproductive cranes lay eggs every year, some females lay every other year, lay occasionally, or lay small or misshapen eggs (CWS and USFWS 2007).

Population Viability Assessment

A whooping crane population viability assessment

(PVA) conducted in 1991 evaluated the role of captive propagation as a component of recovery strategy for the species and served as a basis for a master plan for the captive flock. It included priorities for research and management of the wild and captive populations as a meta-population to maximize retention of genetic heterozygosity and minimize the risk of extinction (Mirande et al. 1993). The PVA also considered: 1) accelerating the expansion of the captive population with an adequate number of pairs to provide the numbers of offspring needed to sustain release efforts, 2) enhancing preservation of genetic diversity through adequate representation of the AWBP in captivity through egg collections to ensure 90% of the genetic diversity represented in the wild flock survives for 100 years should catastrophe strike the AWBP, 3) protecting the population gene pool against fluctuations due to environmental stochasticity in the wild, 4) providing birds for reinforcement of wild populations or establishment of new populations, 5) enhancing conservation efforts through public education, and 6) identifying problems or issues needing analysis and research.

Reintroductions

Three reintroduction experiments have been supported with eggs produced in captivity and eggs taken from the wild. From 1975 to 1988, 216 eggs from WBNP and 73 from captivity were placed in sandhill crane nests at Grays Lake NWR in Idaho (CWS and USFWS 2007). The cross-fostered whooping crane young learned the migration route to New Mexico from their sandhill crane parents. Whooping cranes in that population peaked at 33 cranes in 1985, and the last bird in the wild died in spring 2002. There was no reproduction in the cross-fostered whooping cranes except for 1 male (studbook no. 1118) that paired with a sandhill crane and produced 1 hybrid offspring. One male captured from this population was still living in captivity at ICF in 2009 and paired with a sandhill crane female raised by a pair of captive whooping cranes.

After the failure of the cross-fostered flock, most captive chicks were either parent-reared or costume-reared. To avoid imprinting problems, all costume-reared chicks were raised in auditory and visual contact with live white-plumaged whooping cranes and other chicks. In costume-rearing, cranes are exposed to the human form only during negative, stressful situations.

Additional reintroductions using birds hatched in captivity and soft-released into the wild have taken place in Florida (1993-2005) and in Wisconsin (2001-present). The whooping cranes in central Florida are non-migratory, whereas the cranes released in Wisconsin migrate primarily to the western portions of Florida, with some individuals wintering in other southeastern states. Between 1993 and 2007, captive eggs went to the Florida nonmigratory population (n = 257), and the eastern migratory population (n = 125). These reintroductions have so far failed to produce a self-sustaining population, but have produced second generation wild offspring. The WCRT is considering trying to restore whooping cranes to Louisiana wetlands where the species once roamed (CWS and USFWS 2007).

Growth of the Captive Flock

Prior to collection of wild eggs, whooping crane numbers in captivity equaled 1 bird (1936-1940), 2 birds (1941-1955), and 3 to 8 birds (1956-1964). The growth rate was approximately 10% from 1967 to 1991, a period when eggs in most years were collected in WBNP and split between hatching in captivity and being used for the cross-fostering reintroduction in Idaho. Mirande et al. (1993) found that the captive population had the ability to sustain itself without the eggs from WBNP, but its growth rate was negatively affected by using eggs for reintroductions prior to stabilizing the captive population.

With the Idaho reintroduction ended in 1989 and no other ongoing reintroductions, the whooping crane captive flock doubled in the next 4 years. In 1993, a reintroduction project to establish a non-migratory population in Florida began. Modeling indicated that if the captive population was limited to 100 birds, production would not be able to consistently meet targeted goals for releases in Florida (Mirande et al. 1993). As a result, actions were taken to gradually increase the number of breeding stock in captivity. Another reintroduced flock was developed in Wisconsin beginning in 2001. Despite releases during 1993 to 2007, the captive flock grew to 148 birds by 2007. Overall, the mean annual population growth rate (1980 through 2006) was 5.5% (Jones and Lacy 2007). Demographic analyses show that the captive population without production used to support reintroductions has the potential to grow at a rapid rate (26% in 2006), but this kind of growth rate

would quickly surpass the capacity of the captive holding facilities (Jones and Lacy 2007).

In 1998 the WCRT adopted the following allocation of captive-produced chicks listed in order of priority: maintenance of captive flocks; reintroductions; off-corridor experiments considered essential to reintroductions or propagation; education; other approved populations; and other research experiments (CWS and USFWS 2007). A studbook is updated annually (Jones and Lacy 2007) with genetic analysis done using Sparks 1.4 software (ISIS 1994). Decisions about pairings, production targets for each pair, and whether to retain offspring as future breeding stock or use them in reintroduction experiments are proposed annually by all the captive flock managers and approved by the WCRT.

Genetic Issues

As a consequence of the 1941 wild population bottleneck, the current whooping crane population is derived from an estimated 6 to 8 founders, with a loss of 66% of all historic genetic material (Mirande et al. 1993, Glenn et al. 1999). In the wild, about 87% of the gene diversity that survived the bottleneck has persisted from 1938 to 1990 (Mirande et al. 1993). Between 1980 and 2006, 98% of the existing gene diversity in captivity was retained (Jones and Lacy 2007).

Given current genetic analyses based on captive pedigrees, an estimated 153 whooping cranes (21 productive pairs all passing on their genetic material) are needed in captivity to maintain the flock in good genetic health and retain 90% of genetic diversity of the original founders for 100 years (Jones and Lacy 2007, unpublished report). With limited availability of genetically valuable offspring in captivity, the WCRT recommended building the population slowly to allow maturation of additional pairings whose offspring are needed in future. By 2007 the numerical target of 153 whooping cranes in captivity was nearly reached, with strong emphasis currently placed on maximizing genetic diversity. Current recommendations are 50 captive breeding pairs of whooping cranes (defined as pairs that breed or are intended to breed in the future) by 2010, including 15 pairs at PWRC, 12 at ICF, 10 at the Calgary Zoo, 10 at SSC, and 3 at the San Antonio Zoo (CWS and USFWS 2007). The construction of a new facility at SSC in 2007 has provided needed facilities to bring the captive flock up to the recommended size. Production from these 5 facilities will be the principal source of birds for release to the wild.

DISCUSSION

Early records of captive whooping cranes in Europe and the United States prior to 1948 confirmed no breeding of the species. This changed dramatically in 1966 with the establishment of the first official breeding facility at PWRC as a hedge against possible extinction of the 1 remaining wild flock. Breeding methodology has been developed through many years of research, including multiple clutching and the use of artificial insemination. Two major remaining hurdles for a highly productive captive breeding program are the delayed age of first reproduction of captive cranes and limb development issues affecting crane longevity.

Growth was never the only goal of the captive flock. The use of wild eggs and captive-produced eggs for reintroduction purposes started in 1975, substantially diminishing growth of the captive flock (Mirande et al. 1993). The WCRT in 1998 wisely made the maintenance of the captive flock its top priority for use of captive offspring (CWS and USFWS 2007).

The WCRT recognizes that collection of wild eggs from WBNP has benefited the whooping crane recovery program by providing stock to establish the captive flocks and offspring for release, thus increasing the total number of whooping cranes and helping to preserve the genetics of the species. The team believes that data analyses to date do not indicate that egg collections done every year would increase total recruitment in the AWBP. However, egg pickup in selected years, depending on the timing in relation to the 10-year population cycle, could increase recruitment of the AWBP in some years (CWS and USFWS 2007).

Genetic theory suggests that small populations will continue to lose genetic diversity with each generation, and that continued loss of genetic material leads to inbreeding depression and declining productivity (Jimenez et al. 1994, Frankham 1995, Lacy 1997, Woodworth et al. 2002). A study of the effects of inbreeding in captive red-crowned cranes (*G. japonensis*) showed a decrease in fertility and hatchability (Mirande et al. 1993). The loss of genetic material may have serious implications for both captive and wild whooping crane flocks. Limited genetic diversity is a detriment to a wild

population currently threatened with unprecedented global ecosystem change, human development, and introduced diseases. The AWBP is challenged to increase in number so that the random mutation rate that creates new alleles will offset the loss of genetic diversity (CWS and USFWS 2007). Beginning in the 1990s, birds in captivity have been bred to maintain maximum genetic herterozygosity. Although the current goal of the captive flock is to maintain 90% of genetic diversity over the next 100 years (Jones and Lacy 2007), even meeting this goal means the genetic base will have declined. Management efforts need to continue to minimize loss of genetic material in the captive flock. Genetic studies need to more accurately measure the genetic diversity of both the captive and wild flocks to determine if any additional genetic material exists that could be brought into captivity or reintroduced back out into the wild.

Successful maintenance of the captive flocks faces threats. Lessons learned from the past should be applied to the future of the captive flocks. Politics and lack of information sharing during the initial attempts at breeding captive whooping cranes prior to the 1960s should serve as a reminder that the captive flock can only be maintained through continual cooperation. Experienced and specially trained staff must work with the cranes for multiple years to successfully breed whooping cranes in captivity. Many of the current whooping crane flock managers have dedicated their lives to breeding whooping cranes. Personnel turnover at captive facilities must not occur rapidly so that knowledge is carefully passed on to new flock managers. Government needs to continue to make a long-term financial commitment in partnership with private entities for maintaining the captive flock until the species is recovered. Splitting the entire captive flock amongst the zoo community would at best be problematical because of the tremendous difficulties encountered when breeding whooping cranes and lack of institutional experience and rapid personnel turnover at some zoos.

With only 247 whooping cranes in the AWBP in the spring of 2009, the whooping crane remains endangered. Even though the growth rate has averaged approximately 4.5% for the AWBP over 70 years, unprecedented threats loom. Habitat is being threatened on the wintering grounds by housing developments (Stehn and Prieto 2010) and loss of freshwater inflows. Sea level rise is anticipated to make much of the existing winter marshes too deep for the cranes to use (CWS and USFWS 2007). Climate change with expected temperature increases will dry up wetlands in summer, migration, and winter ranges unless precipitation also increases. Migration corridor habitat is threatened with changes in farm programs and increased construction of obstacles including power lines, wind turbines, cell towers, and airports (CWS and USFWS 2007).

With all of the existing threats facing the sole self-sustaining wild population, it is essential to continue maintaining a captive flock with a minimum of 21 productive pairs in order to protect genetic material until the species is considered recovered in the wild (Jones and Lacy 2007). Effective captive production is also needed to continue reintroduction programs if newly established populations can become self-sustaining.

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