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NATURAL FERTILITY IN WHOOPING CRANES AND MISSISSIPPI SANDHILL CRANES AT PATUXENT WILDLIFE RESEARCH CENTER

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Abstract: The first fertile whooping crane (*Grus americana*; WC) egg produced through natural breeding at Patuxent Wildlife Research Center (Patuxent) was laid in 1991. Prior to that time, all fertile whooping crane eggs were the result of artificial insemination. Since 1991, eight different whooping crane pairs at Patuxent have produced fertile eggs through natural breeding. Mean fertility averages over years for each pair range from 40% to 93%. Fertility rates for each pair also vary greatly between years, from 0% to 100%, but the causes of the variance are unknown. Experiences with natural fertility in Mississippi sandhill cranes (*G. canadensis pulla*; MSC) have been similar. Annual natural fertility rates averaged from 21% to 89% and fertility averages for each of 7 pairs also varied greatly between years. Rearing methods have not determined success in natural breeding for either species. Both hand-reared and parent-reared pairs have been fertile. Wing condition, however, has been an important factor affecting natural fertility. Because artificial insemination (AI) generally results in higher fertility rates than natural breeding, AI should continue for some pairs.

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Key words: artificial insemination, *Grus americana, Grus canadensis pulla*, Mississippi sandhill crane, natural fertility, whooping crane.

In crane husbandry, natural fertility, or fertility through natural breeding, is preferred as less intrusive and less labor intensive than AI, although each has its advantages. This paper provides an overview of natural fertility in 2 endangered crane taxa at Patuxent.

Patuxent has a 35 year history of working to conserve rare and endangered species. Most of our recovery efforts have been focused on the WC and the MSC. Captive flocks at Patuxent are used for research, for reintroduction, to maintain genetic diversity, and to guard against extinction.

The first WC arrived at Patuxent in 1966, a juvenile taken into captivity after being found severely injured in the wild. Eggs from the wild were used to expand the captive flock. The first fertile WC egg produced at Patuxent came in 1975 (Derrickson and Carpenter 1982). Production from Patuxent WCs has supported several WC reintroduction projects (Drewien et al. 1989 unpublished, Ellis et al. 1992*a*, Nesbitt et al. 1997, Clegg and Lewis 2001). As of 1999, 73 eggs laid at Patuxent and 132 birds hatched at Patuxent have been involved in WC reintroductions. Biologists split the captive flock of WCs to guard against catastrophic losses, and there are now breeding pairs of WCs at the International Crane Foundation in Baraboo, Wisconsin; the Calgary Zoo in Calgary, Alberta, Canada; and the San Antonio Zoo in Texas.

The MSC flock began at Patuxent in 1966 with 4 chicks reared by John Lynch from eggs collected from the wild (McMillen et al. 1987). A pair of MSC produced the first fertile egg in 1973 and the flock gradually increased through captive production and from additional eggs brought in from the wild. By 1994, Patuxent held 44 after-hatch-year birds, including 16 productive females. From 1981–95, Patuxent sent captive-produced chicks to the Mississippi Sandhill Crane National Wildlife Refuge in Jackson County, Mississippi for release into the wild (Ellis et al. 1992*b*, Ellis et al. 2000). After several years of producing 20–40 chicks annually for release, the wild flock in Mississippi was believed to be at carrying capacity so Patuxent's role in the recovery of the MSC was diminished. Between 1994–96 Patuxent divided the captive flock between the Audubon Species Survival Center in New Orleans, Louisiana, and the White Oak Conservation Center in Yulee, Florida.

In the early years of production at Patuxent, fertile WC and MSC eggs could only be obtained through AI (Derrickson and Carpenter 1982). AI has many uses, including increasing fertility in mated pairs, fertilizing females kept in pens separate from over aggressive males, and allowing mate choice (i.e., genetic management) (Gee and Mirande 1996). However, AI is very labor-intensive, risks injury to cranes and

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staff (Swengel and Tuite 1997), and causes potentially detrimental disturbance to the AI pair and neighbors. Production through natural fertility requires less manpower and is less risky, so for 15 years we have promoted natural fertility in Patuxent's cranes.

Flight capability is now known to be an important component in the success of naturally breeding cranes. Among 21 pairs of captive red-crowned cranes (*Grus japonensis*), fully-flighted cranes had a fertility rate of 76.3% while fertility in pinioned pairs was only 27.0% (Belterman and King 1993). In the early 1980s, Patuxent recognized the value of flight capabilities for natural breeding, and discontinued the practice of rendering the cranes flightless through tenotomy. At that time, we built two crane pen complexes with overhead nets to allow the occupants to remain full-winged. A few years later, when these young, flighted pairs came into production, they achieved fertility through natural breeding. These birds laid Patuxent's first naturally fertile MSC eggs in 1986.

Natural fertility in WCs came later, due largely to the WCs' slower maturation. Captive MSC females began egg-laying at an average age of 3 years, while in WCs, the average age of first production was 7 years. The first full-winged pair of WCs came into production in 1990, but their eggs were infertile. In 1991, the same pair laid the first naturally fertile WC egg produced by a captive-reared pair at Patuxent. The number of naturally fertile WC and MSC pairs at Patuxent increased gradually as more fully winged birds came into production.

In addition to flight capability, there are many other factors which may influence the success of naturally breeding birds. Physical characteristics affecting mounting, such as toe or leg deformities in the male or an inability for the female to support the male, might prevent copulation and natural fertilization. Poor semen quality can impede both AI and natural fertilization (Brillard 1993). Experience is also important to the breeding success of wild cranes. Of 14 color-banded WCs nesting in or near Wood Buffalo National Park in Canada, the average age of first nesting was 5.0 years, yet average age of first fertile egg production was 5.4 years (Kuyt and Goossen 1987). In one field study, none of 13 wild, inexperienced, Florida sandhill crane pairs were able to successfully reproduce during their initial breeding attempt (Nesbitt and Tacha 1997). Factors which affect egg production, such as pair compatibility, sexual imprinting, physical stress, and disturbance, also potentially affect natural fertility.

In this paper, we examine the influence of rearing, flight capability, and breeding history on the success of natural breeding pairs at Patuxent. We compare natural fertility to fertility through AI, and discuss fluctuations in fertility rates of individual pairs.

METHODS AND STUDY AREA

Patuxent's facilities are located on lands managed by the U. S. Fish and Wildlife Service near Laurel, Maryland. The captive crane colony is located in an area secluded from public use. WC breeding enclosures were well-vegetated 14 x 20 m pens of 2.4 m high chain link, covered with nylon flight netting (Swengel and Besser 1996). The pens are in complexes surrounded by electric perimeter fences. We used photoperiod lights to stimulate WC pairs to begin laying earlier in the season (Kepler 1978, Derrickson and Carpenter 1982, Gee and Pendleton 1992). MSCs were housed in similar pens, approximately 9–15 x 30 m (net covered) or 10 x 18 m (uncovered). Earlier facilities were constructed of wood and galvanized steel poultry wire, but the more recent enclosures were in use during most of the years involved in this paper.

We reared cranes by 1 of 4 methods, or by a blend of the following methods: (1) parent-rearing by conspecifics, (2) foster parent-rearing by cranes of another species (i.e., WCs reared by sandhill cranes), (3) hand-rearing without costumes, and (4) costume-rearing (Ellis et al. 1992*b*, Nagendran et al. 1996, Wellington et al. 1996). We will not elaborate here on the various rearing types, because, they are described in detail elsewhere, and, later in the paper, we show that rearing method was not closely associated with fertility rates. We did not choose the method of rearing for each bird randomly. Rather, birds were reared according to the availability of foster parent cranes and the hand-rearing method in use at Patuxent at the time. Cranes were allowed to remain full-winged, although a few had injuries that restricted wing extension.

Our choices for mates for WCs and MSCs were intended to avoid inbreeding and to optimize unique genetic representation in the captive flock. We also considered behavioral and physical characteristics of the individual birds. We introduced the potential mates gradually under careful monitoring, as described by Swengel et al. (1996). We chose mates for all 8 naturally fertile WC pairs. Of 7 naturally fertile MSC pairs, we arranged 5 pairings, whereas 2 pairs chose their own mates from a subadult flock. In this paper, we refer to each pair by the alphanumeric identification of its breeding pen.

Maximum production from pairs depended on how many eggs and chicks biologists required for various projects. In most cases, we allowed pairs to complete each clutch, then removed the eggs to encourage re-nesting. Normally managers removed eggs so each pair completed 2–4 clutches (rarely 5) in a season. Generally, we incubated eggs under surrogate sandhill crane pairs for the first 2–3 weeks, then placed the eggs in a Petersime, forced air, incubator. We also used broody cochin hens to incubate eggs for short periods (1986–94). Experienced crane pairs were often allowed to incubate their last clutches of the season, full term. Staff assessed viability by candling during routine handling of the eggs. We refrigerated nonviable eggs, then opened them to determine fertility. Upon examination, we could not determine fertility in 10.0% of WC eggs and 12.8% of MSC eggs because of decomposition or lack of a detectable embryo. For this paper, we considered these eggs infertile. Of all eggs laid, 17.7% of WC eggs and 3.9% of MSC eggs were broken before fertility could be determined, usually just after oviposition. We excluded broken eggs from our calculations.

We summarized WC data for the years in which naturally breeding birds were in production, 1990–99. We allowed 10 productive pairs to breed naturally. We eliminated 2 pairs from the comparisons presented here. One pair had a weak pair bond and was split after 1 year. The male of a second pair luxated his wing; it was thereafter stiff at the carpal joint. For this pair, copulation was unlikely, and after 1 year with 0% natural fertility, we reassigned the pair to the AI program. We excluded a third naturally fertile pair (B24) from calculations because mates were together for less than 1 year, too little time to make judgements about their rate of fertility (which, however, was 100% for 5 eggs). We did, however, include this pair as a successful, naturally breeding pair, in our discussions. In 1999, we performed supplemental AI in 2 WC females, but continued to allow natural breeding of the pairs. Because subsequent production could not be credited to a single fertilization method, we omitted eggs laid after we initiated AI. Naturally breeding MSC pairs were present at Patuxent from 1986–94; data presented covers this 9-year period. We allowed 6 females to breed naturally. Because we paired 1 female to a new mate in 1990, we included data for her in 2 pairs, so our total is for 7 pairs of natural breeders.

Our data on AI covers the same years involved in the data on natural fertility: 1990–99 for WCs and 1986–94 for MSCs. During these periods, 4 WC (2–3 at any 1 time) and 11 MSC (5–9 at any 1 time) were in the AI program. We initiated AI ca. 2 weeks before we expected the first egg and performed AI 3 times per week throughout the laying season. AI techniques are described in detail in Gee and Mirande (1996). We did not include production data from females laying for only 1 year. We did an arcsine transformation and unpaired t-test (Steel and Torrie 1960) on fertility averages through natural breeding and AI. We used an ANOVA (Steel and Torrie 1960) to compare egg sequence with egg fertility.

RESULTS

Eight of 8 WC pairs allowed to breed naturally for more than 1 year were naturally fertile. At least 4 pairs produced fertile eggs in their first year of production and 3 in their second year of production. One of the 3 pairs had broken all their eggs in the first year, so fertility could not be determined. The eighth pair broke all their eggs in their first year of production and most eggs in years 2 and 3. The few eggs that we collected were infertile. We finally collected fertile eggs from this pair in their fourth year of production.

Six of 7 naturally breeding MSC pairs laid fertile eggs in their first year of production. The seventh pair (L8) was in a group pen the year the female began laying, and the male was wing-clipped. Both eggs laid that year were infertile. Because the male was wing-clipped, we did not include these eggs in fertility averages. By the following year, the pair had been moved to their own breeding pen and the male had grown in new flight feathers. They produced fertile eggs that second year.

We separated 1 pair of naturally breeding WCs (B2) 2 years after being paired because genetic advisors believed that the 2 birds were closely related. All other naturally fertile pairs have remained together since pairing. One MSC naturally breeding pair, O5, had consistently low fertility, so after 4 years we split the pair. Once in a new pairing, fertility increased for this female (O6) from an average of 12% with the previous mate to an average of 69% with the new mate (Fig. 1). This new pair, and the 5 other naturally breeding pairs, remained intact during their remaining time at Patuxent. We moved the male from the split O5 pair to a new female and incorporated him into the AI program.

Fertility averages of naturally breeding WCs varied from 40% to 94% (Table 1), and, for most pairs, fluctuated greatly from year to year. Two pairs produced very few eggs per year (B10 averaged 1 egg/yr and B14 averaged 3 eggs/yr), so wide fluctuations in annual fertility were expected. However, fertility also fluctuated greatly for 3 other pairs (B4, B12, and B16), even though the number of eggs produced was consistently high (i.e., 3–4 clutches/year). The B2 pair was only in production for 2 years, not long enough to show a

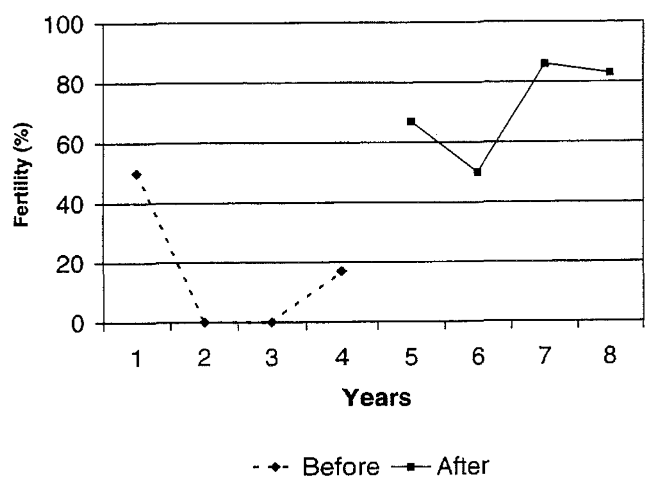

Fig. 1. Fertility of 1 Mississippi sandhill crane female before and after a mate switch.

Table 1. Fertility percentages for naturally breeding WCs at Patuxent 1990–99.[a]

Pair	I.D.	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Pair Totals
B2	84001					**75%**	**83%**					**80%**
	85007					3/4	5/6					8/10
B4	84002			**28%**	**50%**	**75%**	**100%**	**86%**	**75%**	**57%**	**50%**	**65%**
	87043			2/7	3/6	3/4	7/7	6/7	6/8	4/7	3/6	34/52
B10	88022		No mate	-	**100%**	**100%**	**0%**	-	**100%**	-	-	**80%**
	83001		(0/4)	0/0	2/2	1/1	0/1	0/0	1/1	0/0	-	4/5
B12	86027	**0%**	**60%**	**13%**	**40%**	**50%**	**80%**	**60%**	**57%**	**75%**	**0%/AI**	**44%**
	85002	0/4	3/5	1/8	2/5	4/8	4/5	3/5	4/7	3/4	0/4/(1/3)	24/55
B14	83003		-	**0%**	**0%**	**100%**	**20%**	**67%**	**50%**	**43%**	A.I.	**40%**
	83004		0/0	0/2	0/2	2/2	1/5	2/3	2/4	3/7	(3/3)	10/25
B16	88046				**0%**	**83%**	**88%**	**33%**	**57%**	**88%**	**86%**	**65%**
	87042				0/4	5/6	7/8	3/9	4/7	7/8	6/7	32/49
B22	84003			**100%**	**100%**	**83%**	**100%**	**78%**	**100%**	**100%**	**100%**	**94%**
	85001			3/3	4/4	5/6	6/6	7/9	9/9	8/8	8/8	50/53
Year		**0%**	**60%**	**30%**	**48%**	**74%**	**79%**	**64%**	**72%**	**74%**	**68%**	**65%**
Totals		**0/4**	**3/5**	**6/20**	**11/23**	**23/31**	**30/38**	**21/33**	**26/36**	**25/34**	**17/25**	**162/249**

[a] Excludes eggs broken in nest before fertility was determined. Values are presented as number eggs fertile/total number. Eggs in parenthesis are not included in totals (B10 female was unpaired in 1991, and B12 and B14 females received supplemental AI in 1999).

trend. Only 1 pair (B22) maintained a steady rate of fertility throughout its reproductive history. Among MSC naturally breeding pairs, fertility averages varied from 12% to 97% (Table 2). Annual fertility percentages fluctuated widely in 4 pairs (O5, O6, O8, and L3) and minimally in 3 pairs (L1, L6, and L8).

The egg sequence, or order in which each female laid eggs throughout the season, was not related to egg fertility for either species of crane (Fig. 2). An ANOVA comparison showed no correlation between the fertility of eggs and the sequence in which they were laid.

During 1990–99, WCs at Patuxent laid 339 eggs which we collected intact. Natural breeders produced 75% of the eggs; pairs in the AI program produced 23%; and naturally breeding pairs that were also artificially inseminated produced 2%. We examined fertility averages of naturally breeding and AI pairs using an unpaired t-test (Steel and Torrie 1960). The fertility average for the AI pairs (73%) was higher, but not significantly different ($P > 0.05$) from the fertility average of eggs laid by natural breeders (65%) (Table 3). During 1986–94, MSCs laid 541 eggs which were not broken prior to fertility determination. Natural breeders laid 36% of these and AI pairs laid 64%. Average fertility through AI (81%) was significantly higher than average natural fertility (67%, t-test, $P \leq 0.01$).

Rearing histories did not have an apparent affect on the success of naturally breeding WCs or MSCs. None of the differences in Table 4 were statistically significant.

DISCUSSION

At Patuxent, we achieved natural fertility in all full-winged WC and MSC pairs that were allowed to copulate naturally for more than 1 year. While 6 of 7 MSC pairs produced fertile eggs in their first year of production as a pair, only 4 of 8 WC pairs were naturally fertile in their first productive year together. Managers of captive flocks, often under pressure to maximize production of fertile eggs, may be inclined to allow each pair a limited time to lay naturally fertilized eggs before resorting to AI. While 1 year may be sufficient for sandhill cranes, crane managers should consider giving each WC pair at least 2 years to breed naturally before concluding that fertility rates are too low and before implementing AI.

While fertility through AI is often higher and more consistent than fertility through natural breeding (Gee and Mirande 1996), in WCs the differences (Table 3) were not as great as expected. During the study period (1990–99), one of our greatest challenges in the WC AI program was a shortage of high-quality semen samples. This led to a lower than

Table 2. Fertility percentages for naturally breeding Mississippi sandhill cranes at Patuxent Wildlife Research Center 1986–94.[a]

Pair	I.D.	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	Pair Totals
O5	82005	No mate	50%	0%	0%	17%						12%
	81001	(0/2)	½	0/5	0/4	1/6						2/17
O6	84006						67%	50%	86%	83%	60%	69%
	81001						4/6	4/8	6/7	5/6	3/5	22/32
O8	82006		50%	83%	33%	67%	57%	38%	50%	0%	67%	51%
	81002		2/4	5/6	2/6	4/6	4/7	3/8	4/8	0/4	4/6	28/55
L1	84009					100%	88%	100%	100%	100%	100%	97%
	86038					4/4	7/8	7/7	8/8	4/4	6/6	36/37
L3	85009					50%	100%	100%	75%	100%	75%	89%
	84008					½	8/8	6/6	3/4	4/4	3/4	25/28
L6	87023								100%	100%	83%	91%
	90019								2/2	3/3	5/6	10/11
L8	89118							wing clip	50%	33%	50%	38%
	89069							(0/2)	2/4	1/3	2/4	5/13
Year			50%	45%	20%	56%	79%	69%	76%	71%	74%	66%
Totals			3/6	5/11	2/10	10/18	23/29	20/29	25/33	17/24	23/31	128/193

[a] Excludes eggs broken in nest before fertility was determined. Eggs in parenthesis are not included in totals (81001 did not have a mate in 1985, and 89118 was wing clipped in 1991 so copulation was impaired).

expected AI fertility and consequently no significant difference between AI and natural breeding. Conversely, poor semen quality of 1 or more natural breeders could also depress natural fertility averages. Although the differences were not statistically significant, it is possible that, under different circumstances, AI would be more efficient than natural breeding in WCs. The difference between AI and natural breeding fertility rates in MSCs was significant, as expected.

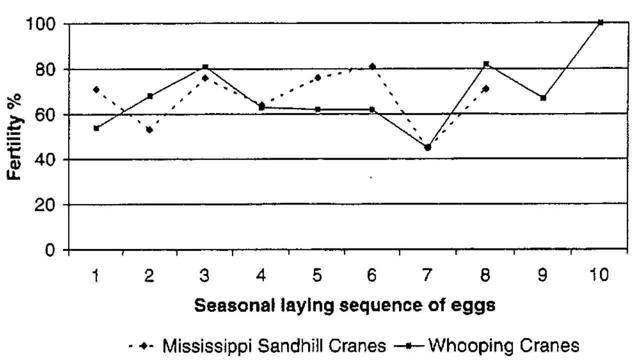

Fig. 2. Average fertility of eggs by sequence of laying: naturally breeding pairs of whooping cranes (1990–99) and Mississippi sandhill cranes (1986–94).

Fertility rates for most of our WC pairs varied greatly from year to year (Table 1). One might expect a low rate of fertility in the first year of production, which would increase with time and experience, then remain stable. Fertility gradually increased in B4 pair in years 1–4 as expected, but then dropped inexplicably thereafter. The great fluctuations for other WC pairs likewise are unknown. Only 1 naturally breeding WC pair at Patuxent (B22) has maintained consistently high fertility averages throughout its production history. In general, management practices regarding reproduction remained constant during the period considered in this paper, except as noted below, therefore, we do not believe husbandry practices greatly altered fertility rates. If a particular disturbance or season of bad weather caused a drop in fertility, we would expect to see a change in all or most pairs during the same time. However, we could find no year effect (Fig. 3). Averages for some pairs increased in the same year that averages for other pairs decreased. The only notable year was 1995 in which 5 of 7 WC pairs had their highest average fertility. We failed to identify any other correlating variable.

MSC pairs showed greater stability in their rates of natural fertility. Most had either consistently high or consis-

Table 3. WC and MSC fertility percentages through natural breeding and artificial insemination.[a]

Species	Natural Breeding	Artificial Insemination	Percent Difference	t-test Probabilities
WC	65 (9)	73 (9)	7.0	$P > 0.05$
MSC	67 (9)	81 (9)	14.0	$P \leq 0.01$
WC & MSC	66.0 (18)	79.6 (18)	13.2	$P \leq 0.01$

[a] Number of years included in average is shown in parenthesis.

tently low fertility rates. Only 1 pair (O8) varied widely between years.

Due to the possibility of great variability in fertility rates, we advise managers of naturally breeding cranes to monitor pairs closely and be willing to adjust strategies to achieve greater fertility. Pairs with consistently high rates of fertility can be left to breed naturally. There are a few options to consider for pairs with low or inconsistent fertility rates: (1) split the pair and provide new mates, (2) supplement natural breeding with a few, well timed, AI bouts, and (3) incorporate the pair into a regular AI program.

From splitting a pair and creating new pairs, increased fertility may result. One MSC female in her first pairing had a fertility average of 12%, but with her second mate she averaged 69%.

Splitting a pair may not be a realistic option due to behavioral or genetic considerations. In such cases, managers could keep the mates together, but also perform supplemental AI. In poultry, the number of sperm available for storage in the sperm storage tubules affects fertility (Brillard 1993).

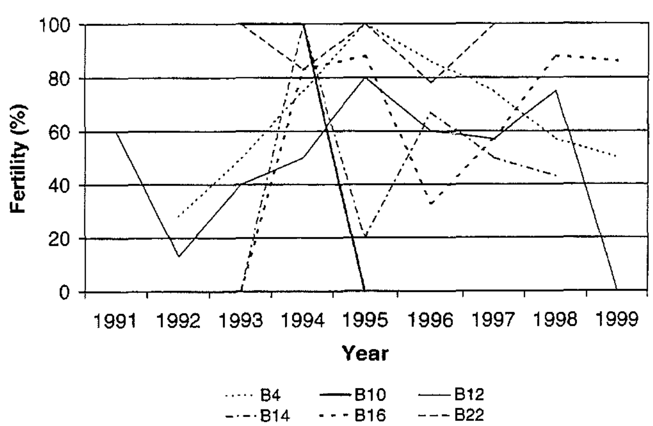

Fig. 3. Whooping crane natural fertility by pair and year, 1992–99.

Table 4. Rearing histories and fertility averages of naturally breeding WC and MSC pairs at Patuxent.

Both members of pair hand-reared			Both members of pair parent-reared			Mixed pair: one hand-reared, one parent-reared		
species	ID	%	species	ID	%	species	ID	%
WC	B14	40	WC	B4	65	WC	B16	65
WC	B12	44	MSC	O5	12	WC	B2	80
MSC	L1	97	MSC	O8	51	WC	B10	80
			MSC	L6	91	WC	B22	94
						MSC	O6	69
						MSC	L3	89
						MSC	L8	38

Brillard (1993:926) also concluded that "in turkey hens, inseminations performed before the onset of lay allow better overall efficiency of sperm storage and, therefore, increase the chances of fertilization of eggs." If these conditions also apply to cranes, a few artificial inseminations early in the season or occasionally throughout the egg-laying period, could significantly increase fertility rates in naturally breeding cranes. In 1999, we artificially inseminated a naturally breeding whooping crane female, B14, over an 8-day period with 4 viable semen samples from a nearby male. B14 pair previously had inconsistent, often low, fertility averages. The female laid the 2 eggs of her first clutch 16 and 19 days after the last insemination. After removing the first clutch, we performed AI one more time 11 days prior to her third and final egg. As determined by genetic testing, all 3 of B14's eggs laid in 1999 were fertile and all were fertilized by the mate, not the AI semen donor. Although the eggs were fertilized through natural breeding, the success of fertilization may have been increased as a result of increasing the supply of semen in the sperm storage tubules early in the season.

In another 1999 attempt to increase fertility in a second pair, B12, we again used supplemental AI. We initiated AI in the middle of the egg laying season because the pair's first 2 clutches were infertile and the pair had a history of poor fertility in some years. We performed AI on 3 occasions and only the fifth of 7 eggs was fertile. It is impossible to determine if the minimal supplemental AI improved fertility.

A third option is to fully incorporate the pair in a regular AI program. This may be the best alternative if natural breeding is consistently unsuccessful and if demand for fertile eggs is high. WC pairs that previously had been infertile or had poor fertility rates as natural breeders have greatly improved fertility rates in AI programs at the International Crane Foundation (S. R. Swengel, unpublished data) and the San Antonio Zoo (J. T. Rouse, unpublished data). At Patuxent, we have not abandoned natural breeding in any established crane pairs, but may do so in the future with particularly unsuccessful pairs.

During 1998 and 1999, we collected semen from 3 of Patuxent's naturally breeding WC males (B4, B12, and B16). In 1998–99, the fertility averages for B16 were much better than they had been in 1996–97, while those for B4 were lower. The B12 pair had particularly low fertility (0 of 4 eggs fertile) in 1999, the year we collected the most samples (12) from the male. This drop in fertility could have been related to the semen collections, or it may have been coincidental.

Egg fertility was not related to the order in which eggs were laid. In Fig. 2, the apparent increase in fertility of WC eggs laid at the very end of the season is misleading. The sample sizes of ninth and tenth eggs are very small, 6 and 2 respectively. In addition, the majority of these late eggs are from our best pair, B22. Normally we allow pairs to incubate their third or fourth clutches and thereby interrupt laying after 6–8 eggs. However, because B22 begins laying early in the season, and because their fertility is so reliable, we occasionally cycle them for up to 10 eggs. Because of this potential bias, our data should not be used to conclude that fertility rises late in the season.

We earlier discussed flight capability as being an important factor in the success of naturally breeding cranes. We also noted earlier that a few of our cranes had varying degrees of flight impairment. Some with minor impairment were naturally fertile, so we included them in the data presented above. However, some birds we included were probably significantly impaired. For example, the wings of MSC male O8 were both stiff at the carpus and elbow with extension restricted by about 25%. This is the one MSC pair that had highly variable annual fertility averages. However, MSC male L5 also had stiffness in the carpus of both wings but his fertility rates were high. Although these instances show us natural fertility is possible with some wing impairment, we believe fertility will on average be highest with no wing impairment, especially with larger species such as the WC.

Our study found no influence of rearing method on fertility. Even individuals with potential problems from improper imprinting were successful. Four WC pairs (B2, B4, B16, and B22) included at least 1 individual that was reared by sandhill crane foster parents. After fledging, we socialized these birds with conspecifics, and they apparently overcame any negative impacts of their rearing. Sample sizes are too small to determine if there is any correlation between rearing method (hand rearing verses parent rearing) and natural breeding success. All breeding pairs have been successful to some degree despite rearing history.

CONCLUSIONS

We achieved fertility through natural breeding in captive WCs and MSCs. At Patuxent, 14 of 15 pairs allowed to breed naturally produced fertile eggs within 2 years. Flight capability is an important factor effecting natural fertility; rearing history probably is not. Throughout a pair's production history, fertility averages can fluctuate greatly, particularly in WCs. We can not account for some of these fluctuations; captive crane managers would benefit immensely from research into this problem. In general, fertility achieved through AI is more consistent, and 7% to 13% higher, than fertility through natural breeding. AI may be used to supplement natural fertilization. Research is needed to determine the magnitude of this effect. The great differences we found in fertility rates within and among our pairs reinforces the need to manage each pair individually and monitor their status regularly.

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