North American Crane Workshop Proceedings   North American Crane Working Group

2001

WHOOPING CRANE EGG MANAGEMENT: OPTIONS AND CONSEQUENCES

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Abstract: Eggs to build captive whooping crane (*Grus americana*) flocks and most eggs for reintroduction experiments have come from second viable eggs in 2-egg clutches in Canada. Four years ago, egg removal ceased. Based on reproductive rates for years when second eggs were removed and for years when eggs were not removed, we project numbers of young fledging in the wild and in captivity for the 2 most likely egg-management strategies. From existing data sets, we find that reproductive performance was, on average, better during the era of routine removal of the second viable eggs than when no manipulation occurred. Further, the number of young produced in captivity from the removed eggs, on average, resulted in a doubling of the number of young birds (wild and captive) alive each autumn.

Enlightened by hindsight, future conservationists will pronounce judgement on today's decisions in whooping crane egg management. It is most important for the survival of the whooping crane through this millennium that today's decisions maximize both genetic diversity and population growth. These goals can only be met by expanding whooping crane populations as rapidly as practical to offset the harmful effects of inbreeding depression caused by the genetic bottleneck of the 1940s. This essay is an attempt to project the effects of the 1990 decision to curtail the routine removal of the second egg from whooping crane nests in Wood Buffalo National Park (Wood Buffalo), Canada. We base our projections on readily available data sets, but we also clarify the informational needs for future, more precise, assessments.

Egg Recovery and Uses

Until 1954, the nesting location of the migratory whooping crane population was a mystery. That year, a pair was discovered near Great Slave Lake in northwestern Canada (Allen 1956). Allen soon began monitoring the associated population. From these early efforts came the discovery that, although whooping cranes almost always lay 2 eggs, seldom are 2 chicks reared (Novakowski 1966). From this observation came the recommendation to recover the second viable egg from each nest to build a captive flock (Hyde 1957) and to provide chicks for reintroduction purposes. Erickson (1968) proposed experimenting a few years with a surrogate species, the sandhill crane (*Grus canadensis*), before starting an egg-removal program with the whooping crane. This was

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done, then the first whooping crane eggs were taken in 1967. From 1967–74, 61 second eggs were recovered for creating a captive colony (Ellis et al. 1992). From 1975–83, 216 eggs from Wood Buffalo and 73 eggs from the Patuxent Wildlife Research Center (Patuxent) went for an experimental reintroduction at Gray's Lake, Idaho. During egg removal in 1985 and continuing in later egg-removal years, 1 viable egg was translocated into many nests with nonviable clutches (Mirande et al. 1991 unpublished).

Of the 176 eggs (128 fertile) that went to Patuxent, 119 hatched and 83 fledged. These birds provided almost all of the founders at the 2 sizeable captive colonies, Patuxent (44 adults) and the International Crane Foundation (29 adults), and also for the smaller colonies at the Calgary Zoo (21 adults) and elsewhere (8 adults) (August 1999 data, T. V. Stehn, U.S. Fish and Wildlife Service [FWS], personal communication). These captive colonies are today the primary source of young for the whooping crane release program in Florida (122 young from Patuxent, 54 from the International Crane Foundation, and 5 from the Calgary Zoo from 1993 through 1999). These colonies are producing about 30 birds for release each year. They also provide replacement breeders within each colony.

In 1990, Parks Canada called for a halt in egg removal from Canada. This decision was made even though Kuyt (1987) concluded that productivity of the flock was actually higher during the era of egg removal. The Canadian and U.S. Whooping Crane Recovery Teams discussed this issue and agreed to stop eventually, but arranged for egg removal until 1996. In 1994, the Memorandum of Understanding (MOU) between the Canadian Wildlife Service (CWS) and FWS concerning whooping crane management issues was being revised. The new MOU included a statement that routine egg removal would stop in 1996. Although the MOU allowed for

the recovery of 1 or more eggs for purposes of genetic management, in the intervening 4 years, only 1 egg/chick has been recovered. The effect of this nonremoval is that each year 45 or more second eggs have been left to the vicissitudes of nature with the expectation that nearly all would die. Although 148 nesting attempts have been documented over the 3-year period ending in 1999, only 2 sibling pairs have been observed during migration and only 1 sibling pair arrived at Aransas National Wildlife Refuge (Aransas) (B. W. Johns, CWS, personal communication). From existing data sets, we calculate that approximately 130 viable whooping crane eggs have been sacrificed to this policy. In this essay, we project the likely results of 2 alternatives in egg management.

MANAGEMENT ALTERNATIVES

The 2 most likely management alternatives are as follows. Option 1: Do not conduct a routine egg-removal program, but allow removal of 1 or a very few eggs each year for genetic management of the captive colonies (this is the current scheme). Option 2: Routinely remove the second viable egg from each nest that contains 2 viable eggs and use these second eggs to replace the nonviable eggs in any nonviable clutches. This would maximize the number of wild nests with 1 viable egg: this was the practice during the late egg-removal years. Effects of these strategies will be the focus of this paper.

Assumptions and Approximations

Before proceeding with our projections of various egg-management strategies, it is important to state the numerical bases for these projections.

1. Clutch size.—Our value for clutch size in Wood Buffalo will be 2.0 eggs. This value is simpler to work with, and very close to, the calculated average of 1.92 eggs for 500 wild clutches from 1966–91 (Kuyt 1995).

2. Fertility rates.—Young pairs and very old adults sometimes have reduced fertility (Patuxent unpublished data, Johnson 1986*a,b*). Because pairs with infertile eggs are likely to be capable parents, during the later egg-removal years, 1 viable egg was often left in non-viable clutches. This practice could significantly increase productivity of the wild population. Our best estimate of the wild fertility rate is 73% (128 of 176 eggs) based on eggs from Wood Buffalo that came to Patuxent. This value is surely lower (biased downward) than the true fertility rate because so many eggs known to be viable were left behind, and all eggs believed to be nonviable were selectively removed and transported south. Because of this bias, for our analyses, we will use the following more

generous viability rates: 80% of the nests will have 2 viable eggs, 5% of the nests will have 1 viable egg, and 15% will have no viable eggs (i.e., an overall fertility rate of 82.5%). Data from the egg-translocation years (so far unpublished) could be used to refine these estimates.

3. Wild and captive hatching success.—Hatching success of either the first or second eggs at Wood Buffalo is poorly known. It would be expected that the hatching success of eggs removed from the nest, artificially incubated and transported long distances, would be much lower than that for eggs left in wild nests. However, this value for wild eggs traveling to Patuxent was 94% ($n = 48$) for a 5-year period from 1992–96 when egg collection and propagation teams were most experienced (unpublished data, Patuxent files). We will use this value as a conservative estimate of wild hatching success and a reasonable estimate of hatching of eggs transported to the propagation centers.

4. Wild fledging success for single chicks and for sibling pairs.—Ultimately the necessary demographic measures for evaluating population growth are the rates of (1) recruitment of breeders, (2) emigration, and (3) immigration. Because there is only 1 known wild migratory whooping crane population, we assume that immigration is zero. Further, we are confident that all birds that breed return to the general area of Wood Buffalo, so the emigration rate is also zero.

The genetic fitness of an adult lies not in the number of young hatched or fledged, but rather in the number of young that themselves reproduce and how successfully these young and their offspring perform as breeders. For each breeding pair or each population, the number or ratio of young birds produced that themselves become breeders is also the true meaning of recruitment. Reproductive fitness, could be compared for chicks reared singly and chicks from sibling pairs by knowing how many survive to breed and how successful they are at fledging young. However, these ultimate estimators have not been calculated for the migrating flock, so we are forced to rely on fledging rates and fall arrival rates as our only convenient measures of reproductive success.

A good estimate of fall arrival rate would be, of course, the number of young per breeding pair. However, for the pre-egg-removal era, we must rely on a far inferior value, the number of young per successful pair. For this early period (prior to 1967), fall arrival rates averaged 1.13 young per successful pair (Drewien et al. 1995). Drewien and coauthors also report only 1.00 young per successful pair during the egg-removal era, even though some pairs were left with 2 eggs. This leads to the conclusion that none of the unmanipulated 2-egg clutches from 1967–91 resulted in sibling pairs arriving at Aransas.

The inferiority of this parameter (i.e., young/successful pair) compared to values for young/breeding pair can be seen from a bit of hyperbole. If a population consists of 100 breeding pairs of which only 2 are successful in rearing a single chick each, then the number of young/breeding pair equals 2/100 or 0.02 (correctly showing extremely poor productivity) while young/successful pair equals 2/2 or 1.0 (a ratio 50 times higher and a value incorrectly suggesting high productivity).

An even more inferior measurement of reproductive performance for K-selected species, such as the whooping crane, where young birds are typically several years old before breeding, is the number (or ratio) of young in the whole population. By including with breeding pairs the non-breeding segment (immature and subadult birds), it is possible to conclude that an expanding population is actually performing poorly. If, for example, in year 1, a population of 50 breeding pairs (100 white birds) and 50 nonbreeding subadults (also white birds) produces 50 young, then productivity is either 1.0 young/breeding pair (extremely good reproductive performance) or 0.5 young/breeding adult (similarly good) or 0.33 young/white bird (confusingly low). If overwinter survival of young and old alike is excellent and in year 2 the population is similarly productive (i.e., 50 pairs produce 50 young: 1.0 young/breeding pair and 0.5 young/breeding adult), then productivity, as measured by number of young/white bird now drops to 0.25 (a value deceptively low unless presented with qualifiers).

Obviously, it is preferable to use the superior measures of productivity whenever possible. For the Aransas-Wood Buffalo population of whooping cranes (AWP), for most of its history, we have good records of young produced per breeding pair. However, in a companion paper in this volume (Cannon et al. 2001), the authors present exclusively the values for young produced/white bird and state the conclusion: "In reality, the average productivity of the AWP (here defined as recruitment or the percent of the AWP that were young of the year) actually declined during egg-collection years." The authors are fully aware that superior measures of productivity are available and, as we will next see, these lead to the opposite conclusion.

Fortunately, we have data on reproductive performance (including failures) from 407 breeding attempts from 1967–89 (Mirande et al. 1991 unpublished). For our purposes, we have eliminated the 1984 data from this treatment because, for that year, the number of breeding attempts was uncertain. For this period, 210 attempts (51.6%) were successful (i.e., a chick arrived at or near Aransas). To simplify our calculations, we will round this value downward to 50% success for manipulated nests even though we are aware that the 51.6% is already biased downward through the inclusion of many nonmanipulated nests in the 407 total.

Because failed breeding attempts are also important in our calculations and because data on this subject are unavailable in the literature for the pre-removal years (i.e., prior to 1967), we must base our estimates of nonremoval productivity per pair on the last 3 years when egg removal was disallowed (B. W. Johns and T. V. Stehn, personal communication). Our calculations could be improved if we were able to include unmanipulated nests for the egg-removal years, but that data is as yet unavailable.

To clarify, the best estimate of wild fledging success (including the frequency of sibling pairs) for unmanipulated nests would be based on 3 data sets: (1) fledging rates (young/breeding pair) prior to the egg-removal years, (2) fledging rates of unmanipulated pairs during the egg-removal years, and (3) fledging rates during the last three years. For the first estimate (success prior to 1967), we have no data on failed attempts so can only calculate the ratio of sibling pairs (15) and single chicks (101) that arrived at Aransas (Drewien et al. 1995). For the second parameter (productivity of unmanipulated pairs during egg-removal years), no published values are available, but we know from records at Aransas that none of these pairs arrived south with sibling pairs. The third value (productivity from 1997–99, 3 non-removal years) can be carefully estimated from surveys during incubation (B. W. Johns, personal communication) and arrival rates on the wintering grounds (T. V. Stehn, unpublished data).

Our calculated productivity estimates are summarized in Table 1. During the recent non-removal years, 148 known nesting attempts (1997–99), resulted in 1 sibling pair and 63 single chicks arriving at Aransas. Simply put, 42.6% of breeding attempts resulted in single young at Aransas, and 0.7% resulted in sibling pairs. Stated differently, 1.5% (1 of 65) chicks of the fall "recruitment" were from second chicks, and 64 pairs (43.2%: we'll use 43%) were successful in arriving at Aransas with one or more chicks. The pre-1967 rate of recruitment from second chicks was 11.5% (Drewien et al. 1995). Combining early with recent values, the estimate for non-egg-removal recruitment for successful pairs only was 131 + 65 chicks, of which 15 + 1 were second chicks, so 8% (16 of 196) of recruitment was from second chicks. We will use this value (8%) as our estimator of the productivity from second surviving chicks in wild, unmanipulated clutches.

5. Captive fledging success.—The fledging rate of chicks hatched in captivity from wild-origin, viable eggs is 75% based on 48 eggs brought to Patuxent from 1992–96.

Pros and Cons

There is an obvious advantage of saving viable second eggs that most likely would not produce a fledged chick if left in the wild. However, there are also known and potential

Table 1. Reproductive performance rates for wild whooping crane pairs and the fate of wild eggs brought into captivity.

A. Productivity Early Years (1938–66)
116 successful attempts ⇒ 131 winter juveniles
so 11.5% (15 of 131) juveniles from second eggs

B. Productivity for Post-Removal Years (1997–99)
148 attempts, 64 successful ⇒ 43.2% successful
1.5% (1 of 65) juveniles from second eggs

A + B. Combined Non-Removal Years
180 successful attempts ⇒ 196 winter juveniles
so 8.2% are from second eggs

C. Productivity for Egg-Removal Years (1967–89)
407 attempts, 210 successful ⇒ 51.6% successful

D. Fertility Rate for Eggs Sent to Patuxent
72.7% (128 of 176) fertile

E. Hatching Rate for Viable Eggs Sent to Patuxent (1992–96)
94% (45 of 48)

F. Fledging Rate for Viable Eggs Sent to Patuxent 1992–96)
75% (36 of 48)

Sources: A. Drewien et al. 1995; B. Mirande et al. 1991; C. B. Johns and T. Stehn, in litt; D. Patuxent files; E. Patuxent files; F. Patuxent files.

problems associated with egg-removal. Whooping cranes have chosen a remote area to rear their young, and the adults are obviously disturbed during egg-removal visits. To reduce this disturbance, egg removal has been, and can be, performed very quickly with the use of a helicopter to transport people to and from the site. On average, 9.1 min (based on 388 visits: Kuyt 1995) were involved from arrival to departure. By shortening these visits and timing them to occur during late incubation, nest desertion was minimized.

A second negative influence on pairs with 2 viable eggs is that if, after removal of the second egg, the first egg or chick dies, the pair will have no offspring that year. Because the strongest (i.e., most active upon floatation) embryo was left to hatch (the normal practice during the removal years), potential damage from the removal operation was minimized. That the proportion of pairs arriving south with a juvenile was actually higher during removal years (51.6% verses 43.2%) suggests that the above 2 negative factors were negligible.

An unquestionably positive influence of egg removal on

reproductive performance for the population is the insertion of a viable egg into the nest of pairs with nonviable eggs. Further, chicks reared as singles rather than as members of a sibling pair have the advantage of increased adult attention and are therefore likely to be more fit for survival. Bergeson and Johns (2001) reported the high incidence (100%) of loss of second chicks through predation and abandonment.

It is axiomatic that, for species that nurture their young, the degree of parental investment influences quality of progeny. As stated by Lack (1968:165), "in broods of above the normal size the young tend to weigh less at fledging, and to survive less well after fledging . . . ." Cranes are among the species for which it is accepted that the second egg provides "hatching insurance." The second chick is available in case the first embryo or neonatal chick dies (Forbes and Mock 2000), but the second chick otherwise has little chance of survival. For those whooping crane nests where the second eggs are abandoned immediately following hatching of the first chick, the first chick probably suffers no disadvantage by non-removal. However, when the surviving chick is reared with a sibling that dies after considerable parental investment, the surviving chick is probably disadvantaged (i.e., it receives less attention than it would if it had no sibling). This disadvantage could be most easily monitored merely by comparing body mass and feather condition of fledgling colts reared singly or with a sibling. At present these data are unavailable.

Other measures of fitness include juvenile survival probability, based on rates of arrival at Aransas, overwinter survival, and survival to adulthood. Are the juveniles that are lost along the way on their first migration, more often than would be expected, birds reared with a sibling? Also, from records of banded birds, how do adults reared as singles or as siblings compare in rates of reproduction? Because we, at present, have none of these fitness indices available, we will here treat all chicks the same, but we emphasize the need for a careful evaluation of existing data sets.

A discussion of the effects of egg removal would be incomplete without stating that there is a possibility that the wild population would be larger today if egg removal had never happened. As presented above, second chicks account for 8% of the recruitment for early and recent non-removal years combined (Table 1). This value is obviously an over estimate because we know that many clutches during the egg-removal years were left with 2 eggs yet no sibling pairs arrived at Aransas. Nevertheless, we will use this generous value in our calculations. This 8% advantage is offset by the reduced breeding success rate for non-removal years (43.2% verses 51.6%; Table 1).

Year Effect

Historically, the reproductive performance of the wild population has been highly variable from year to year (Mirande et al. 1991 unpublished: section 3:28). Even if we consider only those years from 1983 through 1990 wherein the number of breeding pairs was >20, breeding success ranged from 29% to 78%. We ignore year effect in our calculations, but recognize it as a major factor influencing whooping crane production, short term.

PROJECTIONS

Based on the values presented earlier and summarized in Table 1, the following are projections under various management options for 100 viable second eggs produced by a population consisting of 100 pairs with both eggs viable, 5 pairs with 1 egg viable, and 19 pairs with no eggs viable. Projections in Tables 2–5 are based on the following estimators. Line 1: For pairs with 2 live eggs, 43%, if unmanipulated, and 50%, if manipulated, will arrive at Aransas with 1 or more chicks and 8% of the recruitment of unmanipulated nests will come from second chicks. Line 2: we treat pairs with 1 live egg like manipulated pairs in Line 1, namely, we estimate that 50% of these pairs will arrive at Aransas with a chick. Line 3: Without manipulation, all

Table 3. Juvenile survival projections with broad-scale egg removal for a hypothetical population (125 pairs) having 100 retrievable eggs.

Viable eggs produced before manipulation	Number viable eggs after removal and replacement	Number surviving juveniles
100 pairs with 2 viable eggs (200 eggs)	100	50
6 pairs with 1 viable egg (6 eggs)	6	3
19 pairs with no viable eggs (0 eggs)	19	9.5
Increase in captive population	81	60.8
Totals	206	123.3

pairs without live embryos fail; with manipulation 50% of these pairs arrive south with a chick. Line 4: viable eggs will produce fledglings in captivity 75% of the time.

Management Strategy 1: Remove 1–5 eggs per year for

Table 2. Juvenile survival projections with minimal egg removal for a hypothetical population (125 pairs) having 100 retrievable eggs.

Viable eggs produced before manipulation	Number viable eggs after removal	Number surviving juveniles[a]
100 pairs with 2 viable eggs (200 eggs)	195	2.5 + 40.9 + 3.6 = 47.0
6 pairs with 1 viable egg (6 eggs)	6	3
19 pairs with no viable eggs (0 eggs)	0	0
Increase in captive population	5	3.8
Totals	206	53.8

[a] Calculations in line 1 are as follows: 50% of 5 pairs with 1 remaining egg arrive south with a chick (so 2.5 surviving juveniles), of the remaining 95 pairs (all with 2 eggs) 43% (40.9) arrive south with 1 or more chicks and an additional 8% (3.6) of the total production for these 95 pairs comes from a second surviving chick.

Table 4. Juvenile survival projections for a population of 50 pairs without egg removal.

Viable eggs produced before manipulation	Number viable eggs after removal	Number surviving juveniles[a]
40 pairs with 2 viable eggs (80 eggs)	80	17.2 + 1.5 = 18.7
2.5 pairs with 1 viable egg (2.5 eggs)	2.5	1.3
7.5 pairs with no viable eggs (0 eggs)	0	0
Increases in captive population	0	0
Totals	82.5	20.0

[a] Calculations in line 1: of 40 pairs, 43% (17.2) arrive south with 1 or 2 chicks and 8% (1.5) of the total produced by these pairs derives from the second surviving chick.

Table 5. Juvenile survival projections for a population of 50 pairs with egg removal.

Viable eggs produced before manipulation	Number viable eggs after removal and replacement	Number surviving juveniles
40 pairs with 2 viable eggs (80 eggs)	40	20
2.5 pairs with 1 viable egg (2.5 eggs)	2.5	1.3
7.5 pairs with no viable eggs (0 eggs)	7.5	3.8
Increase in captive population	32.5	23.4
Totals	82.5	48.5

genetic management purposes but leave other nests untouched (Table 2).

Management Strategy 2: Remove all second eggs, but leave 1 viable egg in each nest including nests that had no viable eggs (Table 3).

Our calculations show 50 wild juveniles (47 + 3) without removal (Table 2) and 62.5 wild juveniles (50 + 3 + 9.5) plus an additional 60.8 captive juveniles if we allow broad scale removal (Table 3). Wide scale removal should, on average, more than double the number of surviving juveniles.

MANAGEMENT IMPLICATIONS

It is tempting to extrapolate long-term population trends for the 2 egg-management strategies. Such can be done with somewhat improved accuracy after we have better estimates of some of the population variables discussed earlier, but projections will always be tenuous because of year effect. Differences in number of surviving juveniles resulting from the 2 management strategies are vast (54 without removal verses 123 with removal, Tables 2 and 3). With removal, even the number of wild young produced is increased. These projections justify a rethinking of the current non-removal policy.

It is a fundamental principle of population genetics, that following severe population reduction (a genetic bottleneck), it is imperative to rapidly proliferate as many blood lines as possible. Even birds with deleterious genes should not be eliminated lest their valuable rare alleles be lost to future

generations. The recommended strategy is to expand the population and sort out maladaptive traits later (Mirande et al. 1991 unpublished, section 9:2). In this light, it is advisable to recover as many eggs as practical (without jeopardizing the wild population), at least until the number of breeding adults is greater than 500 (Franklin 1980, Frankel and Soulé 1981). To remove all eggs is ill advised because this practice would both discourage the wild breeding pairs and remove the possibility for natural recruitment, but it does seem advisable, considering the infrequency with which both chicks in sibling pairs survive to reach Aransas, to salvage the second eggs.

Using the current breeding population of about 50 pairs and our estimators, without egg removal, about 20 young, on average, should arrive at the wintering grounds (Table 4). With egg removal and replacement (Table 5), about 25 young would arrive at the wintering grounds and another 23 would fledge in captivity. The total productivity more than doubles and wild young reared without a competing sibling are probably better able to survive.

If, in projecting demographics of the population into the future, we assume that habitat is unlimited, then reproductive output would rise in proportion to population growth. We note, however, that while the number of nesting pairs in the Aransas-Wood Buffalo population has increased by 17% in the last decade (from 32 nesting pairs in 1990 to about 50 today), the absolute number of young arriving at Aransas (14 in 1990 to 18 in 1998) has not increased at the same pace (13%) (T. V. Stehn, personal communication). If productivity has become or becomes density dependent (due, for example, to crowding on the summering grounds or, more likely, on the wintering grounds), then it becomes even more advisable to save eggs that would otherwise die.

In light of all the factors, pro and con, and after reviewing the calculations, the preferred management strategy seems obvious.

Epilogue: In the 2 breeding seasons following writing of this paper (2000 and 2001), no sibling pairs have arrived south, so the losses to the nonremoval policy were more severe even than described herein.

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