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# Whooping crane recruitment enhanced by egg removal

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## Abstract

To facilitate recovery through captive breeding and foster-parenting programs of the endangered whooping crane, one of two eggs was removed from 62% of nests in Wood Buffalo National Park during 1967–1996. Egg removals were justified because cranes usually rear a single chick; the other dies to siblicide or predation. Concerns exist that the wild population might have recovered even faster if nests had not been disturbed. Here we show, contrary to expectation, that removing one of two eggs from a whooping crane nest actually increases the probability of nest success, and this effect is highly correlated with the dynamics of predators in the nesting area. These results beg the question: why do whooping cranes lay two eggs? We attribute two-egg clutches to occasional "good years" in which both chicks survive, compensating for higher mortality in two-egg broods. Egg removal has benefited conservation allowing establishment of several captive flocks, supporting reintroduction of two new populations, and reducing the variance in reproductive success of the wild flock thereby minimizing extinction risk.
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## 1. Introduction

The near extinction of whooping cranes (*Grus americana*) in North America mobilized concern about endangered species, leading to the formulation of the Endangered Species Act in the USA, arguably the most powerful conservation legislation in the world (Doughty, 1989). The subsequent effort to restore whooping cranes has been touted as a model for endangered species recovery programs engaging government, university and private sectors (Cannon, 1996). The sole remaining population nesting in Wood Buffalo National Park in NWT and Alberta, and wintering at the Aransas National Wildlife Refuge and adjacent areas in Texas reached a low

of 16 individuals in 1942 (Boyce, 1987). Since then this population has increased to 217 birds, plus 128 in captivity, and reintroduced populations of 48 in Wisconsin and 79 in Florida (2004 December 31; http://www.pnr-rpn.ec.gc.ca/nature/endspecies/whooping/).

Although 90% of whooping crane clutches contain two eggs (Kuyt, 1995), usually only one chick survives the nesting season with the other succumbing to a variety of causes including siblicide and predation (Bergeson et al., 2001). Therefore, to secure stocks for captive breeding, foster-parenting, and reintroduction programs, 496 eggs were taken from nests in Wood Buffalo during 1967–1996 (Canadian Wildlife Service, 2003). Parks Canada prefers that no future egg collections occur in Wood Buffalo National Park due to concerns that egg removals may reduce the productivity of the whooping crane population (Lewis, 2001), and more generally, that ecological-process management in national parks

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should minimize human intervention and disturbance (Sinclair, 1983; Boyce, 1998).

We examined the consequence of these egg removals on recruitment of young whooping cranes (colts), where we define recruitment to be the proportion of nesting pairs that yield a chick that survives to appear with the wintering flock at Aransas. Because field sampling for egg removals was not designed as an experiment, we used statistical methods to control for variables that might influence results. Several ecological factors might influence recruitment including laying date (Price et al., 1988; Ludwigs and Becker, 2002), water levels (Kuyt et al., 1992), and predation (Boyce and Miller, 1985). A suite of carnivores that might prey on whooping crane chicks is influenced by the 10-year cycle of the boreal forest (Krebs et al., 2001). Little variation existed in egg size within a clutch although eggs laid by novice females were smaller and lighter in weight (Kuyt, 1995).

## 2. Methods

### 2.1. Field sampling

Eggs were removed from nests by the end of May each year during 1967–1996, with eggs being taken from nests throughout the nesting area. Selection of nests for egg removals was not affected by visibility because the birds on a nest are easily seen during survey flights. Likewise, sampling of nests was not influenced by access because there were no sites that could not be accessed readily by helicopter. The only nests less likely to be sampled would be those along the Nyarling River because this area is distant from the other areas thus requiring more travel time. Laying date was estimated by flying low over the nest in an aircraft until the incubating adult stood so that the number of eggs could be counted. If no egg was present repeated visits were made until eggs appeared in the nest. At the time of egg collection, eggs often were tested for viability to ensure that the egg left in the nest was fertile (Kuyt, 1996). If neither egg in a nest appeared viable, an egg sometimes was substituted from a nest where both eggs were fertile.

During visits to the nest, pond depth was measured at each nest 1 m from the edge of the nest in 3 random directions. These measurements were averaged over all nests to obtain mean pond depth for each year.

Mink (*Mustela vison*) and lynx (*Lynx canadensis*) harvest records were obtained from registered traplines in the nesting area. Aboriginal traplines are maintained within Wood Buffalo Park.

Flightless chicks were ringed with coloured leg bands on nesting grounds in Wood Buffalo National Park during 1977–1988. Aerial surveys were conducted on the nesting grounds in August, attempting a complete census. Then in December aerial surveys of whooping crane

territories were conducted by US Fish and Wildlife Service staff at Aransas National Wildlife Refuge, and again, a complete census was conducted using methods detailed by Stehn and Johnson (1987). On rare occasions a ringed chick was missed in the August survey that later showed up in Texas, in which case the August survey results were corrected to reflect that the chick was alive in August.

### 2.2. Effect of egg removal

Habitat quality (Timoney, 1999) and location of nest can influence nesting success (Högstedt, 1980), and variation among years could be attributable to density dependence (Lewis, 2001), but a full model would require too many parameters to account for nesting area and year effects with available data. Therefore, we used the Mantel–Haenszel estimator (Agresti, 1990) correcting for year and nesting area effects to compare recruitment from unmanipulated clutches and those where an egg was removed. The Mantel–Haenszel estimator provides an estimate of the ratio of odds of recruitment in nests where an egg was removed versus the odds of recruitment in unmanipulated nests, after adjusting for nesting area and year effects. An odds ratio, $\theta$, greater than 1 indicates that the odds of recruitment are larger for nests where an egg has been collected. Consider two groups where individuals in one group receive treatment and the other group is the 'control' group where the outcome is 'recruitment' or 'no recruitment' (binary outcome). Effectiveness of the treatment is evaluated by computing the odds ratio: if odds ratio $>1$, treatment is effective and if $<1$, treatment is detrimental. If the number of individuals in the treatment and control class is small, the standard estimator of the odds-ratio is not very accurate. The Mantel–Haenszel estimator allows one to combine information about the common odds ratio across several nesting areas and years, thus improving statistical efficiency. This estimator of the odds ratio permits evaluation of the effectiveness of a treatment by combining several $2 \times 2$ tables, each of which might have small sample size and it also controls for the 'environmental effect' that might be different for each table. Assumptions in computing this estimator are that, on the logit scale, treatment effect and the 'environmental effect' are additive, and there are no three-way interactions. The statistical model for a $2 \times 2$ table for the $i$th location and time point $t$ used is

$$\log \frac{\text{pr}(\text{recruit} \mid X)}{1 - \text{pr}(\text{recruit} \mid X)} = \alpha_{it} + \theta^* I_{(X=\text{treatment})},$$

where $I_{(X=\text{treatment})}$ is 1 if eggs were removed and 0 otherwise, $\alpha_{it}$ is the 'location and time effect' and $\theta$ is the 'treatment effect'. The parameter of scientific interest is the common odds ratio, $\theta$; the other parameters $\alpha_{it}$ are termed, in statistical parlance, as the 'nuisance parame-

ters.' Although they might be of scientific interest, there is not enough information in the data to estimate them individually. The Mantel–Haenszel estimator is a statistically efficient estimator of the common odds ratio in the presence of these nuisance parameters.

After finding a significant main effect using the Mantel–Haenszel estimator, there remained the possibility that other covariates were important. So, we also conducted logistic regression analysis to better understand variation in recruitment success including as covariates precipitation, pond water depth, laying date, egg substitution, egg removal, change in lynx (*Lynx canadensis*) harvests, and change in mink (*Mustela vison*) harvests. We also explored a few interaction effects that made biological sense, including interactions between egg removal and change in lynx and mink harvests. Logistic regression involved fitting models of the following form:

$$y(0, 1) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots)}, \tag{1}$$

where $y(0, 1)$ is 0 if no recruits survive or 1 if at least one survives, and the $x_i$s are from the list of covariates. We used $AIC_c$ to select among alternative plausible models to identify those models that best explained variation in the data whilst minimizing the number of variables in the model (Burnham and Anderson, 2002).

## 3. Results

The ratio of colts/adults appearing on wintering grounds in Texas varied considerably among years (Fig. 1), and recruitment varied among nesting sites (Fig. 2; Table 1). Dropping from analysis 32 nests at which egg substitutions were performed, recruitment of colts into the wintering flock was positively influenced by egg removal ($\hat{\theta} = 1.598$, bootstrapped 90%

CI = 1.098–2.35, $n = 53$ tables). Similarly, we found that the survival of chicks to August was likewise positively influenced by egg removal, with an even stronger effect ($\hat{\theta} = 2.863$, bootstrapped 90% CI = 1.855–4.438, $n = 56$ tables). Our conclusion is that the egg removal effect is not confounded by year or site effects. We also note that variation in recruitment is not tied to the number of years that a site (composite nesting area) was used (Fig. 2). The egg removal effect was not influenced by dropping pairs nesting for the first time from the analysis, and the effects of egg removal on recruitment are large. Eliminating from analysis all novice-pair nesters, recruitment from unmanipulated nests was 0.385 ($\pm 0.0013$) whereas recruitment was 0.498 ($\pm 0.0012$) for nests where an egg was removed.

Ten-year cycles in whooping crane recruitment (Boyce and Miller, 1985) have been sustained; declines in lynx and mink pelts taken from the nesting area are highly correlated with reductions in chick recruitment (Fig. 3). The most parsimonious logistic regression models confirm that laying date, egg collection, and predators influence survival of chicks to August and to December (Table 2). Of chicks surviving until August, $317/440 = 72\%$ survived the migration to Texas. The logistic regression coefficient for egg substitution is negative reflecting that on average recruitment is lower from nests where a substitution was done even though some of these egg transfers resulted in surviving chicks that presumably were not possible otherwise. Low success from nests with substituted eggs might be expected if nests with infertile eggs are associated with poor nest sites or young, inexperienced parents. Counter to expectation (Kuyt et al., 1992) we did not find that precipitation or pond water depth contributed significantly to survival of chicks to August or December. We documented a significant interaction between egg collection and predators (Table 2). This interaction appears
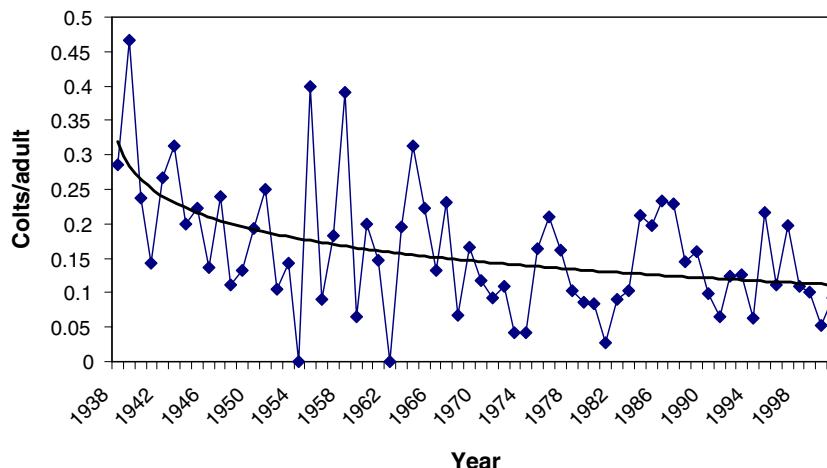


Fig. 1. Among-year variation in the ratio of colts/adults in the Aransas wintering population of whooping cranes.
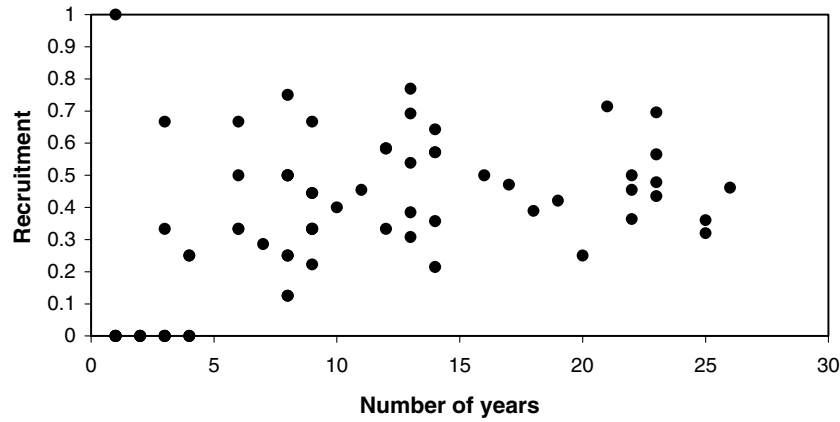
Fig. 2. Average annual recruitment at each composite nesting area plotted against the number of years that the composite nesting area was occupied in Wood Buffalo National Park. A "composite nesting area" is defined to be the general area around a nest site because the precise location for a nest sometimes varied from year to year for the same pair of birds (Kuyt, 1987).

Table 1
Nesting area variation in recruitment of whooping cranes

| Nesting area | Young | Nests | Recruitment | SE |
|---|---|---|---|---|
| Alberta | 17 | 54 | 0.315 | 0.018 |
| Klewi River | 157 | 319 | 0.492 | 0.028 |
| Nyarling River | 13 | 40 | 0.325 | 0.032 |
| Sass River | 92 | 228 | 0.404 | 0.063 |
| Sass-Klewi area | 35 | 89 | 0.393 | 0.074 |
| Total | 314 | 730 | 0.430 | 0.018 |

Standard errors (SE) are based on among-site variances in recruitment.
Data presented are the number of young whooping cranes appearing on wintering grounds at Aransas National Wildlife Refuge, Texas that hatched at nests in each of five primary nesting areas in Wood Buffalo National Park, Canada, 1974–2001.
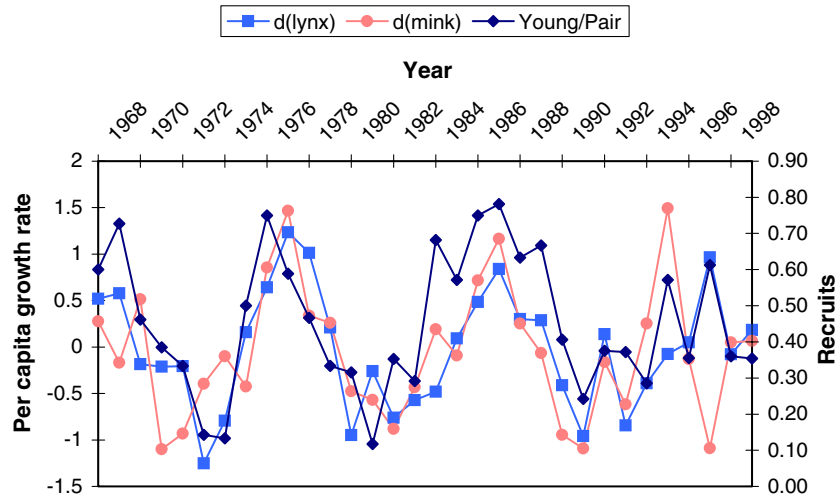


Fig. 3. Recruitment of young whooping cranes to the Aransas wintering population and the per capita growth rate $(\ln[X_t] - \ln[X_{t-1}])$ for reported lynx and mink fur harvests from registered traplines in the immediate vicinity of the nesting grounds in Wood Buffalo National Park. The cross-correlation between the change in lynx and whooping crane recruitment is $r = 0.703$ ($n = 32$, $P < 0.001$); between the change in mink and whooping crane recruitment, $r = 0.518$ ($n = 32$, $P = 0.002$) indicating that recruitment is lowest when fur harvests are declining.

because the difference between unmanipulated clutches and those where an egg was removed only occurs during periods when predators are depressing recruitment (Table 3).

## 4. Discussion

Presumably cranes lay two eggs to provide insurance against loss, i.e., a bet-hedging strategy (Miller, 1973;

Table 2
Factors affecting recruitment of whooping cranes[a]

| Survivors in[b] | August (WBNP) | | December (ANWR) | |
|---|---|---|---|---|
| | $\beta$ | SE | $\beta$ | SE |
| Laying date | −0.04 | 0.022 | −0.054 | 0.022 |
| Viable egg substituted (0, 1) | −1.07 | 0.389 | −0.996 | 0.406 |
| Egg collected (0, 1) | 0.515 | 0.281 | 0.387 | 0.274 |
| Diffs ln(lynx harvests)[c] | 1.46 | 0.406 | 1.48 | 0.414 |
| Egg collected × lynx | −0.921 | 0.445 | −0.895 | 0.451 |
| Constant | 4.91 | 2.83 | 6.44 | 2.83 |

[a] Models presented were selected as most parsimonious from competing biologically plausible models using $AIC_c$ (Burnham and Anderson, 2002).
[b] The table summarizes two logistic regression models (see Eq. (1)) where the response variable was 0 for nests with no survivors and 1 for nests yielding surviving chicks in August (nesting grounds) or December (wintering grounds).
[c] The ln transformed lynx harvests are differenced yielding the per capita growth rate in lynx harvests (see Fig. 3).

Table 3
Influence of predator declines on whooping crane recruitment

| | Chicks | Nests | Recruitment | SE |
|---|---|---|---|---|
| *Low recruitment periods, 1980–1983 and 1990–1993 (predators declining)* | | | | |
| Not collected | 9 | 52 | 0.173 | 0.052 |
| Collected | 18 | 54 | 0.333 | 0.064 |
| Subtotal | 27 | 106 | 0.255 | 0.043 |
| *High recruitment periods, 1984–1986 and 1994–1996 (predators increasing)* | | | | |
| Not collected | 19 | 45 | 0.422 | 0.074 |
| Collected | 28 | 63 | 0.444 | 0.063 |
| Subtotal | 47 | 108 | 0.435 | 0.048 |

We present data on recruitment of whooping cranes during years of low recruitment when predator fur harvest reports were declining (1980–1983 and 1990–1993), and during years of high recruitment when fur harvests were increasing (1984–1986 and 1994–1996) in Wood Buffalo National Park. Predation on whooping cranes as alternate prey is expected to be most severe at the time of predator declines following collapse of snowshoe hare populations (Krebs et al., 2001). Egg collections have the greatest effect on recruitment during nadirs in recruitment.

Forbes, 1991). Increased recruitment from nests where the clutch was reduced to one egg contradicts this hypothesis and raises the question of why whooping cranes lay two eggs. Instead of insurance, we suggest that whooping cranes have adopted a strategy where a two-egg clutch affords opportunity to exploit favourable environments (Orzack and Tuljapurkar, 2001). During years when no egg collections were conducted, 16 of 160 nests produced a pair of chicks (Cannon et al., 2001); no nests produced pairs during years of egg removals even though 38% of the nests were unmanipulated during these years. The occasional survival of both chicks offers sufficient fitness advantage to nearly offset the higher mortality associated with two-egg clutches.

From a long-term perspective and in a large population where the chance of extinction is vanishingly small, the optimal strategy should be based on maximizing the expected number of chicks per pair. For a one-egg strategy, the expected number of chicks is $\varphi$ whereas the expected number of chicks for a two-egg strategy is $(\varphi_1 + 2\varphi_2)$, where $\varphi_i$ denotes the probability of having $i$ surviving chicks arriving at wintering grounds in Texas. With no adjustments for site and year effects, we estimate $\varphi = 0.498$, $\varphi_1 = 0.385$, and $\varphi_2 = 0.05$ thus $\varphi \approx (\varphi_1 + 2\varphi_2)$ indicating little advantage for either strategy.

When populations are small, we are most concerned about risk of extinction. This is related to the probability of having no surviving chicks at the end of the season. With a single egg in the nest, this is given by $(1 - \varphi)$ and for two-eggs this is $(1 - \varphi_1 - \varphi_2)$. Our estimates for these parameters suggest conservation advantage for egg removal with $(1 - \varphi = 0.502) < (1 - \varphi_1 - \varphi_2 = 0.565)$.

Most chick mortality occurred before June 20, in the first few days of life (Bergeson et al., 2001). Chicks have been observed to viciously peck each other, sometimes resulting in the death of the later-hatching chick (Bergeson et al., 2001). Predation on whooping cranes is difficult to document; radiotelemetry studies and field observations documented predation on whooping cranes by wolves (*Canis lupus*; Kuyt et al., 1981) and red fox (*Vulpes vulpes*; Bergeson et al., 2001). Although we have no records of lynx killing whooping cranes, bobcats (*L. rufus*) are the primary predator on whooping cranes introduced to Florida (Nesbitt et al., 2001). Likewise we have no direct observations of whooping crane chicks being killed by mink although mink can be highly effective predators of sandhill crane, *G. canadensis*, chicks (Ivey and Scheuering, 1997). Observations at nests will be necessary to select amongst several alternative mechanisms that might explain higher survival of

chicks from nests where an egg was removed, including: (1) because it is conspicuous, sibling aggression predisposes both chicks to predation, (2) a pair of chicks is more likely to attract the attention of a predator, (3) parents are more attentive/effective against predators if they have a single chick (St. Clair, 1988), or (4) a predator finding an injured, abandoned, or dead chick would search for the surviving sibling, which will not be far away (Bergeson et al., 2001).

The joint US–Canada program of egg removals has enhanced the recovery of whooping cranes in North America (Ellis and Gee, 2001). Even though long-term fitness is nearly equivalent for one-egg and two-egg nests, risk of extinction is lowest when eggs are removed. Egg removals enhance recruitment to the Wood Buffalo/Aransas population and provide birds to supplement recovery efforts elsewhere–multiple populations reduce risk of extinction (Mace and Lande, 1991; Boyce et al., 2002). In addition, studbook management can identify opportunities to sustain genetic variation in the captive flock (Glenn et al., 1999; Jones et al., 2002). Brood management in Wood Buffalo National Park has contributed to the recovery of the whooping crane population, and remains a valuable conservation tool to ensure long-term viability for the species.

The position by Parks Canada that the egg removal program for whooping cranes should be terminated calls to question priorities for park management. Ecological-process management is widely accepted as an important objective for management of national parks, at least in North America (Boyce, 1991, 1998). By minimizing human influence, parks can serve as ecological baseline controls, essential for evaluating the consequences of human developments outside the parks (Sinclair, 1983; Arcese and Sinclair, 1997). However, we believe that management priority should be given to ensure persistence of threatened and endangered species so that diversity is not lost permanently. Surely we cannot appreciate benefits to ecological-process management if components of the ecosystem are missing.

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