Whooping crane Grus americana chick mortality and management intervention

Authors: King, Richard S., Espenshade, Jessica L., Kirkpatrick-Wahl, Sarah K., Lapinski, Monika K., Malekan, Ilana, et al.

Source: Wildlife Biology, 19(4) : 420-428

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/12-133

Wildl. Biol. 19: 420-428 (2013)
DOI: 10.2981/12-133

www.wildlifebiology.com

Original article

Whooping crane *Grus americana* chick mortality and management intervention

Richard S. King, Jessica L. Espenshade, Sarah K. Kirkpatrick-Wahl, Monika K. Lapinski, Ilana Malekan & Jennifer M. Ricket

Translocation of captive-reared animals is widely used as a tool for endangered species recovery. Frequently, translocated populations have relatively low initial productivity, requiring management intervention. A translocated population of whooping cranes *Grus americana* in central Wisconsin is such a case. We examined chick mortality for this population and used daily chick survival rates as our response variable to model several parameters including phenology, chick age, energetics and parent age and experience. We also developed and evaluated adoption techniques using sandhill cranes *Grus canadensis* to mitigate the effects of high chick mortality and increase the probability of fledging. Our results illustrate the challenges that translocated populations can face as they encounter novel breeding conditions. We found that whooping crane daily chick survival was relatively low and most mortality events occurred within the first 20 days. Our results indicated that variables related to age of the parents as well as the pair's previous chick rearing experience were useful for predicting daily chick survival. We found that sandhill crane foster parents readily accepted replacement chicks. We also demonstrated adopted chicks acceptance of foster parents and that the chicks' source (captive-born vs wild-born) did not affect success of the adoption. Chick adoption provides several management options that could be used to bypass the period when chicks experience the greatest mortality. Reducing chick mortality and developing techniques to increase the number of fledged chicks is paramount for whooping crane recovery as well as the recovery of other endangered bird species.

Key words: central Wisconsin, chick adoption, chick mortality, endangered species recovery, Grus americana, whooping crane

Richard S. King, Jessica L. Espenshade, Sarah K. Kirkpatrick-Wahl, Monika K. Lapinski, Ilana Malekan & Jennifer M. Ricket, Necedah National Wildlife Refuge, N11385 Headquarters Road, Necedah, Wisconsin 54646, USA - e-mail addresses: richard_king@fws.gov (Richard S. King); jespenshade@gmail.com (Jessica L. Espenshade); SarahKirkpatrickWahl@gmail.com (Sarah K. Kirkpatrick-Wahl); monsski@gmail.com (Monika K. Lapinski); imalekan@gmail.com (Ilana Malekan); jenniferrickett@gmail.com (Jennifer M. Ricket)*

**Present address: Upper Mississippi River National Wildlife and Fish Refuge, 401 Business Hwy 18 N, McGregor, Iowa 52157, USA*

Corresponding author: Richard S. King

Received 14 December 2012, accepted 14 June 2013

Associate Editor: Kjell Einar Erikstad

Translocation of captive-reared animals within a species' historical range is widely used as an endangered species conservation tool (Griffith et al. 1989, Wolf et al. 1996, Fischer & Lindenmayer 2000). Populations frequently experience low productivity early in translocation programmes (Roche et al. 2008, Evans et al. 2009), requiring management intervention (Reed et al. 1993, Clout & Craig 1994, Elliot et al. 2001), and lending support to the strategy of introducing as many individuals as possible to maximize the probability of success (Griffith et al. 1989, Wolf et al. 1996, Fischer & Lindenmayer 2000).

We studied chick mortality in a population of whooping cranes *Grus americana* that was translo-

cated outside of the species' historical breeding range (Allen et al. 1952) and has experienced low productivity resulting from novel breeding conditions (King et al. 2013). The population began nesting in 2005, and between 2005 and 2009, 41 nest attempts resulted in just one (2.4%) fledged chick. This population is the result of an ongoing release programme that began in 2001. Between 2001 and 2010, 157 captive-reared, costume-imprinted (Horwich 1989, Kreger et al. 2006) whooping crane chicks were released into central Wisconsin, USA. All released whooping cranes were descendants of captive-reared birds that were collected as eggs from nests at Wood Buffalo National Park (Alberta and Northwest Territories, Canada) between 1967 and 1996 (Ellis & Gee 2000, Boyce et al. 2005).

Understanding the factors contributing to high chick mortality rates in the central Wisconsin population and developing management techniques to improve it, or even surpass what could naturally occur, are essential for this population to become self-sustaining. Understanding these factors is complicated by the fact that under normal conditions, cranes have relatively low annual productivity among North American birds (Lovvorn & Kirkpatrick 1982, Drewien et al. 1995), representing a major limiting factor for crane populations (Drewien et al. 1995). Cranes have delayed reproduction (typically 4-7 years of age; Kuyt & Goossen 1987, Tacha et al. 1989, Nesbitt 1992) and relatively high chick mortality rates (typically $>$ 80%; Littlefield 1995). Siblicide (cranes typically have two chicks; Walkinshaw 1973, Kuyt 1981, Littlefield 1995) and parents investing more energy into the larger chick and abandoning the smaller, less able chick (Bergeson et al. 2001) both contribute to high crane chick mortality rates.

Our objectives were to study chick mortality of captive-reared whooping cranes, the variables associated with it and to develop and evaluate techniques to mitigate the effects/limitations of high chick mortality. We hypothesized that crane productivity could be increased with management/manipulation actions including: 1) removing the second egg from a clutch to hand raise the chick for later adoption to either the biological parents or foster parents that lost their first chick, 2) by taking a wild-born chick from parents with two chicks, hand raising that chick, and later giving it to foster parents that lost their own chick, and 3) by replacing young chicks with older, captive- or wild-born chicks, and hand raising the young chicks for release after the period when they would experience highest mortality rates. All research detailed in this manuscript was covered by endangered species (#TE048806-1), migratory bird (#MB09144A-1) and scientific collectors (#SCP-WCR-142-C-2011) permits.

Material and methods

Study area

Our study area (latitude: 44.1499; longitude: -90.1834) was characterized by flat topography, large wetlands complexes and a substrate of coarse sand and totaled 298,240 ha. Some of the wetland complexes were affected by inundation for wildlife management and commercial cranberry production (Jorgensen & Nauman 1993). The wetlands were dominated by sedges *Carex* spp. and bulrushes *Scirpus* spp. with patches of willow *Salix* spp. in drier areas. Mean high temperature during our study was 22.2°C $\pm$ 0.4 (range: 34.4 - 3.3°C). Mean low temperature during our study was 10.7°C $\pm$ 0.4 (range: 24.4 - 2.8°C).

Monitoring wild chicks

In 2010 and 2011, we attempted to make between one and four observations per day of whooping crane chicks/families between hatch and fledge/mortality; four per day for age 1-14 days, three per day for age 14-28 days, two per day for age 29-42 days and one per day after that. In 2012, we attempted to make two observations per day for age 1-42 days, and one per day after that. Our observations, both ground-based and aerial, were aided by every adult crane having individually identifiable colour leg bands and radio-transmitter. We made ground-based observations from a vehicle whenever possible. If not possible, we made ground-based observations from a blind or by foot. Excluding observations from vehicles, we made ground-based observations from a distance of at least 200 m. While conducting observations by foot, we remained hidden from view of the crane family by vegetation and/or topography. Our aerial observations were from fixed-wing aircraft at an elevation of $\geq$ 130 m above ground level.

In the days following hatch, small chicks were often obscured by vegetation. In these cases, we used filial adult behaviours to confirm that the chick(s) was still present. If adult behaviours indicated no chick was present, we searched the last known chick location to collect a carcass for necropsy. We recorded chick/family locations on aerial photo-

graphs and digitized points along with date and time into an ArcMap Geodatabase (ESRI, Redlands, California, USA).

We used the chick/family location information to calculate home-range estimates using the 100% minimum convex polygon and harmonic mean (95% isopleth) methods. While the minimum convex-polygon method is more robust with small sample sizes, it can produce boundaries that encompass areas that are never used (Harris et al. 1990, Borger et al. 2006, Nilsen et al. 2008). Alternately, the harmonic-mean method is more sensitive to small sample size but produces boundaries more accurately limited to areas used (Dixon & Chapman 1980). We calculated all home-range estimates using CALHOME software (Kie et al. 1996).

Modeling daily chick survival rates

We analyzed daily chick survival (DCS) with the logistic-exposure method using a generalized non-linear model with binomial distribution for chick fate and a logit-link function to model DCS with covariates potentially affecting DCS. The logistic-exposure method has been widely used to calculate daily nest survival (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004). We modeled the relationship between DCS and both time-varying (values changed among intervals) and time-invariant (variables changed among chicks but not intervals) covariates. We used the NLMIXED procedure in SAS 9.1 (SAS Institute Incorporated, Cary, North Carolina, USA) for the logistic-exposure models. We calculated the apparent fledge rate (fledged chicks/hatched chicks) to permit comparison with previous research.

Model parameters

We investigated the effects of phenology, energetics and parent age and experience on DCS. We assumed that phenology could affect DCS and used year, ordinal day, chick age and day of chick season, standardized for each chick observation by subtracting the day the first hatch occurred each year from the day of a chick observation, in our DCS models.

We included adult age variables in our models because crane productivity can improve with age (Kuyt & Goossen 1987, Nesbitt 1992). To capture this effect, we included age of both the adult male and female for nesting pairs. This was possible because all whooping cranes are individually colour-banded prior to release and monitored throughout their lives. We also included minimum age as well as combined age for each nesting pair. Crane nest proficiency can improve with experience (Walkinshaw 1947, Kuyt & Goossen 1987, Nesbitt 1992), and we assumed that it could affect chick rearing as well. We captured this potential effect by including whether a whooping crane pair had previous chick-rearing experience.

Energetic demands can affect crane incubation and nest success (Krapu et al. 1985, Tacha et al. 1987), and we assumed that energetics could affect crane chick survival. In our DCS models, we included the distance moved by the chick since the last observation as a measure of the chick's energetic output. If we did not have a measure of the distance moved, we used the mean distance moved for that chick.

Candidate models

We developed *a priori* DCS models with phenology, chick age, parent age and experience, and energetic covariates (detailed above). We introduced a quadratic term for every continuous parameter to capture potential non-linear relationships. As a result of small sample sizes, we limited our analysis to univariate models (Matsuoka & Handel 2007, McWethy & Austin 2009). The use of univariate models also mitigated the effects of overdispersion, which can lead to selection of overparameterized models (Anderson et al. 1994, Rotella et al. 2004, Lusignan et al. 2010).

We evaluated models using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham & Anderson 2002). We assumed that all models containing $> 5\%$ of the model weight (w_i) and within 7 AIC_c units of the model with the smallest AIC_c to be equally supported (Burnham et al. 2011). We assessed whether the data supported covariate effects on DCS with model-averaged coefficients with 95% confidence intervals. We assumed that coefficient intervals that did not overlap 0 to be strong evidence of a covariate effect (Arnold 2010).

Chick adoption

Adoption or alloparental care of chicks by unrelated parents has been reported in > 50 bird species (Riedman 1982). Adoption is usually made by nesting pairs but examples of adoption by subadults or non-breeding pairs have been reported (Holley 1981, Carter & Spear 1986). Adoption rates are affected by a number of proximate factors related to the opportunity for adoption including nest density (Holley 1984, Bustamante & Hiraldo 1990, Roberts

& Hatch 1994), and is therefore most frequently reported in colonial or social species (Pierotti 1991).

Chick adoption as a management or experimental tool has been used in a wide variety of species including barnacle geese *Branta leucopsis* (Loonen et al. 1999), bank swallows *Riparia riparia* (Beecher et al. 1981), pied avocets *Recurvirostra avosetta* (Lengyel 2007), semipalmated sandpipers *Calidris pusilla* (Safriel 1975), Kentish plovers *Charadrius alexandrines* (Szekely & Cuthill 2000), Spanish imperial eagles *Aquila adalberti* (Ferrer & Hiraldo 1991) and piping plovers *Charadrius melodus* (Flemming 1987).

To evaluate the efficacy of bypassing the period of greatest chick mortality, we used greater sandhill cranes *Grus canadensis tabida* for our management/adoption research. Greater sandhill cranes are prevalent in central Wisconsin and have been used to develop techniques later used for whooping cranes including costume-rearing and direct release (Horwich 1989) as well as ultralight-led migration (Duff et al. 2001).

The majority of crane chick mortality occurs within the first two weeks following hatch (Kuyt 1981, Littlefield & Lindstedt 1988, Bennett & Bennett 1990, Bergeson et al. 2001). To simulate predation events during the period of greatest chick mortality, we located sandhill crane families with one or two chicks and captured and removed the chick(s) by hand (Olsen 2004). Captured chicks were either adopted out to another family immediately, or transferred to a captive-rearing facility where we isolation-reared them using costume-imprinting techniques (Horwich 1989). We reared the chicks in captivity until they were used for another adoption, or we released them with adults once fledged. Adopted chicks were held in captivity for varying lengths of time (range: 0-21 days).

Following the simulated predation event, we walked around the area where the chick(s) was captured, acting as a threat to the adults and maintaining visual contact with the pair (Olsen 2004). This prevented the pair from returning to the area where they left the chick and from discovering that it was gone. We maintained visual contact with the pair until we provided a replacement chick either directly from another wild family or from our captive-rearing facility. This was necessary to ensure that we provided a replacement chick to the same pair as none of the adult sandhill cranes were individually identifiable.

We used replacement chicks that had been wild-born (captured during simulated predation events) as well as chicks that were collected as eggs and hatched in an incubator. We weighed chicks upon capture and prior to release with three exceptions. In these cases, we estimated the weight based on weights of similar sized chicks as well as our experience handling and weighing chicks.

Prior to release, we fitted chicks with either a subcutaneous radio-transmitter (in 2011) or a passive integrated transponder (PIT) tag (in 2012). The subcutaneous radio-transmitters used were Model BD-2 by Holohil Systems Ltd (Carp, Ontario, Canada). The transmitters weighed 1.3 g and had a helical antenna coiled around a 10 mm piece of Tygon tubing. The transmitter and antenna were hermetically sealed and subcutaneously implanted (Olsen 2004). We used Trovan PIT tags (model ID-100A Microtransponder, Santa Barbara, California, USA). The PIT tags weighed < 0.1 g and were 2.1 mm in diameter and 11.5 mm long.

We transported replacement chicks to release sites in boxes and released them in thick/tall cover in the area where the original chick(s) was captured. When possible, the chicks were placed so they had visual contact with adults. After release, we left the immediate area. From a distance of ≥ 200 m, we observed the adult sandhill cranes for up to two hours to verify that the adult cranes returned to the release site. We used behavioural observations to confirm that the adults accepted the chicks. These behaviours included: 1) adults and chick observed exhibiting filial behaviours (Ellis et al. 1998) and 2) adult cranes exhibiting filial behaviours while the chick was not visible; vegetation typically obscured the chicks making direct observation difficult and uncommon.

We verified that the replacement chicks accepted the foster parents in one or more of the three following ways: 1) direct observations of the chick with parents exhibiting filial behaviours, 2) confirming that the chick remained with the foster parents for ≥ 1 day via radio-telemetry and that the family moved away from the release site, and 3) confirming that the chick remained with the foster parents for ≥ 1 day via PIT tag scanning following opportunistic recapture of the chick.

Results

We collected 528 whooping crane chick observations from 19 different chicks (13 different nesting pairs) between 2010 and 2012. Three of the pairs produced chicks in subsequent years, but no pair produced

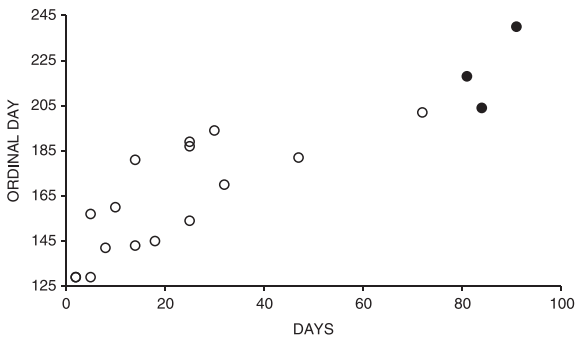

Figure 1. Whooping crane chick mortality and fledge events in central Wisconsin, USA, during 2010 - 2012; ○ represents mortality events and • represents fledge events. Chick age is illustrated on the horizontal axis.

chicks in all years. Our apparent fledge rate was 16% (three of 19). Approximately 56% of chick mortalities occurred prior to day 20. Of the three chicks that survived to fledge, the average fledge age was 85.3 (SE = 3.0) days (range: 81-91 days; Fig. 1). The mean distance between whooping crane chick locations was 264.0 (SE = 12.0) m and mean pre-fledged home range for chicks that survived > 10 days was 40.4 (SE = 11.8) ha (range: 1.6-127.2 ha) and 50.4 (SE = 11.0) ha (range: 3.5-116.3 ha) using the harmonic mean (95%) and minimum convex polygon (100%) methods, respectively.

We collected the carcasses of three dead whooping crane chicks. A chick collected in 2012 (died on day 71) was too decomposed to make any determination other than that radiographs failed to demonstrate any obvious indication of predation. In 2011, a chick died as a result of a predation event (died on day 47), the radiogram indicated thoracic vertebra fracture. This chick was not consumed, indicating that the parents may have guarded/defended the chick (carcass) following the predation event. A chick collected in 2010 (died on day 30) showed no signs of predation but did have a bacterial infection (A. Ballmann, National Wildlife Health Lab, U.S. Geological Survey, unpubl. data).

We found a DCS of 0.972 (CI = 0.957-0.984). Therefore, the probability of fledge (given our average fledge of 85 days) was 9.7% (CI = 2.6-25.7%). Among our DCS models, several variables including age as well as a pair's previous chick-rearing experience were supported (Table 1). Model weights indicated support for adult female age (linear and quadratic forms) over other models (see Table 1). These relationships were all positive and the confidence intervals for model-averaged coefficients did not overlap 0 (indicating a strong covariate effect) with the exceptions of chick day and adult male age of the nesting pair (Table 2).

We performed nine sandhill crane adoptions; four in 2011 and five in 2012. Our adoptions occurred during 28 May - 2 June 2011 and during 24 May - 14 June 2012. Adults accepted chicks during all of the attempts. We confirmed five instances of the chicks accepting the foster parents (Fig. 2). In the remaining four instances, we were unable to evaluate whether the chick accepted the foster parents or not. The time between the simulated predation event and provisioning of a replacement chick ranged from two to 44 minutes.

Five of the replacement chicks were smaller than the pair's original chick and four were larger. The smallest chick weighed 100 g and the largest 518 g. The difference between the original and replacement chick weights ranged from -344 g to 242 g (-77 - 297%; see Fig. 2). Five adopted chicks were wild-

Table 1. Results of models used to evaluate covariate effects on whooping crane daily chick survival in central Wisconsin, USA. Models are ranked by ascending ΔAIC_c; AIC_c is Akaike's information criterion adjusted for small sample sizes; w_i is the model weight. Models presented include only those that were within 7 AIC_c values of the top model ($\Delta AIC_c = 0$).

Variable	AIC_c	ΔAIC_c	Relative Model Likelihood	w_i
Nesting pair female age	131.8	0.0	1.000	0.241
Nesting pair female age^2	132.4	0.6	0.740	0.179
Combined age of nesting pair	133.1	1.3	0.522	0.126
Age of youngest member of nesting pair	133.7	1.9	0.387	0.093
Combined age of nesting pair^2	133.8	2.0	0.368	0.089
Pair with previous nesting experience	134.2	2.4	0.301	0.073
Age of youngest member of nesting pair^2	135.0	3.2	0.202	0.049
Chick day*	135.7	3.9	0.142	0.034
Chick day^2*	135.7	3.9	0.142	0.034
Nesting pair male age	137.8	6.0	0.050	0.012

* Day of chick season, standardized for each chick observation by subtracting the day the first hatch occurred each year from the day of a chick observation.

Table 2. Model-averaged parameter estimates with standard error (SE) and 95% confidence intervals (CI) for all continous covariates used to model whooping crane daily chick survival in central Wisconsin, USA.

			95% Confidence interval	
Covariate	Estimate	SE	Lower	Upper
Nesting pair female age [a]	0.3941	0.1347	0.1295	0.6588
Combined age of nesting pair [a]	0.2225	0.0800	0.0653	0.3797
Age of youngest member of nesting pair [a]	0.4162	0.1627	0.0966	0.7359
Year [a]	0.0018	0.0001	0.0015	0.0020
Chick age	0.0182	0.0131	-0.0076	0.0439
Ordinal day	0.0102	0.0107	-0.0108	0.0311
Chick distance moved	0.0000	0.0010	-0.0021	0.0021
Chick day[*]	0.0142	0.0124	-0.0101	0.0386
Nesting pair male age	0.2690	0.1503	-0.0262	0.5642

[a] Strong evidence of a covariate effect, where CI does not overlap zero.
[*] Day of chick season, standardized for each chick observation by subtracting the day the first hatch occurred each year from the day of a chick observation.

born and four were captive-born. In each of the nine adoptions, we found no differences in the parents' acceptance of the replacement chick whether they were captive-born or wild-born.

Discussion

Our apparent fledge rate was lower than reported for whooping cranes at Wood Buffalo National Park (49.4 - 58.4%; Kuyt 1981 and 33.3%; Bergeson et al. 2001) and for introduced, non-migratory whooping cranes in Florida (47.4%; Spalding et al. 2009). Spalding et al. (2009) studied birds produced at the same captive-breeding facilities as those in our study. Our apparent fledge rate was similar to that reported for some sandhill crane populations (Littlefield 2003) but lower than others (Dimatteo 1992, Dresroberts 1997). Direct comparison among other studies is complicated by the fact that all of these studies included chicks discovered at varying ages. As short-lived chicks are easily missed, much like short-lived nests, apparent fledge rate can be inflated in the same way as apparent nest success (Mayfield 1975). We found that the majority of chick mortalities occurred at or before the chicks reached 20 days of age. Our results are consistent with both whooping crane (Kuyt 1981, Bergeson et al. 2001) and sandhill crane (Littlefield & Lindstedt 1988, Bennett & Bennett 1990) chick mortality studies. To our knowledge, we are first to report whooping crane DCS.

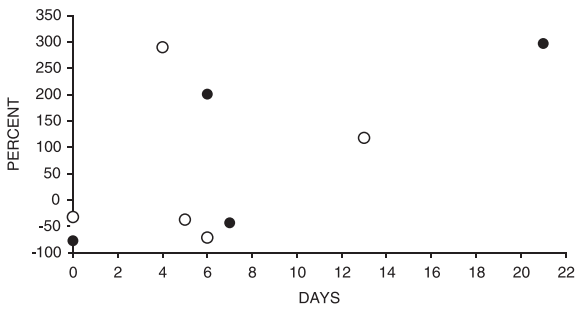

Figure 2. Weight differences (in %) of sandhill crane replacement and original chicks used in adoptions in central Wisconsin, USA. Foster parents accepted replacement (adopted) chicks in all cases. Confirmed examples of chick acceptance of foster parents are illustrated by ○. Chick acceptance of foster parents in the other four adoptions (•) was unconfirmed. Days the chicks were held in captivity prior to adoption are illustrated on the horizontal axis.

Given the effects of age- and experience-related variables on our DCS models and that the central Wisconsin whooping crane population is relatively young, we were not surprised that our apparent fledge rate was lower than that reported elsewhere for whooping cranes and lower than reported for most sandhill crane populations. We note that the fledge rate during our study represented a substantial improvement over the population's fledge rate during the first five years of reproduction. We conclude the central Wisconsin whooping crane population appears to be adjusting to local breeding conditions and that chick fledge rates will likely improve in the future as the population ages and gains chick-rearing experience. However, even if the population's apparent fledge rate rises to levels consistent with other whooping crane and sandhill crane populations, without management intervention, nearly half of all hatched chicks will not survive to fledge.

We provided some insight into our management questions. Adult sandhill cranes appear to readily accept replacement chicks. Our results indicate that,

in the range tested, the size of the replacement chick relative to the original chick was of little consequence to successful acceptance by the parents. We found no evidence that duration in captivity, within the tested range, or whether chicks were wild- or captive-born had an effect on the foster parent acceptance. Though it was much more difficult, we were able to confirm that at least five of the nine replacement chicks accepted the foster parents. We were unable to evaluate this for the other four chicks.

A review of studies investigating the effect of chick size on adoption suggests that there are differences among species, nesting ecology and the level of parent-young recognition. Similar to Mississippi sandhill cranes *Grus canadensis pulla* (Olsen 2004), the foster parent sandhill cranes in our study remained in the area and returned to care for chicks after a range of absence lengths. Our results relative to chick weight are consistent with Carter & Spear (1986), who studied western gulls *Larus occidentalis* and found that adults adopted a range of chicks bigger, smaller and the same size as their own chicks. However, piping plovers, which exhibit synchronized hatching, may not accept adopted chicks of a differing age (Flemming 1987). This suggests that species with asynchronised hatching, such as cranes, may have an increased likelihood of accepting replacement chicks with ages that differ from their own chick.

Our adoption research was limited both in numbers and scope. We recommend that adoption as a management tool receives more detailed study. Most notably, we recommend that techniques be explored with whooping cranes as this species may or may not react in the same way as sandhill cranes. Future studies should aim at monitoring the chicks from adoption to fledging as increasing the number of fledged individuals is the ultimate goal, and we cannot assume that an adopted chick equals a fledged chick. For example, there is some evidence that long-term adoption with emperor penguins *Aptenodytes forsteri* is rare (2.3%) with most lasting only 0.5-10 days (Jouventin et al. 1995).

Our results illustrate the challenges that endangered species recovery programmes can encounter as populations of captive-reared animals struggle to gain the experience needed to become self-sustaining. This demonstrates the need to sustain translocation efforts (Griffith et al. 1989, Wolf et al. 1996, Fischer & Lindenmayer 2000) and develop management techniques to maximize productivity and the likelihood of success. Chick adoption presents several management options to reduce chick mortality and increase productivity including 1) provisioning older, replacement chicks and 2) temporarily provisioning replacement chicks from surrogate species. Both techniques maximize productivity by bypassing the period when the majority of chick mortality occurs. In the case of whooping cranes, this is between hatch and 20 days of age. Developing techniques to maximize the number of fledged chicks is paramount for recovery of many species of endangered birds and may reduce the time required to achieve recovery goals.

Acknowledgements - we thank the National Fish and Wildlife Foundation, U.S. Fish and Wildlife Service, International Crane Foundation, Wisconsin Department of Natural Resources, Natural Resource Foundation of Wisconsin and Operation Migration for providing financial support and/or in-kind services to make this research possible. The field crew was invaluable and included: J. Boysen, J. Brennamen, M. Campbell, K. Gleason, T. Hunter, M. Jones, L. Maas, L. McKinney, C. Morris, J. Trutwin and R. Urbanek. We would like to thank private land owners in the surrounding area who granted researchers access to their property. A. Ballmann provided preliminary necropsy results. B. Hartup and M. Wellington provided valuable aviculture and veterinary advice. We thank the U.S. Fish and Wildlife Service for providing the endangered species and migratory bird permits and Wisconsin Department of Natural Resources providing scientific collectors permit. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

References

Allen, R.P., Livingston, J.A. & National Audubon Society 1952: The whooping crane. - National Audubon Society, New York, New York, USA, 246 pp.

Anderson, D.R., Burnham, K.P. & White, G.C. 1994: AIC model selection in overdispersed capture-recapture data. - Ecology 75: 1780-1793.

Arnold, T.W. 2010: Uninformative parameters and model selection using Akaike's information criteria. - Journal of Wildlife Management 74: 1175-1178.

Beecher, M.D., Beecher, I.M. & Hahn, S. 1981: Parent offspring recognition in bank swallows (*Riparia riparia*): development and acoustic basis. - Animal Behaviour 29: 95-96.

Bennett, A.J. & Bennett, L.A. 1990: Productivity of Florida sandhill cranes in the Okenfenokee Swamp, Georgia. - Journal of Field Ornithology 61: 224-231.

Bergeson, D.G., Johns, B.W. & Holroyd, G.L. 2001: Mortality of whooping crane colts in Wood Buffalo National Park, Canada, 1997-1999. - Proceedings of the North American Crane workshop 8, pp. 6-10.

Borger, L., Franconi, N., De Michele, G., Gantz, A., Meschi,

F., Manica, A., Lovari, S. & Coulson, T. 2006: Effects of sampling regime on the mean and variance of home range size estimates. - Journal of Animal Ecology 75: 1493-1405.

Boyce, M.S., Lele, S.R. & Johns, B.W. 2005: Whooping crane recruitment enhanced by egg removal. - Biological Conservation 126: 395-401.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information theoretic approach. 2nd edition. - Springer-Verlag, New York, New York, USA, 353 pp.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. 2011: AIC model selection and multimodel inference in behavior ecology: some background, observations, and comparisons. - Behavior Ecology 65: 23-35.

Bustamante, J. & Hiraldo, F. 1990: Adoptions of fledgings by black and red kites. - Animal Behavior 49: 321-331.

Carter, L.R. & Spear, L.B. 1986: Costs of adoption in western gulls. - Condor 88: 253-256.

Clout, M.N. & Craig, J.L. 1994: The conservation of critically endangered flightless birds in New Zealand. - Ibis 137: 181-190.

Dresroberts, K.J. 1997: Survival and habitat use of greater sandhill crane colts on Modoc National Wildlife Refuge, California. - In: Urbanek, R.P & Stahlecker, D.W. (Eds.); Proceedings of the North American Crane Workshop. North American Crane Working Group, Grand Island, Nebraska, USA, 262 pp.

Dimatteo, J.J. 1992: Status, production and migration of greater sandhill cranes on Agassiz National Wildlife Refuge, Minnesota. - In: Wood, D.A. (Ed.); Proceedings of the 1988 North American Crane Workshop. State of Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report #12, 270 pp.

Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002: Advanced techniques for modeling avian nest survival. - Ecology 83: 3476-3488.

Dixon, K.R. & Chapman, J.A. 1980: Harmonic mean measure of animal activity areas. - Ecology 61: 1040-1044.

Drewien, R.C., Brown, W.M. & Kendall, W.L. 1995: Recruitment in Rocky Mountain greater sandhill cranes and comparison with other crane populations. - Journal of Wildlife Management 59: 339-356.

Duff, J.W., Lishman, W.A., Clark, D.A., Gee, G.F. & Ellis, D.H. 2001: Results of the first ultralight-led sandhill crane migration in eastern North America. - In: Ellis, D.H. (Ed.); Proceedings of the North American Crane Workshop. North American Crane Working Group, Seattle, Washington, USA, 226 pp.

Elliot, G.P., Merton, D.V. & Jansen, P.W. 2001: Intensive management of a critically endangered species: the kakapo. - Biological Conservation 99: 121-133.

Ellis, D.H. & Gee, G.F. 2000: Post-release survival of hand-reared and parent-reared Mississippi sandhill cranes. - Condor 102: 104-112.

Ellis, D.H., Swengel, S.R., Archibald, G.W. & Kepler, C.B. 1998: A sociogram for the cranes of the world. - Behavioral Processes 43: 125-151.

Evans, R.J., Wilson, J.D., Amar, A., Douse, A., Macclennan, A., Ratcliffe, N. & Whitfield, D.P. 2009: Growth and demography of a re-introduced population of white-tailed eagles *Haliaeetus albicilla*. - Ibis 151: 244-254.

Ferrer, M. & Hiraldo, F. 1991: Evaluation of management techniques for the Spanish imperial eagle. - Wildlife Society Bulletin 19: 436-442.

Fischer, J. & Lindenmayer, D.B. 2000: An assessment of the published results of animal relocations. - Biological Conservation 96: 1-11.

Flemming, S.P. 1987: Natural and experimental adoption of piping plover chicks. - Journal of Field Ornithology 58: 270-273.

Griffith, B., Scott, J.M., Carpenter, J.W. & Reed, C. 1989: Translocation as a species conservation tool: Status and strategy. - Science 245: 477-482.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T. & Wray, S. 1990: Home range analysis using radio tracking data - a review of problems and techniques particularly as applied to the study of mammals. - Mammal Review 20: 97-123.

Holley, A.J.F. 1981: Naturally arising adoption in the herring gull. - Animal Behavior 29: 302-303.

Holley, A.J.F. 1984: Adoption, parent-chick recognition and maladaption in the herring gull *Larus argentatus*. - Zeitschrift für Tierpsychologie 64: 9-14.

Horwich, R.H. 1989: Use of surrogate parental models and age periods in a successful release of hand-reared sandhill cranes. - Zoo Biology 8: 379-390.

Jorgensen, E.E. & Nauman, L.E. 1993: Bird distribution in wetlands associated with commercial cranberry production. - Passenger Pigeon 55: 289-298.

Jouventin, P., Barbraud, C. & Rubin, M. 1995: Adoption in the emperor penguin, *Aptenodytes forsteri*. - Animal Behaviour 50: 1023-1029.

Kie, J.G., Baldwin, J.A. & Evans, C.J. 1996: CALHOME: A program for estimating animal home ranges. - Wildlife Society Bulletin 24: 342-344.

King, R.S., Trutwin, J.J., Hunter, T.S. & Varner, D.M. 2013: Effects of environmental stressors on nest success of introduced birds. - Journal of Wildlife Management 77: 842-854.

Krapu, G.L., Iverson, G.C., Reinecke, K.J. & Boise, C.M. 1985: Fat deposition and usage by arctic-nesting sandhill cranes during springs. - Auk 102: 362-368.

Kreger, M.D., Hatfield, J.S., Estevez, I., Gee, G.F. & Clugston, A. 2006: Behavioral profiles of the captive juvenile whooping crane as an indicator of post-release survival. - Zoo Biology 25: 11-24.

Kuyt, E. 1981: Clutch size, hatching success, and survival of whooping crane chicks, Wood Buffalo National Park, Canada. - In: Lewis, J.C. & Masatomi, H. (Eds.); Crane research around the world International Crane Foundation, Baraboo, Wisconsin, USA, 259 pp.

Kuyt, E. & Goossen, J.P. 1987: Survival, age composition, sex ratio, and age at first breeding of whooping cranes in Wood Buffalo National Park, Canada. - In: Lewis J.C. &

Ziewits, J.W. (Eds.); Proceedings of the 1985 Crane Workshop. Whooping Crane Habitat Maintenance Trust, Grand Island, Nebraska, USA and U.S. Fish and Wildlife Service, Washington, D.C., USA, 415 pp.

Lengyel, S. 2007: Benefits of large broods by higher chick survival and better territories in a precocial shorebird. - Behavioral Ecology and Sociobiology 61: 589-598.

Littlefield, C.D. 1995: Demographics of a declining flock of greater sandhill cranes in Oregon. - Wilson Bulletin 107: 667-674.

Littlefield, C.D. 2003: Sandhill Crane nesting success and productivity in relation to predator removal in southeastern Oregon. - The Wilson Bulletin 115: 263-269.

Littlefield, C.D. & Lindstedt, S.M. 1988: Survival of juvenile greater sandhill cranes at Malheur National Wildlife Refuge, Oregon. - In: Wood, D.A. (Ed.); Proceedings of the 1988 North American Crane Workshop. State of Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report #12, 270 pp.

Loonen, M.J.E., Bruinzeel, L.W., Black, J.M. & Drent, R.H. 1999: The benefit of large broods in barnacle geese: a study using natural and experimental manipulation. - Journal of Animal Ecology 68: 753-768.

Lovvorn, J.R. & Kirkpatrick, C.M. 1982: Recruitment and socially-specific flocking tendencies of eastern sandhill chicks. - Wilson Bulletin 95: 313-321.

Lusignan, A.P., Mehl, K.R., Jones, I.L. & Gloutney, M.L. 2010: Conspecific brood parasitism in common eiders (*Somateria mollissima*): do brood parasites target safe nest sites? - Auk 127: 765-772.

Matsuoka, S.M. & Handel, C.M. 2007: Nesting ecology of boreal forest birds following a massive outbreak of spruce beetles. - Journal of Wildlife Management 7: 51-65.

Mayfield, H.F. 1975: Suggestions for calculating nest success. - Wilson Bulletin 87:456-466.

McWethy, D.B. & Austin, J. 2009: Nesting ecology of greater sandhill cranes (*Grus canadensis*) in riparian and palustrine wetlands or eastern Idaho. - Waterbirds 32: 106-115.

Nesbitt, S.A. 1992: First reproductive success and individual productivity in Sandhill Cranes. - Journal of Wildlife Management 56: 573-577.

Nilsen, E.B., Pedersen, S. & Linnell, J.D. 2008: Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? - Ecological Research 23: 635-639.

Olsen, G.H. 2004: Mortality of Mississippi sandhill crane chicks. - Journal of Avian Medicine and Surgery 18: 269-272.

Pierotti, R. 1991: Infanticide versus adoption: an intergenerational conflict. - American Naturalist 138: 1140-1158.

Reed, C.M., Nilsson, R.J. & Murray, D.P. 1993: Cross-fostering New Zealand's black stilt. - Journal of Wildlife Management 57: 608-611.

Riedman, M.L. 1982: The evolution of alloparental care and adoption in mammals and birds.- Quarterly Review of Biology 57: 405-435.

Roberts, B.D. & Hatch, S.A. 1994: Chick movements and adoption in a colony of black-legged kittiwakes. - Wilson Bulletin 106: 289-298.

Roche, E.A., Cuthbert, F.J. & Arnold, T.W. 2008: Relative fitness of wild and captive-reared piping plovers: Does egg salvage contribute to recovery of the endangered Great Lakes population? - Biological Conservation 141: 3079-3088.

Rotella, J.J., Dinsmore, S.J. & Shaffer, T.L. 2004: Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. - Animal Biodiversity and Conservation 27: 187-205.

Safriel, U.N. 1975: On the significance of clutch size in nidifugous birds. - Ecology 56: 703-708.

Shaffer, T.L. 2004: A unified approach to analyzing nest success. - Auk 121: 526-540.

Spalding, M.G., Folk, M.J., Nesbitt, S.A., Folk, M.L. & Kiltie, R. 2009: Environmental correlates of reproductive success for introduced resident whooping cranes in Florida. - Waterbirds 32: 538-547.

Szekely, T. & Cuthill, I.C. 2000: Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. - Proceedings of the Royal Society of London 267: 2087-2092.

Tacha, T.C., Haley, D.E. & Vohs, P.A. 1989: Age of sexual maturity of sandhill cranes from mid-continental North America. - Journal of Wildlife Management 53: 43-46.

Tacha, T.C., Vohs, P.A. & Iverson, G.C. 1987: Time and energy budgets of sandhill cranes from mid-continental North America. - Journal of Wildlife Management 51: 440-448.

Walkinshaw, L.H. 1947: Some Nesting Records of the Sarus Crane in North American Zoological Parks. - Auk 64: 602-615.

Walkinshaw, L.H. 1973: Cranes of the World. - Winchester Press, New York, New York, USA, 392 pp.

Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. 1996: Avian and mammalian translocations: update and reanalysis of 1987 survey data. - Conservation Biology 10: 1142-1154.