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Translocation of captive-reared animals within a species’ historical range is widely used as a 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; Walkinson 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 ± 0.4 (range: 34.4 - 3.3°C). Mean low temperature during our study was 10.7°C ± 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 fledging/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 ≥ 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). Alternatively, 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 method. We calculated the apparent fledge rate (fledged chicks/hatched chicks) to permit comparison with previous research.

Model parameters
We investigated the effects of phenotype, energetics and parent age and experience on DCS. We assumed that phenotype 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 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 phenotype, 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 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.

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.
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 alexandrinus (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...
chicks in all years. Our apparent fledge rate was 16\% (three of 19). Approximately 56\% of chick mortal-
ities 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
chance 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 (car-
cass) 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 Sur-
vey, 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 confi-
dence 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 provi-
sioning 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 \(\Delta AIC_c\); \(AIC_c\) is Akaike’s information criterion adjusted for small sample sizes; \(w_i\) is the model weight. Models presented
include only those that were within \(7 \Delta AIC_c\) values of the top model (\(AAIC_c = 0\)).

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

\(^*\) 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.

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.

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