



Effects of Environmental Stressors on Nest Success of Introduced Birds

RICHARD S. KING,¹ *Necedah National Wildlife Refuge, N11385 Headquarters Road, Necedah, WI 54646, USA*

JUSTIN J. TRUTWIN, *Necedah National Wildlife Refuge, N11385 Headquarters Road, Necedah, WI 54646, USA*

TRAVIS S. HUNTER, *Necedah National Wildlife Refuge, N11385 Headquarters Road, Necedah, WI 54646, USA*

DANA M. VARNER, *Cooperative Wildlife Research Laboratory, 251 Life Science II, Southern Illinois University, Carbondale, IL 62901, USA*

ABSTRACT Understanding the influence of environmental stressors on daily nest survival of introduced birds is important because it can affect introduction success as well as the ability to evaluate introduction programs. For long-lived birds with low annual production, adjustment to local breeding conditions can take many years. We examined nest success rates of 2 introduced bird species, whooping crane (*Grus americana*) and trumpeter swan (*Cygnus buccinator*), in Wisconsin. Both species are long-lived with low annual reproductive rates. Trumpeter swans were established in our study area approximately 10 years before whooping cranes. We predicted that trumpeter swans would show less sensitivity to environmental stressors. We used daily nest survival rates (DNSRs) as our response variable to model several environmental parameters including weather, phenology, and ornithophilic black flies (Diptera: Simuliidae). Additionally, we examined the influence of captive history, age, release method, energetics, and nesting experience on whooping crane DNSRs. Daily nest survival of whooping cranes was the most sensitive to stressors. Trumpeter swan daily nest survival showed less sensitivity to the same stressors. Daily nest survival for both species peaked later in the nesting season, after 30 April and before 30 May. We also found that the daily nest survival rate (DNSR) for whooping cranes was potentially affected by captive exposure (measured by generations removed from the wild). Our results highlight the difficulties associated with conservation of long-lived birds with low annual productivity as they adjust to local breeding conditions and that nest phenology at the source location can determine how these conditions are interfaced. We recommend that the juxtaposition of source and introduction location nest phenology be considered prior to introduction site selection. Additionally, strategically selecting offspring from captive pairs with nest phenology similar to that of sympatric species at the introduction location should be considered. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS daily nest survival, environmental stressors, introduction, whooping crane, Wisconsin.

The release of captively reared animals into new areas is a widely used conservation tool (Wolf et al. 1996) but has only recently emerged as a discipline referred to as reintroduction science or reintroduction biology (Armstrong and Seddon 2007, Seddon et al. 2007). Reintroduction science incorporates many disciplines that may themselves be poorly understood. Such is the case with demographic variation across species ranges (Fredrickson et al. 2005, Sandercock et al. 2005, Wilson and Martin 2011) and the role of environmental stressors on that variation (Yeh and Price 2004, Yeh et al. 2007). Therefore, understanding natural demographic variation and the effect of stressors on production is a key component to introduction program evaluation. Ostermann et al. (2001) recommended introduction programs receive periodic review and 1 of the evaluation criteria include a

comparison between post-release recruitment rates of captively reared animals and those at the source population, as well as that of similar species. We use the general term introduction to refer to the release of captively reared animals from a source location to a location that may or may not have been part of a historic breeding range.

Introduced populations often encounter conditions substantially differing from those at source locations. These conditions can represent a barrier to successful reproduction lending support to the conservation strategy of introducing animals to the core of their historic range (Griffith et al. 1989, Wolf et al. 1996). Through natural range expansion, animals have shown remarkable plasticity in response to local breeding conditions by adjusting nesting phenology (Hahn et al. 1997, Yeh and Price 2004), nesting habitat (Aitken and Martin 2008), predator avoidance (Forstmeier and Weiss 2004, Peluc et al. 2008), and overall breeding behavior (Yeh et al. 2007, Gross et al. 2010). The time birds require to adjust to local breeding conditions depends on the proximity of the source and introduction location conditions in space and time; the greater the discrepancy, the greater the time

Received: 7 April 2012; Accepted: 21 August 2012

Published: 25 March 2013

¹E-mail: richard_king@fws.gov

required. This has been shown in several introduced populations adjusting to differences in breeding phenology (Hawaiian goose [*Branta sandvicensis*]; Black et al. 1997), altitude (Black et al. 1997), nesting habitat (saddleback [*Philesturnus carunculatus*]; Hooson and Jamieson 2004), predators (trumpeter swan [*Cygnus buccinator*]; Lumsden and Drever 2002), and geography (Hooson and Jamieson 2004).

The rate of adjustment to local breeding conditions is also affected by a bird species' life history. Species that are slow to mature and produce few eggs or young per year can take much longer to adjust to local conditions than species with earlier maturity and greater yearly productivity (Ricklefs 1977, Erikstad et al. 1998). Exposure to captivity can affect a bird's ability to adapt to local conditions (Leopold 1944, Voss 2001, Roche et al. 2008) and birds resulting from captive breeding programs can face additional genetic challenges affecting their ability to adapt to local breeding conditions (Lynch and O'Hely 2001, Williams and Hoffman 2009).

We studied 2 introduced bird species, the whooping crane (*Grus americana*) and trumpeter swan in Wisconsin. Both are long-lived (>15 years; Kennard 1975, Kuyt and Goossen 1987, Klimkiewicz and Futcher 1989), have delayed reproduction (typically 4–7 years of age; Monnie 1966, Kuyt and Goossen 1987), and have low annual productivity (<2 fledge young per breeding female; Kuyt 1981a, Gale et al. 1987). Trumpeter swans historically nested in Wisconsin (Shea et al. 2002); however, evidence that whooping cranes ever nested in Wisconsin prior to the current introduction is lacking (Allen 1952).

Wisconsin's whooping crane population is the result of an ongoing introduction program 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. At approximately 40 days of age, the chicks were shipped from captive breeding facilities (Fig. 1) to Necedah National Wildlife Refuge (NNWR) where they were reared in isolation. The chicks were released with 2 methods. The first involved costumed handlers, aided by ultralight aircraft, leading the chicks from Wisconsin to Florida between October and January to teach them a migratory path. During their first winter in Florida they were captive reared, spending each night in a predator-proof isolation pen (Urbanek et al. 2010a). These birds were released by early February to migrate north on their own. The second release method involved the direct release of chicks in October with flocks of sandhill cranes (*Grus canadensis*) or older whooping cranes to complete the fall migration on their own.

Between 2001 and 2010, 122 whooping cranes were released into central Wisconsin via the ultralight technique. Between 2004 and 2010, 35 whooping cranes were released via the direct release technique. All released whooping cranes were the descendants of captive reared birds that were collected as eggs from nests at Wood Buffalo National Park (Alberta and Northwest Territories, Canada; Ellis and Gee 2001, Boyce et al. 2005) between 1967 and 1996.

Trumpeter swans were extirpated as a breeding bird from Wisconsin early in the 20th century, and by the 1930s as few as 100 individuals may have survived in the wild (Shea et al. 2002). Starting in 1991, trumpeter swans were introduced to central Wisconsin using 2 techniques. The first involved releasing decoy-imprinted cygnets at age 3–5 days, whereby a parental decoy was manipulated by a camouflaged handler until the cygnets fledged at approximately 100 days of age. The second involved the release of 2-year-old, captive reared birds via hard releases. Eggs used for the Wisconsin introduction were collected from the Minto Flats area of central Alaska and the Nelchina Basin of southeast Alaska (Fig. 1), transported to the Milwaukee County Zoo, incubated until hatch, and captive reared or decoy-reared (Matteson et al. 2007).

The introduction program released 355 trumpeter swans in Wisconsin; 196 via decoy-rearing and 159 captive reared, 2-year-old sub-adults. Wisconsin's trumpeter swan breeding population expanded slowly over the first 15 years (Matteson et al. 2007). By the beginning of our study, more than half of Wisconsin's trumpeter swan population was wild-produced, whereas captive-reared and decoy-reared birds comprised 14% and 11% of the population, respectively (Matteson et al. 2007). A few individuals from Wisconsin's trumpeter swan population immigrated from Minnesota and Michigan where similar introduction programs occurred (Johnson 2000, Corace et al. 2006).

Our objective was to evaluate how DNSRs of the 2 species were affected by environmental stressors. We hypothesized that environmental stressors would affect our study species differently and nesting performance, relative to other populations, would be greatest for trumpeter swans as this species was established in our study area approximately twice as long as whooping cranes. We analyzed DNSRs as our measure of nesting performance. Our goal was to evaluate the role of environmental stressors on daily nest survival of introduced birds to determine how these interactions could limit introduction programs.

STUDY AREA

Our research area in central Wisconsin was composed of 298,240 ha within the footprint of Glacial Lake Wisconsin (Fig. 1). This lake was the result of inundation by water from melting glaciers (Latitude: 44.1499; Longitude: -90.1834). Our study area was characterized by flat topography, large wetlands complexes, and a substrate of coarse sand. Some of the wetland complexes were affected by inundation for wildlife management and commercial cranberry production (Jorgensen and Nauman 1993). The wetlands were dominated by sedges (*Carex* spp.) and bulrushes (*Scirpus* spp.) with patches of willow (*Salix* spp.) in drier areas. All were located largely in open prairie. The prairies were maintained with prescribed burning and mowing since the 1940s. The only exceptions were wetlands in wooded areas with black oak (*Quercus velutina*), northern pin oak (*Quercus ellipsoidalis*), jack pine (*Pinus banksiana*), and aspen (*Populus grandidentata* and *P. tremuloides*). Mean high temperature during our study was $19.2 \pm 0.2^\circ\text{C}$ (range 36.7 to -1.3°C). Mean low



Figure 1. Location of study area and whooping crane (*Grus americana*) and trumpeter swan (*Cygnus buccinator*) source and introduction locations and captive facilities in North America.

temperature during our study was $6.1 \pm 0.2^\circ \text{C}$ (range 29.4 to -7.8°C).

METHODS

Nest Monitoring

We searched for and monitored trumpeter swan nests from March until July between 2006 and 2011 and whooping crane nests between 2005 and 2011. Additional trumpeter swan nest monitoring data (2002–2010) from within our study area were provided by S. Matteson (Wisconsin Department of Natural Resources, unpublished data). We located nests by systematically searching potential nest areas

from the ground and using fixed-wing aircraft. Fixed-wing aircraft were also used by the Wisconsin Department of Natural Resources to locate trumpeter swan nests (S. Matteson, unpublished data). As most of the whooping cranes were fitted with radio transmitters, we used radio telemetry to locate nests when possible. We included nest observations from 80 whooping crane nests and 28 trumpeter swan nests.

We observed nests from the maximum distance possible, typically more than 100 m, to determine if at least 1 egg was present or if the egg(s) were being incubated. In addition to nest observations, trumpeter swan nests were visited once during incubation (S. Matteson, unpublished data) to candle

and age eggs (Westerkov 1950). We monitored a subset of nests ($n \leq 7$ at any time) with remote cameras. We collected video files with surveillance cameras (model VCC-ZM300A, Sony Corporation, Tokyo, Japan) with coaxial cable running from the camera to a digital video recorder (DVR; model SSC-758, Advanced Security, Belleville, IL) or a mobile time-lapse videocassette recorder (model NCL 3300, Gallagher Security, Kansas City, MO). We programmed the DVRs and video recorders to record true-color video between 0500 and 2200.

We defined nest initiation as the start of incubation. When we could not precisely determine the start of nest initiation, we assumed it occurred at the midpoint between the last observation of the pair not nesting and first nest observation. We considered nests successful if they hatched at least 1 chick. In most cases, we determined success by observing the chick with the adults on or near the nest. In cases where the chick was not observed, we examined eggshells to determine if a hatch had occurred.

We made no attempt to distinguish between first nests of the year and subsequent nest attempts because: 1) the decreased probability of finding short-lived nests can result in misclassification of nest attempts (McPherson et al. 2003, Holloran et al. 2005, Moynahan et al. 2007), which would lead to bias similar to that documented in apparent nest success estimates (Mayfield 1975), 2) our study species included unmarked individuals, preventing differentiation among nest attempts, and 3) our study focus was comparison of nest success among study species throughout the nesting season. We recognize that avian demography can be substantially affected by the ability to produce young on the first versus subsequent nest attempts. We believe this to have minimal impact on our study because: 1) we are unaware of any renests among trumpeter swans during our study, and 2) during our study, the majority of full-term whooping crane nests resulting in a hatched chick and all nests resulting in a fledged chick were not initial nest attempts of the year.

Modeling Daily Nest Survival Rates

We calculated apparent nest success (successful nests/total nests) to permit comparison with previous research. We analyzed daily nest survival with the logistic exposure method (Shaffer 2004) using a generalized nonlinear model with binomial distribution for nest fate and a logit link function to model DNSR with covariates potentially affecting nest survival (Dinsmore et al. 2002, Shaffer 2004). We treated intervals between nest checks as observations, which allowed the use of time-dependent covariates. We modeled the relationship between DNSR and both time-varying (values changed among intervals) and time-invariant (variables change among nests but not intervals) covariates. We used the NLMIXED procedure in SAS 9.1 (SAS Institute, Inc., Cary, NC) for the logistic exposure models.

Environmental Parameters

We investigated the effects of 3 environmental stressor groups (phenology, weather, and ornithophilic black flies [Diptera: Simuliidae]) on DNSR of whooping cranes and trumpeter swans. We assumed nesting phenology in our

study area could differ from those encountered by source populations. To account for this, we included 4 measures of nest phenology. Our first measure was day of nesting season, standardized for each nest visit by subtracting the day the first nest was initiated for each year from the day of a nest visit. We included a second phenology variable, ordinal day, because factors affecting DNSR could change seasonally, and the seasonal variation might be independent of the nesting season phenology. We included year to account for annual variation in nesting conditions. We used nest age as our final phenology variable. Researchers have long understood the bias of nest age on DNSR (Mayfield 1975) and developed analytical tools to account for this bias, including the logistic exposure method. We determined nest age by subtracting the nest start date from the date of a nest visit. We used published incubation lengths (32 days for trumpeter swans, Hansen et al. 1971, Mackay 1988; 30 days for whooping cranes, Kuyt 1981*b*) to further refine the nest start dates for nests found with hatched eggs.

Weather conditions can vary markedly across a relatively small geographic scale and can affect DNSR (Ivey and Dugger 2008, Spalding et al. 2009). We assumed weather conditions encountered during the central Wisconsin breeding season could differ from those encountered by source populations in northern Canada, Alaska, and at various captive breeding facilities (Fig. 1). To capture the potential effects of weather on DNSR, we included daily maximum temperature, daily minimum temperature, and daily precipitation totals as recorded at a remote automated weather station located within our study area at Necedah, Wisconsin.

Central Wisconsin has a diverse ornithophilic black fly assemblage (Anderson and DeFoliart 1961, DeFoliart et al. 1967) known for several decades to affect nesting birds (Trainer et al. 1962). We hypothesized black flies in central Wisconsin may present different nesting stressors than those at source locations. Black flies are known to use trumpeter swans (Bennett et al. 1981) and cranes (Anderson and DeFoliart 1961, Malmqvist et al. 2004, King and Adler 2012) as hosts and have been associated with whooping crane nest abandonments (Urbanek et al. 2010*b*). We observed black flies at nests of both of our study species between 2009 and 2011. We collected 2 black fly species, *Simulium annulus* and *S. johannseni*, at whooping crane nests and at a small sample of trumpeter swan nests.

We included 3 measures of black flies at nests including: 1) *S. annulus* abundance, 2) *S. johannseni* abundance, and 3) a sum of *S. annulus* and *S. johannseni*. We tracked population levels of both *S. annulus* and *S. johannseni* in 2009, 2010, and 2011 by visiting whooping crane nests throughout the nesting season and obtaining population estimates by summing the results of 3 methods including: 1) glueboards, 2) high-resolution images, and 3) specimens drowned in the contents of damaged or hatched eggs. We collected data from the 3 methods upon completion of a whooping crane nesting effort (i.e., a nest desertion or a successful hatching). At each nest site, we deployed $40 \times 65\text{-mm}^2$ glueboards (Professional Pest Control, Columbus, GA) on top of the head of a sandhill crane decoy (Model Q1600, Carry-Lite Decoys,

Ft. Smith, AR) painted to resemble a whooping crane. We exposed the glueboards for 5 minutes, following the procedure of Weinandt (2006). To avoid collecting black flies attracted to humans, we remained at least 25 m from the decoy during the 5-minute exposure. After the glueboard sampling, we removed the decoy and obtained an image of the nest from 2 m, with a superfine-resolution ($2,816 \times 2,112$ pixels) Canon PowerShot (model SD630, Canon USA, Lake Success, NY). Finally, we collected any drowned black flies from damaged or hatched eggs in the nest. We summed results of all 3 counts by species to give a count per nest. For black flies counted on high-resolution images, we applied the species ratio from the glueboard and egg samples.

We interpolated black fly abundance for days with missing values by extending measured values to the midpoint between 2 known measures. We used the mean measure when we measured black flies at more than 1 nest on a given day. To replicate nest counts in space, we multiplied nest values by a random variable equal to the coefficient of variation (\pm) provided by *S. annulus* and *S. johannseni* counts obtained with carbon-dioxide traps (Centers for Disease Control MiniLight Trap, Bioquip Products, Rancho Dominguez, CA). We deployed the carbon dioxide traps between April and July at 3–7 randomly selected meadows representative of whooping crane nest locations between 2005 and 2008. We did not use the carbon dioxide trap results for mean values because carbon dioxide alone is a limited attractant for *S. annulus* (Fallis and Smith 1964, Bennett et al. 1972, as *S. euryadminiculum*) and results from these traps inadequately describe *S. annulus* and *S. johannseni* activity at whooping crane nests (King and Adler 2012).

We logarithmically transformed ($n + 1$) all black fly data. We recognize black fly abundance variation could exist among nests from different bird species. However, we expect inter-species differences to be minor because weather, nest phenology (Martinez-de la Puente et al. 2009), and host size (Anderson and DeFoliart 1961), not bird species, typically account for the majority of black fly abundance at bird nests. This assumption is further supported by our observations of black flies at the nests of both study species and by the seasonal variability of black flies at whooping crane nests (King and Adler 2012).

We euthanized black flies by freezing them for 2 hours and removed those on glueboards with Xylene (CITGO Petroleum Corporation, Rolling Meadows, IL). We boiled specimens in 10% potassium hydroxide (KOH) to remove soft tissues, washed them twice in 10% mineral spirits, fixed them in 95% ethanol, and identified them to species by microscopic examination of genitalic features (Adler et al. 2004). We deposited representative specimens in the Clemson University Arthropod Collection, Clemson, South Carolina.

Parameters Specific to Whooping Crane Pairs

All whooping cranes are uniquely color banded prior to release. As a result, we were able to obtain data for individual birds and nesting pairs. To investigate the effect of 17 pair-

specific variables (from 5 different groups) on DNSR, we used the following variables from whooping crane pairs in additional models: age of nesting birds, nesting experience, energetics, captive exposure, and release method. Nesting ability can improve with age (Kuyt and Goossen 1987, Nesbitt 1992). To capture this effect, we included age of both the male and female for nesting pairs. We also included minimum age as well as combined age for each nesting pair.

Crane nest proficiency improves with experience (Walkinshaw 1947, 1951; Kuyt and Goossen 1987; Nesbitt 1992). Experience may not necessarily be related to age because individual cranes become reproductively active at different ages. To capture this potential effect on DNSR, we included the number of apparent previous nests attempts for each pair. This number represents a minimum as short-lived nests can be easily missed.

Nest success can be affected by energetic demands of migration and incubation (Krapu et al. 1985, Tacha et al. 1987, Henson and Cooper 1993). We used 2 measures potentially related to the energetic demands of migration. These measures included the distance from each pair's winter location to its breeding territory and the days between migration completion and nest initiation. The implied assumption of the latter measure is that cranes can potentially replenish their energy stores after arrival on the breeding grounds. These measurements were made possible by year-round tracking of nesting pairs via radio telemetry.

Nesting birds can be affected by captive exposure (Lynch and O'Hely 2001, Ford 2002, Williams and Hoffman 2009). We included a cumulative measure of captive exposure for each whooping crane. We obtained this measure by summing the cumulative generations a bird was separated from wild ancestors. For example, birds whose parents were born in captivity and had wild grandparents were assigned a captive index value of 4, 2 generations from both the sire and dame. For a bird whose parents and grandparents were both born in captivity and had wild great grandparents, we assigned a captive index value of 6. We included the minimum value for each pair, as well as the sum of the male and female values in our models. Given the distribution of whooping crane captive breeding facilities across North America (Fig. 1), we hypothesized some may produce birds more suitable than others for nesting conditions in central Wisconsin. Therefore, we also included the captive breeding facility that produced each of the whooping cranes with dummy variables.

Costume-imprinting affects whooping crane behavior (Kreger et al. 2005). We hypothesized differences in release methods (ultralight vs. direct release) might exist because the 2 methods have far different levels of interaction between birds and costumed handlers. To capture this potential effect, we used a dummy variable for pairs including at least 1 bird reared with the direct release method and a dummy variable for pairs including at least 1 bird reared with the ultralight method.

Candidate Models

We developed a priori candidate models with covariates we hypothesized could affect nest survival, using a hierarchical

approach (Esley and Bollinger 2001, Stephens et al. 2005, Smith and Wilson 2010). We hypothesized environmental stressors would affect whooping cranes and trumpeter swans differently and applied each of those variables to species-specific models. Next, we expanded our species-specific base models with the addition of ornithophilic black fly data. The addition of black fly data did limit the data used for whooping crane and trumpeter swan models because we had to exclude nests monitored prior to 2009. As a result, models with black fly parameters represented 30% and 54% of the total whooping crane ($n = 54$; 906 exposure days) and trumpeter swan nests ($n = 10$; 176 exposure days), respectively. Next, we evaluated 51 whooping crane models that included base environmental parameters and pair-specific parameters. These models included data from all years. Lastly, we added ornithophilic black fly parameters to our whooping crane pair-specific and base environmental parameters for a fourth set of models. The addition of black fly parameters for these models resulted in the same data reduction noted above. For all models, we introduced a quadratic term for every continuous parameter to capture potential nonlinear relationships.

As a result of small sample sizes, we limited our analysis to univariate models (Matsuoka and Handel 2007, McWethy and Austin 2009). The use of univariate models also mitigated the effects of overdispersion, which are often ignored in DNSR analyses (Hazler 2004), and if present, can lead to selection of over-parameterized models (Anderson et al. 1994, Rotella et al. 2007, Lusignan et al. 2010). Data overdispersion presents a serious challenge for nesting studies of captive produced, long-lived birds because individuals reared with the same method or at the same location lack independence, as do nests from the same pair. Additionally, nests in the same general area lack independence because they may be exposed to the same conditions or environmental stressors. Mixed models can account for overdispersion with the inclusion of random and fixed effects. However, we chose not to use mixed models because they are difficult to fit (Heisey et al. 2008) and presently can only accommodate a single random effect (Schmidt et al. 2010) unless multiple random effects can be associated with just 1 variable (Rotella et al. 2007).

We evaluated models, using an information theoretic approach (Burnham and Anderson 2002), using Akaike's Information Criterion adjusted for small sample size (AIC_c). We acknowledged model instability potentially resulting from small sample sizes (Long 1997) by using liberal measures of model support. We assumed 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). Additionally, we used evidence ratios to contrast models (Roche et al. 2010). We assessed whether the data supported covariate effects on daily nest survival with model-averaged coefficients with 85% confidence intervals (Arnold 2010, Giovanni et al. 2011). We assumed coefficient intervals that did not overlapped 0 to be strong evidence of a covariate effect. Our certainty of covariate effect for those with coefficient confidence intervals that did overlap 0 was weakened. We did not

dismiss the potential for a covariate effect when confidence intervals overlapped 0 because these models can still be informative when using an information-theoretic approach (Arnold 2010, Jacobs et al. 2012). To aid biological interpretation, we report parameter estimates, standard errors, and 85% confidence intervals.

RESULTS

We analyzed 1,253 and 389 nest exposure days for whooping cranes and trumpeter swans, respectively. The median interval length between nest checks was 1 day for both whooping cranes and trumpeter swans. Whooping cranes were the first species to initiate nesting in all years (Fig. 2). Trumpeter swan apparent nest success was 78.6%, whereas that for whooping cranes was 20.0%. If we assumed constant survival, daily nest survival was 0.983 (CI = 0.970–0.997) and 0.951 (CI = 0.939–0.963) for trumpeter swans and whooping cranes, respectively.

We were able to determine the cause of failure for 29 whooping crane nests and 2 trumpeter swan nests. Our video review indicated nest abandonment was the cause of failure for all of these nests. We collected intact (unpredated) eggs from 21 of the 29 whooping crane nests and both of the trumpeter swan nests. The time between abandonment and egg collection ranged from 2 to 50 hours. Our video review provided examples of both American crows (*Corvus brachyrhynchos*; $n = 2$) and a raccoon (*Procyon lotor*; $n = 1$) depre-dating unattended whooping crane eggs following abandonment.

Of the 12 DNSR base models including only environmental stressor parameters (no black fly data), 4 whooping crane models related to phenology and 1 recognizing the effects of precipitation were supported. Confidence intervals for mod-

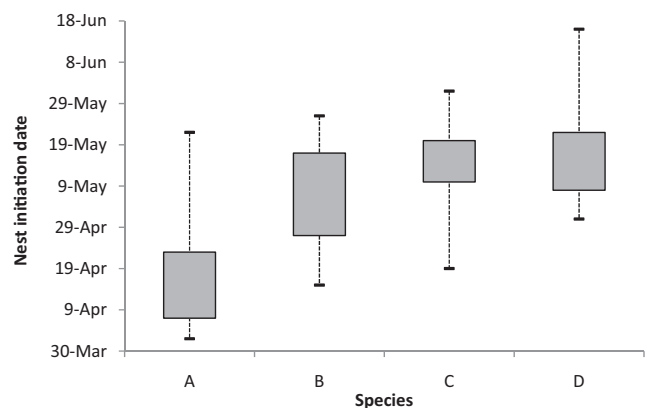


Figure 2. Whooping crane (*Grus americana*; 2005–2011), trumpeter swan (*Cygnus buccinator*; 2006–2011), common loon (*Gavia immer*; 2009–2011), and sandhill crane (*Grus canadensis*; 2009–2011) nest initiation in central Wisconsin, USA. The boxes indicate interquartile ranges (25–75%). Whiskers indicate the range (highest and lowest values). (A) Whooping cranes, (B) trumpeter swans, (C) common loons, and (D) sandhill cranes. Sandhill crane nest data represent 20 nests monitored within our study area (R. King, Necedah National Wildlife Refuge, U.S. Fish and Wildlife Service, unpublished data). Common loon nest data represents 65 nests monitored within our study area (K. Kenow, Upper Midwest Environmental Sciences Center, U.S. Geological Survey, unpublished data).

Table 1. Base environmental models for whooping crane (*Grus americana*; 2005–2011) and trumpeter swan (*Cygnus buccinator*; 2006–2011) daily nest survival rates in central Wisconsin, USA.

Variable ^a	AIC _c ^b	ΔAIC _c ^c	Relative model likelihood	w _i ^d	Evidence ratios
Whooping crane					
Nest start date ²	474.95	0.00	1.000	0.421	
Year ²	475.41	0.46	0.795	0.247	1.26
Precipitation	477.78	2.83	0.243	0.075	4.11
Ordinal date ²	477.94	2.99	0.224	0.094	4.46
Nest start date	478.05	3.10	0.212	0.089	4.71
Ordinal date	478.53	3.58	0.167	0.070	5.99
Trumpeter swan					
Nest age ²	36.90	0.00	1.000	0.111	1.11
Nest age	37.10	0.20	0.91	0.101	1.14
Temperature (daily min.)	37.16	0.26	0.878	0.098	1.21
Temperature (daily min.) ²	37.28	0.38	0.827	0.093	1.25
Start date	37.34	0.44	0.802	0.090	1.30
Start date ²	37.43	0.53	0.767	0.086	1.38
Ordinal date	37.55	0.65	0.723	0.081	1.41
Ordinal date ²	37.59	0.69	0.708	0.079	1.41
Precipitation ²	37.59	0.69	0.708	0.079	1.41
Precipitation	37.64	0.74	0.691	0.077	1.45
Temperature (daily max.)	37.66	0.76	0.684	0.077	1.46

^a Precipitation = total daily rainfall.

^b Akaike's Information Criterion adjusted for small sample sizes.

^c difference in AIC_c relative to the top model.

^d Akaike weight.

el-averaged coefficients did not overlap 0 with the exception of precipitation. The effects were all positive. Nearly all the trumpeter swan base models showed support, but evidence ratios indicated weak support for all models (Table 1) and all model-averaged coefficients overlapped 0 (Appendix A). With the exception of nest age and daily maximum temperature, the effects were negative.

The addition of ornithophilic black fly parameters (limited to data from 2009 to 2011) resulted in only whooping crane models with *S. annulus* abundance parameters (linear and quadratic forms) receiving support (Table 2). Evidence ratios indicated little distinction between the linear and quadratic

forms of *S. annulus* models and model-averaged coefficient intervals did not overlap 0 and indicated a negative effect. Trumpeter swan models showed a similar pattern with models including black fly parameters receiving support as well as 2 with phenology parameters. Evidence ratios, however, did not indicate clear distinction among the supported models (Table 2) and all model-averaged coefficients overlapped 0 (Appendix A). While the black fly effects on trumpeter swan DNSR were positive, both phenology effects were negative.

Among the 51 whooping crane base models with pair-specific parameters added (included data from all years), 2 models recognizing captive history of the pair (linear and

Table 2. Base environmental + black fly models for whooping crane (*Grus americana*) and trumpeter swan (*Cygnus buccinator*) daily nest survival rates in central Wisconsin, USA for years when black fly data were collected (2009–2011).

Variable ^a	AIC _c ^b	ΔAIC _c ^c	Relative model likelihood	w _i ^d	Evidence ratios
Whooping crane					
<i>Simulium annulus</i>	282.35	0.00	1.000	0.521	
<i>Simulium annulus</i> ²	282.74	0.39	0.823	0.428	1.22
Trumpeter swan					
Black fly sum ²	21.10	0.00	1.000	0.100	
Black fly sum	21.60	0.50	0.779	0.078	1.28
<i>Simulium johannseni</i> ²	21.70	0.60	0.741	0.074	1.35
<i>Simulium annulus</i> ²	21.80	0.70	0.705	0.071	1.41
Nest start date	21.90	0.80	0.670	0.067	1.49
Nest start date ²	22.00	0.90	0.638	0.064	1.53
<i>Simulium annulus</i>	22.20	1.10	0.577	0.058	1.73
<i>Simulium johannseni</i>	22.30	1.20	0.549	0.055	1.82
Ordinal date	22.40	1.30	0.522	0.052	1.91
Ordinal date ²	22.40	1.30	0.522	0.052	1.91

^a *Simulium annulus* = estimated log (*n* + 1) abundance at nest for *Simulium annulus*. *Simulium johannseni* = estimated log (*n* + 1) abundance at nest for *Simulium johannseni*, and black fly sum = sum of population estimates for both *Simulium annulus* and *Simulium johannseni*.

^b Akaike's Information Criterion adjusted for small sample sizes.

^c difference in AIC_c relative to the top model.

^d Akaike weight.

Table 3. Model ranking of daily nest survival rates for whooping cranes (*Grus americana*) for all years (2005–2011) and for years with black fly data (2009–2011) in central Wisconsin, USA.

Variable ^a	AIC _c ^b	ΔAIC _c ^c	Relative model likelihood	w _i ^d	Evidence ratio
Models for all years					
Captive exposure pair ²	474.60	0.00	1.000	0.096	
Captive exposure pair	474.92	0.32	0.852	0.081	1.17
Nest start date ²	474.95	0.35	0.839	0.080	1.19
Year ²	475.41	0.81	0.667	0.064	1.50
Models with black fly data (2009–2011)					
<i>Simulium annulus</i>	282.35	0.00	1.000	0.521	
<i>Simulium annulus</i> ²	282.74	0.39	0.823	0.428	1.22

^a *Simulium annulus* = estimated log ($n + 1$) abundance at nest for *Simulium annulus*, captive exposure pair = the cumulative measure of captive exposure of the male and female of nesting pair. Models including black fly parameters (2009–2011) include the parameters used in the base environmental + whooping crane-specific models.

^b Akaike's Information Criterion adjusted for small sample sizes.

^c difference in AIC_c relative to the top model.

^d Akaike weight.

quadratic forms; negative), 1 including the quadratic form of nest start date (positive), and 2 containing a year effect (linear and quadratic forms; positive) were supported. Evidence ratios among these models indicated weak support for any model over another (Table 3). Analysis of models including base, whooping crane pair-specific, and black fly parameters (limited to 2009, 2010, and 2011 data) indicated the same support as models without whooping crane pair-specific parameters (Table 3). None of the model-averaged coefficients from the supported whooping crane pair-specific models overlapped 0.

DISCUSSION

Context of Our Results

Our whooping crane apparent nest success rate was lower than previously reported. In years egg collection occurred (eggs collected from nests containing more than 1 egg; Ellis and Gee 2001, Boyce et al. 2005), hatch success at Wood Buffalo National Park ranged between 76% and 82% (Kuyt 1981a). In this case, hatch success accurately approximates apparent nest success because each nest contained just 1 egg. Spalding et al. (2009) reported costume-imprinted, non-migratory whooping cranes released in Florida and produced at the same captive breeding facilities as those in the current study had an apparent nest success rate of 30.2%. Our trumpeter swan apparent nest success is comparable to that reported for the source population (Hansen et al. 1971). To the best of our knowledge, we report whooping crane and trumpeter swan DNSR for the first time.

Hypothesis Support

Griffith et al. (1989) and Wolf et al. (1996) suggested introduction programs focus on releasing animals within the core of their historic range. Our DNSR modeling indicated a strong, negative ornithophilic black fly effect on whooping crane DNSR in central Wisconsin. If ornithophilic black flies had a similar effect on trumpeter swan DNSR it was neither strong nor consistent as our standard error estimates were larger than the coefficient estimates themselves and all confidence intervals overlapped 0. In their

core range, neither species would be expected to interact with *S. annulus* or *S. johannseni* because neither black fly species is known to occur in the core nesting areas (Adler et al. 2004). However, we note insect distribution information can be limited. Regardless, both whooping cranes and trumpeter swans likely encountered breeding conditions in central Wisconsin significantly differing from their source populations.

We predicted that trumpeter swans would show less sensitivity to environmental stressors than whooping cranes. Although our results indicated both species showed sensitivity to environmental stressors, this sensitivity was not reflected in trumpeter swan apparent nest success rates, which now rival those of the source population in Alaska (Hansen et al. 1971). We conclude the central Wisconsin trumpeter swan population is stable or increasing and although sensitive to environmental stressors, is not currently limited by those stressors.

As expected, we found whooping cranes showed sensitivity to environmental stressors (i.e., ornithophilic black flies and phenology). This was confirmed by our DNSR modeling and apparent nest success rate compared to other whooping crane populations. Among the stressors affecting whooping crane DNSR, *S. annulus* abundance (linear and quadratic forms) represented the greatest stressors. Our examination of whooping crane models with parameters from all years (black fly data not included; 2005–2011) demonstrated central Wisconsin's whooping crane DNSR may be negatively influenced by pair captive history (linear and quadratic forms) and positively influenced by nest start date (quadratic form), and year (linear and quadratic forms). These models, however, received little support relative to the models that included black fly parameters. We note that models with black fly parameters included data from only 3 years (2009, 2010, and 2011).

Given the effect of environmental stressors and pair-specific variables on our DNSR models, we were not surprised our apparent nest success rate was the lowest ever reported for whooping cranes. We conclude central Wisconsin's nesting whooping crane population is sensitive to environmental

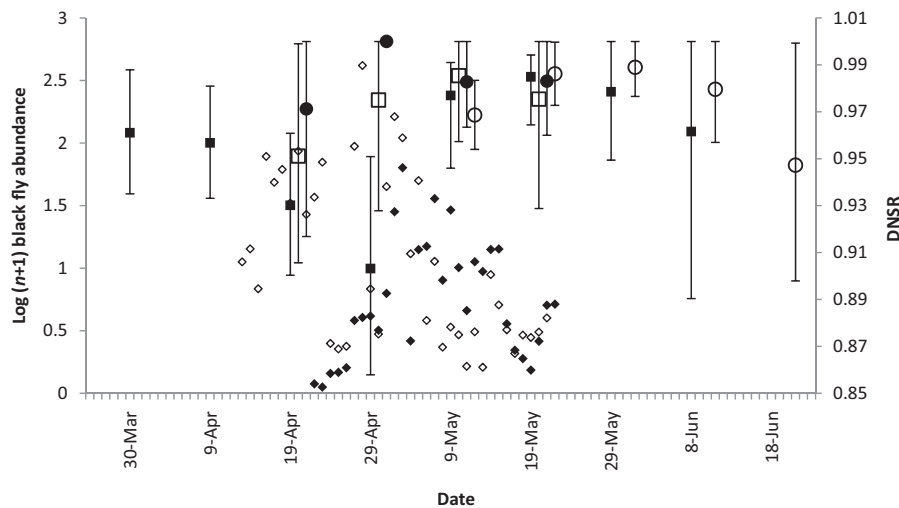


Figure 3. Daily nest survival rate (DNSR) by date (grouped by 10 day intervals) during the entire nesting season for whooping cranes (*Grus americana*; solid squares; 2005–2011), trumpeter swans (*Cygnus buccinator*; solid circles; 2006–2011), common loons (*Gavia immer*; hollow circles; 2009–2011), and sandhill cranes (*Grus canadensis*; hollow squares; 2009–2011) in central Wisconsin, USA. We also present *Simulium annulus* (hollow diamonds), and *Simulium johannseni* (solid diamonds) log transformed ($n + 1$) abundance (2009–2011) by date. Error bars represent standard error. Daily nest survival rate symbols without an error bar represent an interval with no failed nests. Sandhill crane nest data represent 20 nests monitored within our study area (R. King, Necedah National Wildlife Refuge, U.S. Fish and Wildlife Service, unpublished data). Common loon nest data represents 65 nests monitored within our study area (K. Kenow, Upper Midwest Environmental Sciences Center, U.S. Geological Survey, unpublished data). All daily nest survival rates were calculated with the logistic exposure method (Shaffer 2004).

stressors and the effects of those stressors on productivity are potentially accentuated by this population’s history of captive exposure and nest phenology.

Phenology of Local Breeding Conditions

An examination of seasonal changes to DNSR provided insight into the association between DNSR and ornithophilic black fly phenology. We made 3 major conclusions. Although trumpeter swan DNSRs is represented by a bell-curve with the greatest rates of success occurring in the middle of the nesting season, whooping crane DNSR appears bimodal (Fig. 3). The dip in whooping crane DNSR coincides with the phenology of peak *S. annulus* abundance; whereas peak DNSR for both species occurs after *S. annulus* abundance has peaked but is still present. Lastly, whooping crane nesting is initiated well before that for trumpeter swans (Fig. 2) and well before we would predict based on optimal DNSR performance (Fig. 3).

During our study, most whooping cranes also appeared to initiate nesting before sandhill cranes (R. King, Necedah National Wildlife Refuge, U.S. Fish and Wildlife Service, unpublished data) and common loons (*Gavia immer*; K. Kenow, Upper Midwest Environmental Sciences Center, U.S. Geological Survey, unpublished data) that nested within our study area (Fig. 2). Sandhill crane and common loon DNSRs in our study area (2009–2011) appear to peak at the same time as that for whooping cranes and trumpeter swans (Fig. 3). Nest phenology and DNSR of these sympatric species is noteworthy because they nest in the same wetland habitats as whooping cranes and trumpeter swans and cranes (Anderson and DeFoliart 1961, Malmqvist et al. 2004) and common loons (Fallis and Smith 1964, Lowther and Wood 1964, Bennett et al. 1972) are black fly hosts, including *S. annulus*. Additionally, common loon

nest abandonments associated with black fly outbreaks have been reported at rates exceeding most, if not all, North American birds (McIntyre 1988) and *S. annulus* was once thought to be a common loon specialist (Lowther and Wood 1964; as *S. euryadminiculum*).

Early in Wisconsin’s trumpeter swan and whooping crane introduction programs, both species encountered obstacles to production (Matteson et al. 2007, Urbanek et al. 2010b). In the case of trumpeter swans, the number of active nests increased little during the first 10 years of the introduction despite continuous augmentation with birds from captivity (Fig. 4). In colonizing central Wisconsin, trumpeter swans may have had an advantage over whooping cranes. Although all trumpeter swans introduced into Wisconsin were exposed to at least some captivity, they were collected from wild nests in Alaska where nest phenology (Hansen et al. 1971) is approximately 1 month later than what we observed in central Wisconsin. Trumpeter swans started breeding in

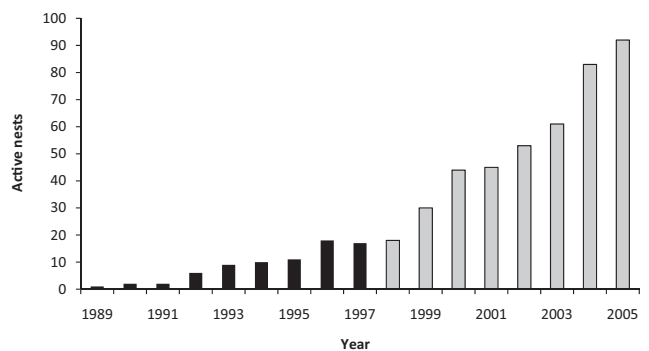


Figure 4. Number of active trumpeter swan (*Cygnus buccinator*) nests in Wisconsin, USA by year. Black bars represent years when the population was augmented with captively reared cygnets. Gray bars represent years without population augmentation.

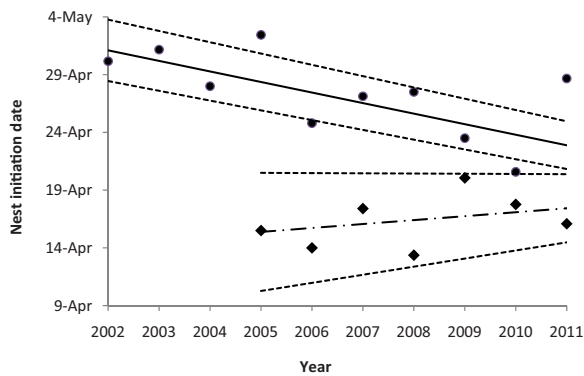


Figure 5. Trumpeter swan (*Cygnus buccinator*; solid line) and whooping crane (*Grus americana*; hatched line) nest initiation by year in central Wisconsin, USA. Dotted lines represent 95% confidence intervals. Solid circles represent mean nest initiation dates for trumpeter swans and solid diamonds represent mean nest initiation dates for whooping cranes.

the area approximately 15 years ago and the population's nesting dates continue to trend toward earlier nesting (Fig. 5). Starting with a later nesting phenology, similar to the source population, and adjusting it to early nesting dates, likely resulted in a gradual interface between nesting trumpeter swans and *S. annulus* and *S. johannseni*.

We found whooping crane nest phenology in central Wisconsin is approximately 1 month earlier than at Wood Buffalo National Park (Kuyt 1996) but closely resembles nest phenology at the captive breeding facilities following just 1 generation of captivity (Fig. 6). It is also ahead of *S. annulus* phenology. As a result, the nesting whooping crane population in central Wisconsin interfaces with black flies much differently than the trumpeter swan population; early nesting phenology cannot gradually be adjusted to later dates without first overcoming what appears to be the major stressor. Compounding the problem, early nesting whooping cranes may face the full brunt of black fly harassment simply because few, if any, alternate hosts are nesting at that time (Fig. 2). Support for this is provided by whooping crane DNSR performance in the second half of the nesting season, which is comparable to trumpeter swans and sympatric birds despite the presence of black flies (Fig. 3).

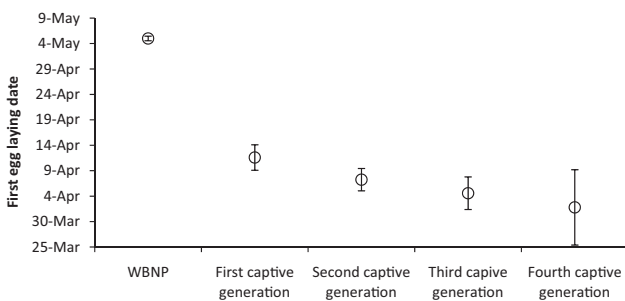


Figure 6. First egg laying dates of the year for whooping crane (*Grus americana*) pairs by generations removed from the wild. WBNP represents eggs hatched in captivity but collected from nests within Wood Buffalo National Park, Alberta and Northwest Territories, Canada. Initiation date data were obtained from the Whooping Crane Studbook (1967–2006). Initiation dates were calculated by subtracting 30 days from egg hatch dates. Error bars represent standard errors.

Our results illustrate a gradual trend toward later nesting dates for central Wisconsin's whooping cranes over 6 years (Fig. 5). This trend is largely the result of increased apparent reneest rates although examples of within-pair delayed nesting between years do exist. Wisconsin's whooping crane population's apparent reneest rate is 16.7% (yearly range 0.0–33.3%), which greatly exceeds the rate reported for the Wood Buffalo National Park population (<1%; Kuyt 1981a) and is slightly greater than reported for introduced, non-migratory whooping cranes nesting more than 2,000 km south in Florida (15.3%; M. Folk, Florida Fish and Game Commission, unpublished data). Increased reneest rates resulting from high failure rates early in the nesting season has been observed for a wide range of bird species (Fondell et al. 2006, Moynahan et al. 2007, Lehman et al. 2008).

Our results have potential ramifications related to climate change. Both and Visser (2005), Pearce-Higgins et al. (2005), and Both et al. (2009) demonstrated a negative, bottom-up trophic level asynchrony potentially related to climate change. A bottom-up asynchrony can have negative consequences because breeding birds may produce young at a time when insect prey is not available, for example. We provide evidence that phenology asynchrony in regard to ornithophillic flies offers a competitive advantage to breeding birds. In contrast to bottom-up trophic level interactions, climate change could negatively affect breeding birds if it results in greater synchrony with stressors such as biting insects. Phenology synchrony could occur if climate change exerts disproportionate effects on breeding birds and ornithophillic flies. This has been referred to as "insufficient adjustment" (Visser and Both 2005).

Although some information is available detailing adjustment of short-lived birds with relatively high productivity to local breeding conditions (Yeh and Price 2004), our results are the first, to our knowledge, to explore this with long-lived birds with low productivity. Although challenges related to predator avoidance and social and foraging behavior of captive produced, introduced bird populations have been studied (Snyder et al. 1994, Black et al. 1997, Meretsky et al. 1997), to our knowledge, our study is the first to detail post-release nesting performance challenges for populations of long-lived birds following up to 4 generations of confinement.

MANAGEMENT IMPLICATIONS

Our results suggest nesting phenology may have resulted in nesting trumpeter swans interfacing black fly populations much differently than whooping cranes. Results indicate that the juxtaposition of source and introduction location nest phenology should be considered in selecting introduction locations. Additionally, strategically selecting offspring from captive pairs with nest phenology similar to that of sympatric species at the introduction location should be considered. Wisconsin's trumpeter swan introduction also had the advantages of more than twice the number of released individuals and had some individuals with far less captive exposure (decoy-reared) than whooping cranes. Both the number of released individuals (Wolf et al. 1996) and

captive exposure (Snyder et al. 1996, Tweed et al. 2006) can limit the potential for successful introductions. We found limited evidence that exposure to captivity, measured in cumulative generations, might be limiting whooping crane breeding performance. Our results and observations are consistent with a failed whooping crane introduction in Florida where whooping cranes encountered breeding conditions different from the source population and experienced low reproductive success. The Florida introduction was also outside the whooping crane's core breeding area and involved relatively few (122) released individuals (Spalding et al. 2009).

ACKNOWLEDGMENTS

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, International Crane Foundation, Windway Capital Corporation, Clemson University, and Operation Migration for provide financial support and/or in-kind services to make this research possible. The field crew was invaluable and included: L. Bauson, M. Bean, C. Bedwell, J. Boysen, J. Brennamen, M. Campbell, K. Finger, K. Gleason, M. Jones, L. Maas, L. McKinney, C. Morris, E. Ulrey, A. VanLanaan, and G. VanVreedy. Aerial reconnaissance was provided by K. Gullickson, B. Paulan, E. Szyszkowski, and R. VanHuevlan. L. Fara, M. Fitzpatrick, S. Houdek, P. Liebel, M. Lupec, K. McGuire, M. Putnam, J. Thompson, R. Urbanek, and S. Zimorski kindly provided ground-based observations of whooping cranes, common loons, and/or sandhill cranes. The International Crane Foundation provided carbon-dioxide trap results from 2010. P. Adler identified samples containing more than 300,000 black flies for this project. S. Matteson provided trumpeter swan nest phenology and nest monitoring data. K. Kenow provide common loon nest monitoring data and provided useful suggestions for improving the manuscript as did P. Adler, B. Gray, S. Matteson, P. Pfost, D. Pfost, and R. Urbanek.

LITERATURE CITED

Adler, P. H., D. C. Currie, and D. M. Wood. 2004. The black flies (Simuliidae) of North America. Cornell University Press, Ithaca, New York, USA.

Aitken, K. E. H., and K. Martin. 2008. Resource selection plasticity and community responses to experimental reduction of critical resources. *Ecology* 89:971–980.

Allen, R. P. 1952. The whooping crane. Research report 3. National Audubon Society, New York, New York, USA.

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

Anderson, J. R., and G. R. DeFoliart. 1961. Feeding behavior and host preference of some black flies (Diptera: Simuliidae) in Wisconsin. *Annals of the Entomological Society of America* 54:716–729.

Armstrong, D. P., and P. J. Seddon. 2007. Directions in reintroduction biology. *Trends in Ecology and Evolution* 23:20–25.

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

Bennett, G. F., A. M. Fallis, and A. G. Campbell. 1972. The response of *Simulium (Eusimulium) euryadmiculatum* Davies (Diptera: Simuliidae) to some olfactory and visual stimuli. *Canadian Journal of Zoology* 50:793–800.

Bennett, G. F., B. Turner, and G. Holton. 1981. Blood parasites of trumpeter swans, *Olor buccinator* (Richardson), from Alberta. *Journal of Wildlife Diseases* 17:213–215.

Black, J. M., A. P. Marshall, A. Gilburn, N. Santos, H. Hoshide, J. Medeiros, J. Mello, C. Natividad, and L. Katahira. 1997. Survival, movements, and breeding of released Hawaiian geese: an assessment of the reintroduction program. *Journal of Wildlife Management* 61: 1161–1173.

Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78:73–83.

Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life history traits. *Global Change Biology* 11:1606–1613.

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

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

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

Corace, R. G. III, D. L. McCormick, and V. Cavalieri. 2006. Population growth parameters of a reintroduced trumpeter swan flock, Seney National Wildlife Refuge, Michigan, USA (1991–2004). *Waterbirds* 29:38–42.

DeFoliart, G. R., M. R. Rao, and C. D. Morris. 1967. Seasonal succession of bloodsucking Diptera in Wisconsin during 1965. *Journal of Medical Entomology* 4:363–373.

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

Ellis, D. H., and G. F. Gee. 2001. Whooping crane egg management: options and consequences. *Proceedings of the North American Crane Workshop* 8: 17–23.

Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788.

Esley, J. D., and E. K. Bollinger. 2001. Habitat selection and reproductive success of loggerhead shrikes in northwest Missouri: a hierarchical approach. *Wilson Bulletin* 113:280–296.

Fallis, A. M., and S. M. Smith. 1964. Ether extracts from birds and CO₂ as attractants for some ornithophilic simuliids. *Canadian Journal of Zoology* 42:723–730.

Fondell, T. F., J. B. Grand, D. A. Miller, and R. M. Anthony. 2006. Rensetting by dusky Canada geese on the Copper River Delta, Alaska. *Journal of Wildlife Management* 70:955–964.

Ford, M. J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16:815–825.

Forstmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* 104:487–499.

Fredrickson, M., M. P. Harris, and S. Wanless. 2005. Inter-population variation in demographic parameters: a neglected subject? *Oikos* 111:209–214.

Gale, R. S., E. O. Garton, and I. J. Ball. 1987. The history, ecology, and management of the Rocky Mountain population of trumpeter swans. U.S. Fish & Wildlife Service, Montana, Cooperative Wildlife Research Unit, Missoula, USA.

Giovanni, M. D., M. Post van der Burg, L. C. Anderson, L. A. Powell, W. H. Schacht, and A. J. Tyre. 2011. Estimating nest density when detectability is incomplete: variation in nest attendance and response to disturbance by western meadowlarks. *Condor* 113:223–232.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.

Gross, K., G. Pasinelli, and H. P. Kunc. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *American Naturalist* 176:456–464.

Hahn, T. P., T. Boswell, J. C. Wingfield, and G. F. Ball. 1997. Temporal flexibility in avian reproduction: patterns and mechanisms. Pages 39–80 in V. Nolan, Jr., E. D. Ketterson, and C. F. Thomson, editors. *Current ornithology*. Volume 14. Plenum, New York, New York, USA.

Hansen, H. A., P. E. K. Shepard, J. G. King, and W. A. Troyer. 1971. The trumpeter swan in Alaska. *Wildlife Monograph* 26:1–83.

- Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. *Auk* 121:707–716.
- Heisey, D. M., T. L. Shaffer, and G. C. White. 2008. The ABCs of nest survival: theory and application from a biostatistical perspective. *Studies in Avian Biology* 34:13–33.
- Henson, P., and J. A. Cooper. 1993. Trumpeter swan incubation in areas of differing food quality. *Journal of Wildlife Management* 57:709–716.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management* 69:638–649.
- Hooson, S., and I. G. Jamieson. 2004. Variation in breeding success among reintroduced populations of South Island saddlebacks *Philesturnus carunculatus carunculatus*. *Ibis* 146:417–426.
- 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.
- Ivey, G. L., and B. D. Dugger. 2008. Factors influencing nest success of greater sandhill cranes at Malheur National Wildlife Refuge, Oregon. *Waterbirds* 31:52–61.
- Jacobs, R. B., F. R. Thompson III, R. R. Koford, F. A. La Sorte, H. D. Woodward, and J. A. Fitzgerald. 2012. Habitat and landscape effects on abundance of Missouri's grassland birds. *Journal of Wildlife Management* 76:372–381.
- Johnson, J. W. C. 2000. Interior population of trumpeter swans: status, trends, management and research priorities. *North American Swans* 29:24–31.
- Jorgensen, E. E., and L. E. Nauman. 1993. Bird distribution in wetlands associated with commercial cranberry production. *Passenger Pigeon* 55:289–298.
- Kennard, J. H. 1975. Longevity records of North American birds. *Bird Banding* 46:55–59.
- King, R. S., and P. H. Adler. 2012. Development and evaluation of methods to measure black flies at nests of the endangered whooping crane (*Grus americana*). *Journal of Vector Ecology* 37:298–306.
- Klimkiewicz, K. M., and A. G. Fitcher. 1989. Longevity records of North American birds. *Journal of Field Ornithology* 60:469–494.
- Krapu, G. L., G. C. Iverson, K. J. Reinecke, and C. M. Boise. 1985. Fat deposition and usage by arctic-nesting sandhill cranes during springs. *Auk* 102:362–368.
- Kreger, M. D., J. S. Hatfield, I. Estevez, G. F. Gee, and D. A. Clugston. 2005. The effects of captive rearing on the behavior of newly-released whooping cranes (*Grus americana*). *Applied Animal Behaviour Science* 93:165–178.
- Kreger, M. D., J. S. Hatfield, I. Estevez, G. F. Gee, and A. Clugston. 2006. Behavioral profiles of the captive juvenile whooping crane as an indicator of post-release survival. *Zoo Biology* 25:11–24.
- Kuyt, E. 1981a. Clutch size, hatching success, and survival of whooping crane chicks, Wood Buffalo National Park, Canada. Pages 126–129 in J. C. Lewis and H. Masatomi, editors. *Crane research around the world*. International Crane Foundation, Baraboo, Wisconsin, USA.
- Kuyt, E. 1981b. Population status, nest site fidelity, and breeding habitat of whooping cranes. Pages 119–125 in J. C. Lewis and H. Masatomi, editors. *Crane research around the world*. International Crane Foundation, Baraboo, Wisconsin, USA.
- Kuyt, E. 1996. Reproductive manipulation in the whooping crane *Grus americana*. *Bird Conservation International* 6:3–10.
- Kuyt, E., and J. P. Goossen. 1987. Survival, age composition, sex ratio, and age at first breeding of whooping cranes in Wood Buffalo National Park, Canada. Pages 230–244 in J. C. Lewis and J. W. Ziewits, editors. *Proceedings 1985 Crane Workshop*. Whooping Crane Habitat Maintenance Trust, Grand Island, Nebraska, USA and U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Lehman, C. P., M. A. Rumble, L. D. Flake, and D. J. Thompson. 2008. Merriam's turkey nest survival and factors affecting nest predation by mammals. *Journal of Wildlife Management* 72:1765–1774.
- Leopold, A. S. 1944. The nature of heritable wildness in turkeys. *Condor* 46:133–197.
- Long, J. S. 1997. *Regression models for categorical and limited dependent variables (advanced quantitative techniques in the social sciences)*. Sage Publications Incorporated, Thousand Oaks, California, USA.
- Lowther, J. K., and D. M. Wood. 1964. Specificity of a black fly, *Simulium euryadminiculum* Davies, toward its host, the common loon. *Canadian Entomologist* 96:911–913.
- Lumsden, H. G., and M. C. Drever. 2002. Overview of the trumpeter swan reintroduction program in Ontario, 1982–2000. *Waterbirds* 25:301–312.
- Lusignan, A. P., K. R. Mehl, I. L. Jones, and M. L. Gloutney. 2010. Conspecific brood parasitism in common eiders (*Somateria mollissima*): do brood parasites target safe nest sites? *Auk* 127:765–772.
- Lynch, M., and M. O'Hely. 2001. Captive breeding and the genetic fitness of natural populations. *Conservation Genetics* 2:263–378.
- Mackay, R. H. 1988. Trumpeter swan investigations, Grand Prairie, Alberta, 1953–75. Pages 5–10 in E. Compton, editor. *Proceedings and Papers of the 10th Trumpeter Swan Society Conference*. The Trumpeter Swan Society, Maple Plain, Minnesota, USA.
- Malmqvist, B., D. Strasevicius, O. Hellberg, P. H. Adler, and S. Bensch. 2004. Vertebrate host specificity of wild-caught blackflies revealed by mitochondrial DNA in blood. *Proceedings of the Royal Society of London* 271:152–155.
- Martinez-de la Puente, J., S. Merino, E. Lobato, J. Rivero-de Aguilar, S. del Cerro, R. Ruiz-de-Castaneda, and J. Moreno. 2009. Does weather affect biting fly abundance in avian nests? *Journal of Avian Biology* 40:653–657.
- Matsuoka, S. M., and C. M. Handel. 2007. Nesting ecology of boreal forest birds following a massive outbreak of spruce beetles. *Journal of Wildlife Management* 7:51–65.
- Matteson, S. W., P. F. Manthey, M. J. Mossman, and L. M. Hartman. 2007. Wisconsin trumpeter swan recovery program: progress toward restoration, 1987–2005. Pages 11–19 in M. H. Linck and R. E. Shea, editors. *Selected Papers of the Twentieth Trumpeter Swan Society Conference*. Trumpeter Swan Society, Plymouth, Minnesota, USA.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- McIntyre, J. W. 1988. *The common loon: spirit of northern lakes*. University of Minnesota Press, St. Paul, USA.
- McPherson, R. J., T. W. Arnold, L. M. Armstrong, and C. J. Schwarz. 2003. Estimating the nest-success rate and the number of nests initiated by radiomarked mallards. *Journal of Wildlife Management* 67:843–851.
- McWethy, D. B., and J. Austin. 2009. Nesting ecology of greater sandhill cranes (*Grus canadensis*) in riparian and palustrine wetlands of eastern Idaho. *Waterbirds* 32:106–115.
- Meretsky, V. J., N. F. R. Snyder, S. R. Beissinger, D. A. Clendenen, and J. W. Wiley. 1997. Demography of the California condor: implications for reestablishment. *Conservation Biology* 14:957–967.
- Monnie, J. B. 1966. Reintroduction of the trumpeter swan to its former prairie breeding range. *Journal of Wildlife Management* 30:691–696.
- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. *Journal of Wildlife Management* 71:1773–1783.
- Nesbitt, S. A. 1992. First reproductive success and individual productivity in sandhill cranes. *Journal of Wildlife Management* 56:573–577.
- Ostermann, S. D., J. R. Deforge, and W. D. Edge. 2001. Captive breeding and reintroduction evaluation criteria: a case study of peninsular bighorn sheep. *Conservation Biology* 15:749–760.
- Pearce-Higgins, J. W., D. W. Yalden, and M. J. Whittingham. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia* 143:470–476.
- Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghallambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. *Behavioral Ecology* 19:830–835.
- Ricklefs, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *American Naturalist* 111:453–478.
- Roche, E. A., J. B. Cohen, D. H. Catlin, D. L. Amirault-Langlais, F. J. Cuthbert, C. L. Gratto-Trevor, J. Felio, and J. D. Fraser. 2010. Range-wide piping plover survival: correlated patterns and temporal decline. *Journal of Wildlife Management* 74:1748–1791.
- Roche, E. A., F. J. Cuthbert, and T. W. Arnold. 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., M. Taper, S. Stephens, and M. Landberg. 2007. Extending methods for modeling heterogeneity in nest-survival data using generalized mixed models. *Studies in Avian Biology* 34:34–44.
- Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* 86:2176–2186.

- Schmidt, J. H., J. A. Walker, M. S. Lindberg, D. S. Johnson, and S. E. Stephens. 2010. A general Bayesian hierarchical model for estimating survival of nests and young. *Auk* 127:379–386.
- Seddon, P. J., D. P. Armstrong, and R. E. Maloney. 2007. Developing the science of reintroduction biology. *Conservation Biology* 21:303–312.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- Shea, R. E., H. K. Nelson, L. N. Gillette, J. G. King, and D. K. Weaver. 2002. Restoration of trumpeter swans in North America: a century of progress and challenges. *Waterbirds* 25:296–300.
- Smith, P. A., and S. Wilson. 2010. Intra-seasonal patterns in shorebird nest survival and related nest age and defense behavior. *Oecologia* 163:613–624.
- Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10:338–348.
- Snyder, N. F. R., S. E. Koenig, J. Koschmann, H. A. Synder, and T. B. Johnson. 1994. Thick-billed parrot releases in Arizona. *Condor* 96:854–862.
- Spalding, M. G., M. J. Folk, S. A. Nesbitt, M. L. Folk, and R. Kiltie. 2009. Environmental correlates of reproductive success for introduced resident whooping cranes in Florida. *Waterbirds* 32:538–547.
- Stephens, S. E., J. J. Rotella, M. S. Lindberg, M. L. Taper, and J. K. Ringelman. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. *Ecological Applications* 15:2137–2149.
- Tacha, T. C., P. A. Vohs, and G. C. Iverson. 1987. Time and energy budgets of sandhill cranes from mid-continent North America. *Journal of Wildlife Management* 51:440–448.
- Trainer, D. O., C. S. Schildt, R. A. Hunt, and L. R. Jahn. 1962. Prevalence of *Leucocytozoon simondi* among some Wisconsin waterfowl. *Journal of Wildlife Management* 26:137–143.
- Tweed, E. J., J. T. Foster, B. L. Woodworth, W. B. Monahan, J. L. Kellerman, and A. Lieberman. 2006. Breeding biology and success of a reintroduced population of the critically endangered puaiohi (*Myadestes palmeri*). *Auk* 123:753–763.
- Urbanek, R. P., L. E. A. Fondow, S. E. Zimorski, M. A. Wellington, and M. A. Nipper. 2010a. Winter release and management of reintroduced migratory whooping cranes *Grus americana*. *Bird Conservation International* 20:43–54.
- Urbanek, R. P., S. E. Zimorski, A. M. Fasoli, and E. K. Szyszkoski. 2010b. Nest desertion in a reintroduced population of migratory whooping cranes. *Proceedings of the North American Crane Workshop* 11: 133–141.
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for yardstick. *Proceedings of the Royal Society of London* 272:2561–2569.
- Voss, M. 2001. Wild turkey ecology and management in Wisconsin. Wisconsin Department of Natural Resources, Madison, USA.
- Walkinshaw, L. H. 1947. Some nesting records of the sarus crane in North American zoological parks. *Auk* 64:602–615.
- Walkinshaw, L. H. 1951. Nesting of white-napped crane in Detroit Zoological Park, Michigan. *Auk* 68:194–202.
- Weinandt, M. L. 2006. Conservation implications of common loon (*Gavia immer*) parasites: black flies, haematozoans, and the role of mercury. Thesis, Northern Michigan University, Marquette, USA.
- Westerkov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14:56–67.
- Williams, S. E., and E. A. Hoffman. 2009. Minimizing genetic adaption in captive breeding programs: a review. *Biological Conservation* 142: 2388–2400.
- Wilson, S., and K. Martin. 2011. Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range. *Population Ecology* 53:459–471.
- Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* 10:1142–1154.
- Yeh, P. J., M. E. Hauber, and T. D. Price. 2007. Alternative nesting behaviors following colonization of a novel environment by a passerine bird. *Oikos* 116:1473–1480.
- Yeh, P. J., and T. D. Price. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. *American Naturalist* 164:531–542.

Associate Editor: Michael Morrison.

Appendix A: Parameter estimates, standard errors, and lower and upper 85% confidence intervals (LCI and UCI) for whooping crane (*Grus americana*) and trumpeter swan (*Cygnus buccinator*) daily nest survival models in central Wisconsin, USA.

Model	Parameter ^a	Estimate	SE	LCI	UCI
Whooping crane all years (2005–2011)	Nest start date ^b	0.0162	0.0077	0.0051	0.0273
	Ordinal date ^b	0.0167	0.0079	0.0053	0.0281
	Precipitation	0.8581	0.6433	–0.0685	1.7847
	Captive ^b	–0.4726	0.1274	–0.6561	–0.2890
	Year ^b	0.0060	0.0001	0.0059	0.0061
Trumpeter swan all years (2006–2011)	Nest start date	–0.0303	0.0546	–0.1095	0.0489
	Nest age	0.0401	0.0518	–0.0350	0.1152
	Ordinal date	–0.0175	0.0557	–0.0983	0.0633
	Temperature (daily min.)	–0.0452	0.0657	–0.1405	0.0501
	Precipitation	–0.4623	3.4502	–5.4653	4.5406
	Temperature (daily max.)	0.0000	0.0472	–0.0684	0.0684
Whooping crane years with black fly data (2009–2011)	<i>Simulium annulus</i> ^b	–0.6016	0.1334	–0.7939	–0.4094
Trumpeter swan years with black fly data (2009–2011)	<i>Simulium annulus</i>	0.8363	1.3364	–1.1049	2.7774
	<i>Simulium johannseni</i>	1.0623	1.6816	–1.3802	3.5049
	Black fly sum	1.0387	1.2839	–0.8262	2.9035
	Nest start date	–0.0740	0.0741	–0.1817	0.0335
	Ordinal date	–0.0597	0.0753	–0.1691	0.0497

^a *Simulium annulus* = estimated log ($n + 1$) abundance at nest for *Simulium annulus*. *Simulium johannseni* = estimated log ($n + 1$) abundance at nest for *Simulium johannseni*, and black fly sum = sum of population estimates for both *Simulium annulus* and *Simulium johannseni*.

^b Strong evidence of a covariate effect, where CI does not overlap 0.