



Population Ecology

Annual and Seasonal Survival of Trumpeter Swans in the Upper Midwest

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ABSTRACT The reintroduction of trumpeter swans to the north central United States appears to be a conservation success story. For the most part, population management goals have been met or exceeded. The population cannot be considered self-sustaining, however, because 90% of the swans migrate short distances to wintering sites where supplemental feeding occurs. The remaining 10% migrate longer distances to areas where adequate open water and forage occur naturally. To determine how these 2 different wintering habits might affect mortality, we used mark-resight data gathered between 2000 and 2008 to estimate and compare annual survival rates for long- and short-distance migrant swans marked in Wisconsin. Apparent annual survival rates were similar for long- (0.81, SE = 0.019) and short- (0.81, SE = 0.022) distant adult migrants but were higher for long-distance sub-adult (0.86, SE = 0.036) migrants than for short-distance sub-adult migrants (0.7, SE = 0.046). We also estimated seasonal survival of long-distance migrants to determine if the migratory periods are a time of high mortality. We found little evidence for seasonal variation in survival and estimates for both migratory and non-migratory seasons were very high (>0.97). Overall, the results suggest that little mortality occurs during migration and long-distance migrants are able to survive at rates at least equal to, but probably higher than, short-distance migrants. © 2011 The Wildlife Society.

KEY WORDS annual survival, *Cygnus buccinator*, migration, reintroduced species, seasonal survival, trumpeter swan, winter.

Each season poses a new set of challenges for migratory birds; harsh weather conditions and limited natural foods in winter, the risks and costs of reproduction in summer, and a dangerous and energetically demanding migration in spring and fall. Migration allows birds to exploit seasonally available resources, increasing survival and overall fitness (Cox 1968, Lack 1968). The costs of migration, however, may include high mortality during the migratory period and lower productivity (Greensberg 1980, Nichols 1996, Newton 2006). Migration may be a period of high mortality in some species of birds (Greensberg 1980, Pienkowski and Evans 1985, Nichols 1996, Newton 2006). For large-bodied birds such as geese and swans, however, the relationship between mortality and migration is less clear (Francis et al. 1992, Sedinger et al. 1995, Gauthier et al. 2001, Menu et al. 2005, Eichholz and Sedinger 2007). Overall, few studies have explored seasonal survival of non-hunted waterfowl species and little is known about how natural mortality rates change during each part of the annual cycle.

In the last 50 years, many Midwestern states (states located in the north central United States) have initiated or completed reintroduction programs to restore trumpeter swans

(*Cygnus buccinator*), which had been extirpated by the early 1900s. When these trumpeter swan reintroduction programs began, organizers released swans in areas of the upper Midwest (Michigan, Wisconsin, Ohio, Iowa, and Minnesota), which were ideal for nesting (Matteson et al. 2007). In those states, however, winter snow and ice cover prevented access to food and open water. As a result, swans concentrated on a few areas near nesting sites that remained ice-free due to warm water release from power plants and other anthropogenic activities. Supplemental feeding was initiated because of concern over winter mortality and a possible lack of traditional southern wintering habitat. Because trumpeter swans are philopatric to both the breeding and wintering grounds, the areas where supplemental feeding occurred quickly became traditional wintering grounds for 90% of the population, which numbered nearly 5,000 swans in 2005 (Moser 2006). Less than 10% of these swans currently migrate to wintering sites below 40° N latitude, the latitude at which water typically remains ice-free most of the winter (Slater 2006). The lack of natural migratory habits and dependency on humans during the winter are considered the major factors preventing the complete recovery of the Midwestern trumpeter swan to a healthy, self-sustaining population (Mitchell 1994).

It is unclear if supplemental feeding of swans in ice-free areas enabling shorter winter migrations allows for increased annual survival, thus increased population growth. To test this, we compared apparent survival of long- and

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short-distance migratory swans that breed in Wisconsin. We also estimated seasonal survival for a long-distance migratory flock of swans to determine if migration is a time of high mortality.

STUDY AREA

Our study population included 5 wintering flocks of trumpeter swans in northern and central Wisconsin (Fig. 1). The 3 long-distance migrant flocks wintered at the Burning Star Number 5 Mine (BS5), the Universal Mine (Universal), and the U. S. Army Corps of Engineers Riverlands Migratory Bird Sanctuary (Riverlands). The BS5 flock was located approximately 10 km east of De Soto, Illinois, in Jackson County (37° 51' 40" N, 89° 10' 4" W) and was owned by Consolidation Coal Company. Riverlands was a migratory waterfowl refuge owned by the U. S. Army Corps of Engineers located on the Mississippi River in St. Charles County, Missouri (38° 51' 16" N, 90° 10' 22" W). Universal, a reclaimed surface coal mine owned by Peabody Coal Company, was located on the border between Illinois and Indiana about 19 km north-northwest of Terre Haute, Indiana (39° 39' 6" N, 87° 32' 15" W). Over 100 swans wintered at each of these 3 sites and foraged primarily in aquatic areas and crop fields, including corn, winter wheat, and soybeans (Varner 2008).

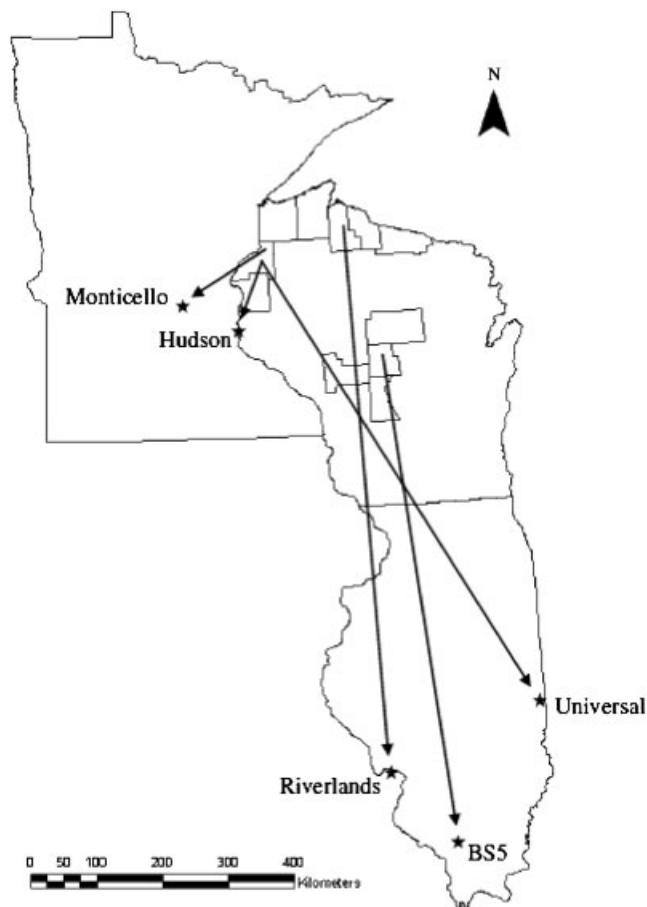


Figure 1. Location of wintering areas (starred) and migration routes (indicated by arrows) of the 5 study populations of trumpeter swans in Illinois, Wisconsin, and Minnesota, 2000–2008.

Two short-distance migrant flocks wintered near the towns of Hudson, Wisconsin, (44° 58' 39" N, 92° 45' 47" W) and Monticello, Minnesota (45° 17' 53" N, 93° 46' 15" W). The Hudson area was surrounded by residential neighborhoods and one nearby resident provided approximately 50 kg of corn each day. Trumpeters were also observed foraging on submerged aquatic vegetation and, in recent years, field-feeding. Over 400 trumpeter swans have been seen at Hudson during the winter in recent years but less than 200 typically stay for the entire winter. More than 1,000 swans wintered in a residential area in Monticello on the Mississippi River below the Monticello Nuclear Generating Plant in Wright County, Minnesota. A local resident began supplying food for the swans in the mid-1980s and provided more than 450 kg of corn each day during this study. The swans were also seen foraging in the river and in nearby crop fields, primarily corn.

We also monitored swans on the central Wisconsin breeding grounds during the summers of 2006 and 2007. A previous study found that the majority of marked swans at BS5 originated in 2 adjacent central Wisconsin counties, Juneau and Wood, so we focused our efforts on those, as well as surrounding counties (Babineau 2004). We studied swans on known breeding territories as well as areas where non-breeders were known to gather such as Necedah National Wildlife Refuge, Sandhill Wildlife Area, and cranberry farm impoundments.

METHODS

Annual Survival of Long- and Short-Distance Migrants

As part of the reintroduction program, approximately 50% of trumpeter swans in Wisconsin have been banded and neck collared (S.W. Matteson, Wisconsin Department of Natural Resources, personal communication). All released swans were marked with aluminum leg bands and neck collars as part of the reintroduction program. Wisconsin Department of Natural Resources (WDNR) personnel also attempted to capture and collar breeding adults and their broods each year in the late summer as resources allowed. Non-breeding adults were also opportunistically captured and collared during molt. We attempted to read and record all neck collars at all 3 southern Illinois study sites weekly during the winter. We obtained winter collar sightings for Hudson and Monticello from 2 local residents who regularly fed and monitored the swans. Band attachment and resighting records were provided by WDNR personnel and the United States Geological Survey (USGS) Bird Banding Lab. Also, we used previous records of neck-banded swans wintering in southern Illinois from the Illinois Department of Natural Resources, the Cooperative Wildlife Research Lab at Southern Illinois University, and the general public. To estimate annual survival, we used only resightings made during the winter (21 Dec–20 Mar) between 2000 and 2008, for a total of 8 encounter occasions. Because we used observations collected during the winter, each swan was included in the dataset after the first time it was observed on the

wintering grounds, not at the time of banding as with most live encounter studies.

We used prior resighting data, as well as data collected during this study, to estimate apparent annual survival, detection, and movement probabilities using the multi-strata model in Program MARK (<http://www.phidot.org/software/mark>, accessed 25 Feb 2011). We allowed apparent survival to vary by age and migratory strategy and detection probability to vary by effort level. Effort was categorized as low during those years when data were collected opportunistically by volunteers, moderate during years when hired researchers collected data, and high during the 2 years of this study. For each set of models, we tested fit of the most general model using the bootstrap goodness-of-fit method (Burnham and Anderson 2002). We ran 1,000 simulations for each bootstrap test. If we detected a lack of fit (deviance estimated using original data greater than 900 of 1,000 bootstrap deviance estimates), we adjusted the variance of the point estimates using the variance inflation factor (\hat{c}). We estimated \hat{c} either by dividing the deviance estimated using the original data by the mean deviance estimated using the bootstrap simulations or by dividing the \hat{c} estimated using the original data by the mean \hat{c} estimated using the bootstrap simulations (White and Burnham 1999). We used the larger of the 2 values to avoid underestimation. We used Quasi Akaike's Information Criterion, corrected for small sample size (QAIC_c), for model comparison.

Age for each swan was determined using band attachment data provided by the WDNR. We defined 2 age classes; we considered swans sub-adults during the time between their first and second winter after hatching and adults by their second winter. We considered swans observed north of 40° N latitude during winter short-distance migrants, and swans observed at wintering areas south of that line, such as BS5, Riverlands, and Universal, long-distance migrants as defined by the ad hoc drafting committee for the Interior Population of trumpeter swans (Mississippi and Central Flyway Councils, unpublished report). Only swans collared in Wisconsin were included in the analysis. Furthermore, in 2004 the WDNR began using plastic-coded leg bands in addition to the standard U.S. Fish and Wildlife Service metal bands. For swans that did not have collars, we attempted to read the leg band if present. This allowed us to identify and remove from the analysis swans that had lost their collars minimizing bias in survival estimates due to collar loss.

Seasonal Survival of Long-Distance Migrants

To estimate seasonal apparent survival of a group of long-distance migrants, we recorded band resightings in central Wisconsin early in the breeding season (17–30 May) and again towards the end of the breeding season (4–17 Aug). We also used resightings collected at BS5 early (6–19 Dec) and late (8–21 Feb) in the winter season. Data collection for the seasonal survival analysis began in December 2005 and ended in December 2007. We excluded swans that we did not resight during the winter from the dataset because we could not determine whether they were long-distance migrants. We used the Cormack–Jolly–Seber model in Program MARK to estimate apparent seasonal survival. We allowed apparent survival to vary by all seasons (summer, fall, winter, spring) or 2 seasons (spring and fall, summer and winter) to determine if apparent survival varied seasonally or if apparent survival decreased during migratory periods. We also allowed apparent survival to vary by age class to determine if the changing seasons affected sub-adults differently than adults. We defined 3 age classes: swans in their first winter, swans in their first spring migration, and swans ≥ 1 year of age. We allowed detection probabilities to vary by all seasons (summer, fall, winter, spring) or site (central Wisconsin and BS5). We considered models with a ΔQAIC_c of < 2 to be competitive.

RESULTS

Annual Survival of Long- and Short-Distance Migrants

We used 576 encounter histories to test for differences in apparent annual survival between short- and long-distance migrants. Over half of the swans in the dataset were first seen as sub-adults but proportions varied by site, sex, and origin (Table 1). Most swans were banded in 2000 or later (84%) but some were banded as early as 1990. Estimates of collar loss were 2% at Universal, 4% at BS5 and Hudson, 6% at Riverlands, and 9% at Monticello. We detected a lack of fit using the goodness-of-fit test (984 of 1,000 iterations) so we used the calculated \hat{c} of 1.223 to adjust the variance of the data. The best model had more than twice as much support as any other model and indicated that apparent survival varied in an interactive manner between short- and long-distance migrants and between adults and sub-adults (Table 2). We estimated apparent survival of long-distance migrants as 0.808 (SE = 0.019) for adults and 0.858 (SE = 0.036)

Table 1. Characteristics of trumpeter swans wintering at the 5 study sites in Illinois, Wisconsin, and Minnesota as well as those that moved from one site to another between winters (switchers), 2000–2008.

Site	n	Age ^a		Sex			Origin ^b				
		Adult	Sub-adult	Male	Female	Unknown	Wild	Decoy	CP	CT	U
BS5	132	37.1	62.9	45.7	54.3	62.3	84.4	3.3	2.5	1.6	8.2
Riverlands	60	65.0	35.0	44.4	55.6	44.9	83.7	2.0	4.1	6.1	4.1
Universal	76	64.5	35.5	62.5	37.5	44.2	91.9	0.0	0.0	0.0	8.1
Hudson	220	39.1	60.9	53.2	46.8	44.1	87.4	0.9	0.5	2.7	8.6
Monticello	17	47.1	52.9	37.5	62.5	57.9	84.2	5.3	10.5	0.0	0.0
Switchers	71	33.8	66.2	52.9	47.1	52.1	91.5	0.0	1.4	0.0	7.0

^a Age at first observation.

^b Wild, wild-hatched; decoy, decoy-reared; CP, captive parent-reared; CT, captive reared; U, unknown.

Table 2. Model selection criteria for models of apparent annual survival of trumpeter swans at 5 study sites in Illinois, Wisconsin, and Minnesota, 2000–2008.

Model ^a	QAIC _c	ΔQAIC _c	AIC _c weights	Model likelihood	Parameters	Deviance
phi(a*m) p(e) psi(ss)	2436.09	0	0.4929	1	27	989.78
phi(.) p(e) psi(ss)	2437.81	1.7261	0.2079	0.4219	24	997.75
phi(m) p(e) psi(ss)	2437.88	1.7968	0.2007	0.4072	25	995.74
phi(a) p(e) psi(ss)	2439.31	3.2209	0.0985	0.1998	25	997.16
phi(a*m) p(e) psi(.)	2511.27	75.1786	0	0	8	1104.03

^a m = migratory strategy (long- and short-distance), a = 2 age classes (first year after hatch and all subsequent years), e = level of effort (low, moderate, and high). ss = site-to-site movements, phi = survival probability, p = resighting probability, psi = movement probability.

for sub-adults. Apparent survival of short-distance migrants was 0.808 (SE = 0.022) for adults and 0.697 (SE = 0.046) for sub-adults. Detection probabilities varied by level of effort and were 0.0, 0.727 (SE = 0.022), and 0.945 (SE = 0.018) for low, medium, and high efforts, respectively. The highest movement probabilities were from Universal to Hudson (0.129 ± 0.029), Monticello to Hudson (0.12 ± 0.056), and Hudson to Universal (0.08 ± 0.015). All other movement probabilities were less than 0.03 (Table 3). We also used model averaging capabilities in Program MARK to generate survival estimates based on the top 3 models which all had a ΔQAIC_c < 2. These estimates were 0.83 (SE = 0.04) for long-distance migrant sub-adults, 0.809 (SE = 0.018) for long-distance migrant adults, 0.744 (SE = 0.059) for short-distance migrant sub-adults, and 0.802 (SE = 0.022) for short-distance migrant adults.

Seasonal Survival of Long-Distance Migrants

We observed 91 collared swans wintering at BS5 in the winters of 2005–2006 and 2006–2007. Swans were banded as early as 1993, but 58% were banded in 2005 or 2006. Nearly 95% of swans wintering at BS5 were banded in Juneau, Wood, or Jackson County in central Wisconsin. Eighty-five percent of all wintering swans resighted were

wild-hatched birds banded as cygnets. When testing for age effects on apparent seasonal survival, the goodness-of-fit test indicated that the most general model did not fit the data (998 of 1,000 iterations) therefore the variance inflation factor (\hat{c}) was adjusted to 1.347. There were 2 models with a ΔQAIC_c < 2 which had nearly an equal amount of support (Table 3). Both models indicated that apparent survival varied by age. According to the most parsimonious model, apparent survival was 1.0 for sub-adults during their first winter, 0.971 ± 0.013 for sub-adults during their first spring migration, and 0.995 ± 0.002 for all seasons and age classes thereafter. Detection probabilities were 0.927 ± 0.021 during the early and late winter and 0.583 ± 0.036 during the early and late summer. The second most parsimonious model (Table 4) had identical survival rates, but recognized slight differences in detection probabilities during early and late winter (0.89 ± 0.036 and 0.954 ± 0.021) and early and late summer (0.542 ± 0.051 and 0.621 ± 0.05).

DISCUSSION

Annual Survival of Long- and Short-Distance Migrants

Our results indicated adult survival was similar between short- and long-distance migrants and greater for sub-adult long-distance migrants relative to short-distance migrants. Both short- and long-distance migrants originated in the same region, thus, factors affecting mortality on the breeding grounds should be similar between groups and would not explain any differences in apparent annual survival (Varner 2008). Swans wintering in Minnesota and Wisconsin, subsist primarily on supplementally fed corn, which is lacking in some necessary minerals and amino acids (Petrie et al. 1998). Alternatively, swans wintering in southern Illinois consume waste grain scavenged in grain fields with substantial amounts of submersed aquatic vegetation and winter wheat (Varner 2008). If nutrients acquired during winter also influence mortality the following spring and summer, any differences in apparent survival between short- and long-distance migrant sub-adults may be due to winter diet. Because of the lack of dietary variation, sub-adults wintering at these supplemental feeding locations may be nutritionally stressed, thus more susceptible to inclement weather, disease, or starvation. During exceptionally harsh winters or power plant disruptions, the water surface may freeze for extended periods. Furthermore, high densities of birds at the feeding sites may lead to higher rates of disease and competition for food.

Table 3. Movement probabilities (psi) and standard errors for trumpeter swans at 5 study sites in Illinois, Wisconsin, and Minnesota, 2000–2008.

Transition ^a	psi	SE
B to R	0.0212	0.0086
B to U	0.0104	0.0066
B to H	0.0082	0.0058
B to M	0.0038	0.0038
R to B	0.0308	0.0155
R to U	0.0189	0.0132
R to H	0.0178	0.0125
R to M	Not estimable	
U to B	0.0105	0.0074
U to R	0.0057	0.0057
U to H	0.1290	0.0259
U to M	0.0102	0.0079
H to B	Not estimable	
H to R	0.0081	0.0042
H to U	0.0796	0.0133
H to M	0.0169	0.0064
M to B	Not estimable	
M to R	Not estimable	
M to U	0.0243	0.0239
M to H	0.1197	0.0502

^a B, BS5; R, Riverlands; U, Universal; H, Hudson; M, Monticello.

Table 4. Model selection ranking for models of apparent seasonal survival for trumpeter swans wintering near Burning Star Number 5, Jackson County, Illinois, 2005–2007.

Model ^a	QAIC _c	ΔQAIC _c	QAIC _c weights	Parameters	Deviance
phi(a) p(2s)	461.93	0	0.3780	5	139.70
phi(a) p(4s)	462.26	0.3362	0.3195	7	135.91
phi(2s) p(2s)	464.84	2.9124	0.0881	4	144.66
phi(.) p(2s)	465.07	3.1387	0.0787	3	146.93
phi(.) p(4s)	465.64	3.7132	0.0590	5	143.41
phi(2s) p(4s)	466.42	4.4944	0.0400	6	142.14
phi(4s) p(2s)	467.48	5.5541	0.0235	6	143.20
phi(4s) p(4s)	468.63	6.704	0.0132	8	140.20
phi(a) p(.)	523.80	61.8712	0	4	203.62
phi(4s) p(.)	525.77	63.8447	0	5	203.55
phi(2s) p(.)	528.53	66.6007	0	3	210.39
phi(.) p(.)	529.94	68.0164	0	2	213.83

^a 2s = migratory and non-migratory seasons; 4s = winter, spring, summer, and fall; a = 3 age classes (first winter after hatch, first spring migration, and all subsequent seasons); phi = survival probability; p = resighting probability.

We found evidence indicating survival of sub-adults was greater than that of adults for long-distance migrants. This is a somewhat surprising result until you consider that survival estimates of sub-adult swans in our study do not include 2 periods of typically high mortality in waterfowl, their first fall migration and reproduction. Young swans enter into our analysis when they are first observed on the wintering grounds following their first fall migration, a period of high natural mortality for juvenile geese (Owen and Black 1989, Francis et al. 1992, Sedinger et al. 1995, Eichholz and Sedinger 2007). Furthermore, trumpeter swans do not begin breeding until 3–4 years of age. Young swans remain under the care of their parents for much of their first year (Banko 1960). They often travel, roost, and forage in groups with other young non-breeders which also likely provides for better survival overall (Banko 1960, Mitchell 1994). However, we did not find this same pattern among short-distance migrant swans.

Inherent biases in our estimates could lead to differences in apparent annual survival between short- and long-distance migrants. Biases could be caused by markers affecting survival of swans, marker loss, or permanent emigration from our study areas. Although there is building evidence indicating neck collars may affect survival of geese (Castelli and Trost 1996, Schmutz and Morse 2000, Alisauskas and Lindberg 2002), we can think of no reason why neck collars would have a greater effect on survival of short-distance migrants relative to long-distance migrants. It is possible that icing of collars may cause mortality. However, iced collars are not a common occurrence and, for swans, it is unlikely that iced collars would affect sub-adults and adults differently.

Additionally, tag loss is not expected to differ between short- and long-distance migrants as all collars were identically attached on the breeding grounds by WDNR personnel. Differences in estimates of collar loss among sites likely reflected our ability to identify leg-band-only swans, not differences in collar loss. The leg bands are difficult to read so apparent survival estimates for both short- and long-distance migrants are likely biased low because of collar tag loss. However, survival estimates from swans wintering at

Monticello (short-distance migrants) are likely the least biased due to tag loss because swans in this area are more habituated to people and observers are able to closely approach the swans and identify birds that have lost their collars by their leg bands. Therefore, the 9% estimate of tag loss for Monticello is probably more accurate than the lower estimates for our other study areas. This would bias survival estimates lower for long-distance migrants and thus would not account for the greater survival estimates we observed in long-distance migrant sub-adults.

Differential rates of permanent emigration could also lead to differences in estimates of apparent annual survival. Estimates could be lower for short-distance migrants relative to long-distance migrants if short-distance migrants are more likely to permanently emigrate from the study areas. We found little evidence, however, that the likelihood of a migratory strategy change was greater for short- than long-distance migrants. We only observed 12.3% of swans at >1 wintering site and movement rate estimates were low overall.

The goal of supplemental feeding was to increase annual survival of the newly reintroduced trumpeter swans, maximizing population growth. Currently, both long- and short-distance migrant swans survive at rates that support population growth. From 2000 to 2005, the average annual growth rate of Wisconsin's swan population, more than half of which are long-distance migrants, was 17%, which is comparable to growth rates in states where most swans are short-distance migrants, ranging from 13% in Michigan to 17% in Minnesota (Caithamer 2001, Moser 2006). Results of our annual survival analysis indicate that long-distance migrant swans that are not dependent on supplemental feeding survive at least as well as, but possibly better than short-distance migrants that are fed, particularly sub-adults.

Seasonal Survival of Long-Distance Migrants

Alerstam (1990) proposed several factors that might cause increased mortality in birds during migration including: starvation, adverse weather, collisions, and predation. The factors that typically lead to high mortality during migration may have little influence on trumpeter swans in this study.

The distance between the central Wisconsin breeding areas and our southern studies sites was 700–800 km. This distance is quite short when compared to other migratory species of swans. Tundra swans (*Cygnus columbianus*) and Bewick's swans (*Cygnus bewickii*) travel more than 4,500 km each fall and spring (Bowler 1994, Petrie and Wilcox 2003). Because the migration distance of our population of trumpeter swans was relatively short and swans had ample opportunities for resting and feeding, it was unlikely that starvation or adverse weather influenced swan mortality during this season. In addition, the swan's large body size likely prevents predators from appreciably influencing mortality. Collisions with obstructions, such as power lines, are thought to be a primary mortality factor for swans (Matteson et al. 2007). However, we did not expect more collisions during migration since birds typically fly well above any obstacles (Engelhardt 1997).

Swans that winter at BS5 may undergo a drop in apparent survival during their first spring. This is likely due to parental abandonment, however, and not migration-related factors. Apparent survival rates during summer and winter are also very high in spite of the stresses associated with each season. It appears that BS5 is a safe and good-quality wintering area as survival rates were high at this site, especially among sub-adults. These results suggest that, migration does not cause a reduction in survival rates for these swans and it may be advantageous for swans to trade off the minor costs of migration for the benefits of wintering at BS5 and other southern sites with similar habitat features.

MANAGEMENT IMPLICATIONS

Initial concerns about high winter mortality due to a lack of adequate wintering habitat were reasonable when considering the lack of knowledge regarding trumpeter swan wintering ecology when trumpeter swans were first reintroduced to the Midwest. Recent evidence, however, indicates large open bodies of water in proper juxtaposition to a variety of agricultural habitats provide quality wintering habitats for trumpeter swans (Babineau 2004, Varner 2008). Information on IP trumpeter swan wintering locations south of 40° latitude in conjunction with results from this study indicate the continued provisioning of resources during winter near breeding grounds is unnecessary. The primary goal of the IP Flyway Management Plan is “to restore self-sustaining migratory meta-population of trumpeter swans” (Ad hoc drafting committee for the Interior Population of trumpeter swans, Mississippi and Central Flyway Councils, unpublished report). Winter feeding in northern areas contradicts that goal. We recommend managers encourage migration of these flocks through a carefully monitored reduction or discontinuation of supplemental feeding programs. Furthermore, our results indicate, unlike smaller-bodied birds, large-bodied waterfowl that migrate intermediate distances are subject to only minor costs of migration. Combined, these results suggest artificially minimizing migration distances when reintroducing large-bodied migratory birds is likely unwarranted.

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LITERATURE CITED

- Alerstam, T. 1990. Bird migration. Cambridge University Press, New York, New York, USA.
- Alisauskas, R. T., and M. S. Lindberg. 2002. Effects of survival and fidelity of white-fronted and Canada geese captured as non-breeding adults. *Journal of Applied Statistics* 29:521–537.
- Babineau, F. M. 2004. Winter ecology of trumpeter swans in southern Illinois. Thesis, Southern Illinois University, Carbondale, USA.
- Banko, W. E. 1960. The Trumpeter Swan. *North American Fauna* No. 63. Fish and Wildlife Service, Washington, D.C., USA.
- Bowler, J. M. 1994. The condition of Bewick's swans *Cygnus columbianus bewickii* in winter as assessed by their abdominal profile. *Ardea* 82: 241–248.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Caithamer, D. F. 2001. Trumpeter swan population status, 2000. Division of Migratory Bird Management, U.S. Fish and Wildlife Service, Laurel, Maryland, USA.
- Castelli, P. M., and R. E. Trost. 1996. Neck bands reduce survival of Canada geese in New Jersey. *Journal of Wildlife Management* 60:891–898.
- Cox, G. W. 1968. The role of competition in the evolution of migration. *Evolution* 22:180–192.
- Eichholz, M. W., and J. S. Sedinger. 2007. Survival and recovery rate of Canada geese staging in interior Alaska. *Journal of Wildlife Management* 71:36–42.
- Engelhardt, K. A. M. 1997. Evaluation of translocation criteria for trumpeter swans reintroduced to Northern Utah: habitat quality and interactions with tundra swans. Thesis, Utah State University, Logan, Utah, USA.
- Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Changes in survival rates of lesser snow geese with age and breeding status. *Auk* 109:731–747.
- Gauthier, G., R. Pradel, S. Menu, and J.-D. Lebreton. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. *Ecology* 82:3105–3119.
- Greensberg, R. 1980. Demographic aspects of long distance migration. Pages 493–504 in A. Keast and E. S. Morton, editors. *Migrant birds*

- in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.
- Matteson, S. W., P. F. Manthey, M. J. Mossman, and L. M. Hartman. 2007. Wisconsin trumpeter swan recovery program: progress toward restoration, 1987–2005. Proceedings and Papers of the Trumpeter Swan Society Conference 20: 11–16.
- Menu, S., G. Gauthier, and A. Reed. 2005. Survival of young greater snow geese (*Chen caerulescens atlantica*) during fall migration. *Auk* 122:479–496.
- Mitchell, C. D. 1994. Trumpeter swan (*Cygnus buccinator*). Account 105 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.
- Moser, T. J. 2006. The 2005 North American trumpeter swan survey. Division of Migratory Bird Management, U.S. Fish and Wildlife Service, Denver, Colorado, USA.
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* 147:146–166.
- Nichols, J. D. 1996. Sources of variation in migratory movements of animal populations: statistical inference and a selective review of empirical results for birds. Pages 147–197 in O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, Illinois, USA.
- Owen, M., and J. M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. *Journal of Animal Ecology* 58:603–617.
- Petrie, M. J., R. D. Drobney, and D. A. Graber. 1998. True metabolizable energy estimates of Canada goose foods. *Journal of Wildlife Management* 62:1147–1152.
- Petrie, S. A., and K. L. Wilcox. 2003. Migration chronology of eastern population tundra swans. *Canadian Journal of Zoology* 81:861–870.
- Pienkowski, M. W., and P. R. Evans. 1985. The role of migration in the population dynamics of birds. Pages 331–352 in R. M. Sibly and R. H. Smith, editors. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford, United Kingdom.
- Schmutz, J. A., and J. A. Morse. 2000. Effects of neck collars and radio-transmitters on survival and reproduction of emperor geese. *Journal of Wildlife Management* 64:231–237.
- Sedinger, J. S., P. L. Flint, and M. S. Lindberg. 1995. Environmental influence on life history traits: growth, survival, and fecundity in black brant (*Branta bernicla*). *Ecology* 76:2404–2414.
- Slater, G. L. 2006. Trumpeter swan (*Cygnus buccinator*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region, Washington, USA.
- Varnier, D. M. 2008. Survival and foraging ecology of Interior Population trumpeter swans. Thesis, Southern Illinois University, Carbondale, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.

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