MUTE SWAN POPULATION GROWTH

Rapid increase in the lower Great Lakes population of feral mute swans: a review and a recommendation

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Abstract Mute swans (*Cygnus olor*) are an exotic species whose population has increased throughout the lower Great Lakes since their introduction during the mid-twentieth century. We used 3 independent data sources to estimate the rate of increase of mute swans on the lower Great Lakes: aerial surveys in spring and autumn at Long Point, Lake Erie, Ontario, Canada 1971–2000; midwinter waterfowl inventory of the north shore of Lake Ontario, 1980–2000; and Christmas Bird Counts on both the United States and Canadian shores of the lakes, 1980–2000. The average estimated population growth rate varied from 10 to 18% per year. The most conservative growth-rate estimate of 10% per year indicates a doubling of the mute swan population every 7–8 years.

> These high growth rates indicate that mute swans have found a favorable environment in the lower Great Lakes. That area is climatically somewhat similar to their native range in Europe, with low natural predation rates and minimal human interference (the birds are protected in Canada and the United States under the Migratory Birds Convention of 1916). If the mute swan carrying capacity of the lower Great Lakes is similar to portions of the species' native European range and growth rates continue, the Canadian population could reach as many as 30,000 birds within 30 years. Given that the species is nonnative and its ecological impact potentially could be large, we suggest that control measures be implemented before the population grows much larger.

Key words Cygnus olor, exotic species, Great Lakes, mute swans, population growth

The accidental and intentional introduction of exotic waterfowl can have negative ecological impacts on native species (Weller 1969). Adverse effects are particularly likely if the introduced species is aggressive, competes with other waterfowl for food or habitat, and hybridizes with native species. For example, North American ruddy ducks (*Oxyura jamaicensis*) threaten white-headed ducks (*O. leucocephala*) in Europe through hybridization and competition, and Canada geese (*Branta canadensis*) introduced into the United Kingdom

have caused numerous ecological and economic concerns (Hughes et al. 1999). Mute swans (*Cygnus olor*), endemic to Eurasia, were introduced to North American city parks, zoos, avicultural collections, and estates in the late 1800s and early 1900s (Bellrose 1980). The intentional release and accidental escape of these birds resulted in the establishment of populations along the northeastern Atlantic Coast of the United States, portions of the Pacific Coast, and more recently, the lower Great Lakes.

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Mute swans occupy and defend large territories (up to 6 ha) of wetland habitat during nesting, brood rearing, and foraging (Birkhead and Perrins 1986, Ciaranca 1990, Ciaranca et al. 1997). They can attack and displace native waterfowl from breeding and staging habitats (Willey 1968a, Reese 1975, Ciaranca 1990, Ciaranca et al. 1997), and they have been reported to kill adult and juvenile ducks and geese as well as other wetland-dependent birds (Willey 1968a, Ciaranca 1990). They also have been reported to cause nest abandonment in least terns (Sterna albifrons), black skimmers (Rynchops niger), forster's terns (S. forsteri), and common terns (S, birundo) (Ciaranca et al. 1997). Mute swans consume and uproot large amounts of aquatic vegetation (Gillham 1956, Mathiasson 1973, Owen and Cadbury 1975, Allin 1981, Fenwick 1983). Competition for space and food imposed by mute swans has the potential to reduce the carrying capacity of breeding, staging, and wintering habitats for native species of migratory waterfowl in areas where feral populations of mute swans are established (Cobb and Harlan 1980, Allin 1981, Allin et al. 1987).

The lower Great Lakes coastal wetlands provide important staging habitat for migrating waterfowl (Crowder and Bristow 1988, Prince et al. 1992). However, these coastal wetlands have been reduced by drainage and development (Crowder and Bristow 1988, Smith et al. 1991, Prince et al. 1992); only about 20-25% of the original wetland area of western Lake Ontario (Whillans 1982) and less than 5% of western Lake Erie's original wetlands remain (Herdendorf 1987). This wetland loss has concentrated birds on a reduced habitat base, thus increasing the importance of the remaining lower Great Lakes wetlands for staging waterfowl. Pressures from coastal development, human disturbance, and exotic introductions of plants and animals exacerbate the problem (Mills et al. 1993, Petrie and Knapton 1999, Knapton et al. 2000).

Mute swans began colonizing the lower Great Lakes in the mid-1960s and 1970s. Since then, breeding and wintering populations have become well established throughout Ontario's lower Great Lakes coastal regions. Mute swans are currently considered to be protected in Canada and the United States following the Migratory Birds Convention of 1916, which lists swans as game birds without differentiating native and non-native species.

We used several data sets to estimate the rate of population growth of mute swans in the lower Great Lakes in the past 20-30 years. The first data set was from spring and autumn aerial surveys flown over Long Point, Lake Erie from 1971-2000. This area supports some of the largest and most important marshes in the lower Great Lakes. The second was from ground-based midwinter waterfowl surveys on the Canadian side of Lake Ontario, 1980-2000. The last was from Christmas Bird Counts from both the United States and Canadian sides of the Great Lakes, 1980-2000. We also examined available weather data because we hypothesized that increased winter temperatures were contributing to increased mute swan numbers on the lower Great Lakes. The objectives of this paper were to determine the rate of mute swan population growth on the lower Great Lakes, predict how big the population potentially could become, and make recommendations for future management of mute swans in the region.

Methods

Data collection

Long Point aerial surveys (1971-2000). Spring and autumn waterfowl populations were monitored at Long Point by the Canadian Wildlife Service during 7 years in the 1970s and 1980s (1971, 1974, 1975, 1979, 1984, 1987, 1988), and subsequently by the Long Point Waterfowl and Wetlands Research Fund annually from 1991-2000 (Figure 1). Aerial surveys were conducted along a regular route by 2 observers in a fixed-wing aircraft flying at an altitude of 100 m above the ground. Survey routes were designed to cover all major wetlands and waterfowl concentration sites in the area, currently including 27 transects covering >250 km. Survey crews identified and estimated the numbers of each species of waterfowl seen along each of the transects. Usually 5 or 6 survey flights were flown during each season. Because mute swans are large and conspicuous and were generally segregated from other species of swans in the area (mainly tundra swans [Cygnus columbianus columbianus]), these counts likely were fairly comprehensive for this species. Because the same birds likely were present at Long Point for much of each season (spring and autumn), we based our analysis on the peak count in each season.

Midwinter waterfowl inventory (1980-2000). Ground-based surveys forming part of the continental midwinter inventory (MWI) of waterfowl have been conducted along the northern shoreline of

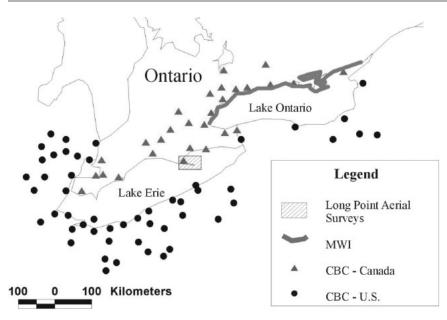


Figure 1. Distribution of surveys used to estimate the rate of population growth of mute swans on the lower Great Lakes: Long Point Aerial Surveys: spring and autumn aerial surveys (1971–2000); MWI: Midwinter inventory on the north shore of Lake Ontario (1980–2000); CBC: Christmas Bird Counts in Canada and the United States within the catchments of the lower Great Lakes where mute swans have been reported (1980–2000).

ally in terms of the number of circles surveyed and the number of participants per circle. We used data from all count circles surveyed for at least 2 years and that reported swans in at least 1 year within the drainage basins of lakes St. Clair, Erie, and Ontario and within about 200 km of the shore (Figure 1). The most consistently available measure of survey effort was party-hours, a measure of the total number of hours spent in the field by independent survey teams (parties).

We downloaded the CBC data through the 1996 count (version 5.10, 4 August 1998) from a publicly available web-

Lake Ontario since 1980 (Figure 1). Surveys are conducted as close to 5 January as scheduling and weather permit. Numerous naturalist clubs conduct the surveys, and the Toronto Ornithological Club compiles the data for all waterfowl species. We labeled all counts based on the year in January (e.g., counts conducted in December 1980 were labeled 1981). Because mute swans tend to be concentrated in a limited number of areas due to harsh weather conditions in January, these surveys are likely to provide a good estimate of the total population of this species along the shore at this time of year.

Christmas Bird Count (1980-2000). The National Audubon Society has been coordinating Christmas Bird Counts (CBCs) in North America since 1900 (in collaboration with Bird Studies Canada starting in 2000). Volunteers count all birds they can identify within pre-selected 24-km-diameter circles on a fixed date within about 1.5 weeks on either side of 25 December (Butcher 1990). Although some counts took place in January, we referred to all counts based on the year in December (thus, the 2000 CBC refers to the count between December 2000 and January 2001). In most instances each circle was surveyed close to the same date each year. Survey effort varied annu-

site (ftp://ftp.nmt.edu/pub/people/john/cbc/). We extracted data from 1997-2000 from the BirdSource database (9 Feb 2001).

Data analysis

We analyzed count data using Poisson regression with a loglink function, corrected for overdispersion, to estimate rate of increase. We fitted models assuming exponential growth and with second order year terms to test for changes in the rate of population growth.

For analysis of CBC data, we included sites as covariates, to allow for the fact that some counts were not conducted every year. In effect, this method analyzes trends within each site and estimates the average trend across sites. We also included effort (measured as party-hours, ξ) as a covariate. Following Link and Sauer (1998), we used a Box-Cox transformation of effort, $b_p(\xi) = B(\xi^p - 1)/p$ with a value of p = -1.5. Because swans are relatively conspicuous and may be fairly readily counted irrespective of the number of observers, we also tested models without the effort covariate. To control for overdispersion of the response variable, we used an SAS program that implements the method of iterative reweighting developed by Link and Sauer (1999). We back-transformed all trend

coefficients and converted them to percentages. We fitted all models using PROC GENMOD in SAS version 8.0 (SAS Institute Inc. 1999).

Climate data

We obtained winter temperature data from the United States Historical Climatology Network (Easterling et al. 1996) for Erie, Pennsylvania (station 362682, 42°05′N, 80°11′W). We downloaded the mean monthly data, adjusted for bias due to station changes and urbanization effects, from the NOAA website (http://lwf.ncdc.noaa.gov/oa/climate/research/ushcn/ushcn.html) and averaged the November-March monthly temperatures for the winters 1969-1970 through 1999-2000. We then used linear regression to estimate the average rate of change in winter temperature over this period.

Results

Long Point migration counts

The first mute swans were recorded at Long Point during spring surveys in 1984, when 4 birds were observed. Because spring surveys were conducted during only 3 years between 1971 and 1984, this probably does not represent the first occurrence of this species at Long Point in spring (see McCracken et al. 1981). Peak spring counts increased to 154 in 2000, following a sharp decline in the early 1990s (Figure 2A). The overall average rate of increase based on spring data, estimated assuming an exponential population growth model, was $16\% \pm 3\%$. However, from 1970-1992 (prior to the drop in 1993), the estimated rate of increase was $30\% \pm 5\%$ per year.

On autumn surveys the first mute swan was recorded in 1971, and most surveys revealed relatively small numbers until the early 1990s, when there was a marked increase (Figure 2B). A sharp decrease occurred in the mid-1990s, followed by an increase to a peak count of 203 birds in 2000. The average rate of increase over the whole time period was $12\%\pm2\%$ per year, but prior to 1993 the growth rate had been about $30\%\pm5\%$ per year.

For neither data set was there evidence that a model allowing the growth rate to increase or decrease over time (a second-order polynomial on the log scale) provided a better fit than the basic exponential model. Nevertheless, it was clear from the graphs (Figure 2) that the exponential model was not a particularly good fit to the data, due to substantial drops in the mid-1990s.

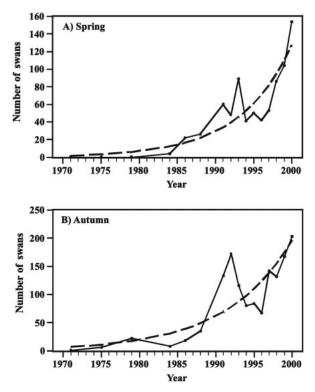


Figure 2. Peak spring (A) and autumn (B) mute swan counts at Long Point, Lake Erie, 1971–2000 (solid line), and estimated population trajectory assuming exponential population growth (dashed line).

Lake Ontario midwinter inventory

The number of mute swans recorded during this survey increased from 49 birds in 1980 to 327 in 2000 (Figure 3). The average rate of population growth during this period, based on an exponential population growth model, was $10\% \pm 1\%$ per year. However, a second-order curve, allowing the growth rate to change over time, was a better fit to

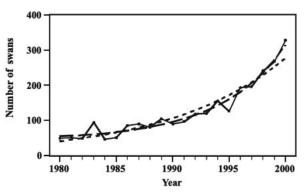


Figure 3. Midwinter inventory of mute swans on the Canadian side of Lake Ontario, 1980–2000, and estimated population trajectory assuming exponential population growth (short dashes) or a growth rate that changes over time (long dashes).

the data (P < 0.01). Based on this model, the growth rate increased from about 3% per year in the early 1980s to about 16% per year in the late 1990s.

Christmas Bird Counts

For data sets on both sides of the Great Lakes, there was a statistically significant, albeit relatively small, effect of effort on the counts (P<0.01), so effort was retained as a covariate. After incorporating this correction, assuming exponential growth rates, counts on the Ontario side of Lake Erie and Lake Ontario increased by about $14\% \pm 1\%$ per year from 1980-2000 (Figure 4A), while those on the United States side increased by about $18\% \pm 1\%$ per year during the same time period (Figure 4B). If we had not corrected for changes in effort, which generally increased over time, the estimated growth rate would have been about 1% per year higher in both data sets.

On both sides of the lakes, there was some evidence that the growth rate has been slowing over time, in that a second-order polynomial (on a log scale) was a better fit than a simple exponential curve (P<0.01). Based on the second-order growth

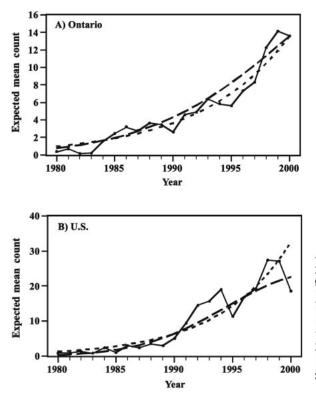


Figure 4. Annual indices for mute swans based on Christmas Bird Count data for the Canadian (A) and United States (B) side of the lower Great Lakes, 1980–2000, and estimated population trajectories assuming exponential population growth (short dashes) or decreasing growth rates (long dashes).

curve, the estimated growth rate decreased from about 19% to 12% per year in Ontario and from 35% to 13% per year in the United States.

Changes in winter temperature

From 1969–1970 through 1984–1985, mean winter temperatures from November through March were below freezing in 10 out of 15 years, while from 1985–1986 through 1999–2000 temperatures were below freezing in only 2 of 15 years (Figure 5). Based on linear regression, the mean temperature increased by an average of 0.064 ± 0.028 degrees Celsius per year over this time period (*P*= 0.03).

Discussion

Population growth

All 3 data sets indicated rapid growth of the mute swan population around the lower Great Lakes, with estimated average growth rates between 10% and 18% per year. Data from the MWI suggest that the growth rate may have increased from about 3% per year to about 16% per year over the time period. Increasing growth rates could be due to increased immigration, decreased emigration, or increasing survival or fecundity. Increased winter temperatures on the lower Great Lakes may have resulted in a reduced tendency for birds to move south to the United States in winter. Also, increased mean winter temperatures could influence both overwinter survival and nutrient reserves of females for breeding in the following year (Esselink and Beekman 1991, Perrins 1991, Walter et al. 1991).

In contrast, data from CBC suggested that the growth rate may have decreased over time, from between 19% (Canada) and 35% (United States) per

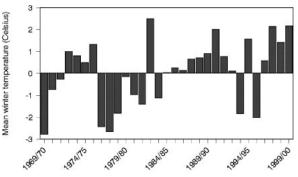


Figure 5. Mean winter temperatures (1 Nov–31 Mar) at Erie, Pennsylvania, as an index of annual variation in winter temperature in the lower Great Lakes region, 1970–2000.

year in the early 1980s to about 12-13% per year in 2000. However, data from these counts must be treated somewhat cautiously because only a limited portion of the wintering range was sampled and sampled areas were not randomly selected. As the mute swan population expands, the proportion of the population wintering outside the sampled areas could potentially be increasing more rapidly as the birds expand into new areas. An additional consideration is that the analysis methods used assumed individual counts were independent, which would be violated if mute swans moved among counts. For example, in the winter of 2000-2001, when substantial portions of Lake Erie were frozen, many counts were lower than the previous year, leading to a decline in the index, but the total count of mute swans was actually higher than the previous year (1,673 compared to 1,270) owing to large increases on a few counts where the birds were presumably concentrated. Such limitations are unlikely to cause much long-term bias but do indicate a need for caution when interpreting annual indices and also in concluding that the rate of increase has declined.

Data from Long Point do not provide evidence for a long-term change in growth rate, but those estimates were strongly affected by sharp drops in counts in the mid-1990s. These drops were most likely related to decreased winter temperatures (Figure 5) and an unsanctioned localized human control effort at that time. The rapid regrowth of population after this disturbance highlights the fact that control, if it is to be effective, must be sustained, and suggests that the estimate of a 30% increase per year prior to 1993 was a good indication of potential growth rate.

Despite some variation in estimates, even the most conservative estimate indicates a growth rate of at least 10% per year. If this growth rate continues, it would correspond to a doubling of population approximately every 7 years. By comparison, the Atlantic Flyway (United States only) population increased by approximately 8% per year between 1986 and 1999 and now numbers nearly 13,000 birds (Matt Perry, Biological Resources Division, United States Geological Services, personal communication).

Mute swan populations also have been increasing during this period within most of their native western Palearctic and southeast Asian range (Wieloch 1991, Delany et al. 1999). For instance, the East Mediterranean-Black Sea population increased from an estimated 20,000 birds in the mid-1980s to 45,000 birds in the mid-1990s (Delany et al. 1999). Similarly, mute swan populations doubled in Estonia, Latvia, and Lithuania between 1987 and 1995 (Delany et al. 1999). A number of factors could have led to those increases, including legal protection, milder winters, and reduced mortality due to lead poisoning (Wieloch 1991). Given the availability of suitable habitat in the lower Great Lakes, the strong competitive abilities of mute swans, their high reproductive rate when expanding into new areas (Wieloch 1984), and their almost total lack of predators (Perrins and Reynolds 1967, Wieloch 1991, Ciaranca et al. 1997), it seems probable that mute swans will continue to increase rapidly in the lower Great Lakes, much as they have in their native Eurasian range.

The potential carrying capacity for mute swans in the lower Great Lakes is unknown, but estimates based on various sources suggest it could be quite high. Territory size in other areas varies from <1ha in high-quality areas to about 6 ha on large open water (Ciaranca et al. 1997). The Canadian side of the lower Great Lakes includes about 47,000 ha of coastal wetland habitat. At 6 ha per territory, these wetlands potentially could support about 8,000 pairs. Including nonbreeders (Czapulak 1991, Krivonosov 1991), this could easily represent 20,000-30,000 individuals. If mute swan territories are smaller in high-quality habitats or if swans start breeding in inland habitats (e.g., Wieloch 1984, Circana et al. 1997), an even larger population could be supported. The most recent Christmas Bird Count for the Canadian side of the lower Great Lakes in 2000, which did not sample all areas, recorded about 1,700 birds. At a growth rate of 10% per year, this population would reach 30,000 birds in 30 years.

What factors might limit the population from reaching its potential carrying capacity? Severe winters can cause increased winter mortality (particularly of cygnets) and reduced future reproductive output in mute swans (Esselink and Beekman 1991, Perrins 1991, Walter et al. 1991). So increasing winter temperatures may be contributing to the rapid growth rates of mute swans on the lower Great Lakes, as it is thought to be doing in the Palearctic (Wieloch 1991). Since winter temperatures are projected to continue to increase (Environmental Protection Agency 1997), it seems unlikely this factor will inhibit continued population expansion.

Lead poisoning was a substantial mortality factor in Europe and the United Kingdom prior to the banning of lead fishing weights and shotgun pellets in many regions (O'Halloran et al. 1988, MacDonald et al. 1990, Brown et al. 1992, Pennycott 1999). Postmortem examination of birds revealed that almost 70% of mute swans examined in Ireland died from lead poisoning and >40% of captured swans had elevated levels of blood lead; birds that died from collisions also had elevated blood lead levels (O'Halloran et al. 1991). Lead poisoning was implicated in the local population decline of mute swans in a number of areas in Europe (Hardman and Cooper 1980, Birkhead and Perrins 1985). Since lead was banned, lead poisoning deaths have declined dramatically and mute swan populations have increased in several European countries (Sears and Hunt 1991, Pennycott 1999). Because lead shot for hunting waterfowl was banned in the United States in 1991 (Anderson 1992) and Canada in 1999 (Rodrigue and Reed 1999) and the use of lead sinkers is declining through legislation and education, we doubt that lead poisoning is or will be a major limiting factor.

Natural mortality of adults generally has been reported to be low (Ciaranca et al. 1997). Unless widespread disease outbreaks or serious degradations in wetland quality occur, it seems unlikely that mute swans will be limited before they reach carrying capacity, except by human intervention.

Ecological impacts of feral mute swans

Mute swans are aggressive toward other waterfowl and may displace them from breeding and foraging areas. Unlike tundra swans, which use the lower Great Lakes region for brief periods in the spring and autumn (Petrie and Wilcox 2003), mute swans remain on the Great Lakes throughout the year, although they move locally in response to weather conditions. Also, whereas tundra swans often forage in fields (Petrie et al. 2002), mute swans using the lower Great Lakes presently rely entirely on wetlands (personal observation). They consume daily at least 3-4 kg (wet weight) of submerged aquatic plants, including leaves, stems, roots, stolons, and rhizomes (Willey 1968a, Mathiasson 1973, Owen and Cadbury 1975, Allin 1981, Fenwick 1983), uproot additional vegetation that is not eaten (Gillham 1956, Willey 1968b, Ciaranca et al. 1997), and use emergent vegetation for nest building (Gillham 1956). At high densities, mute swans can overgraze an area, causing a substantial decline in the availability of submerged aquatic vegetation (Cobb and Harlan 1980, Allin 1981, Allin et al. 1987), with the potential to eliminate some plant species from an ecosystem (Mathiasson 1973). During winter mute swans may also consume nutrient storage and overwintering structures such as tubers, which could reduce the future availability of perennial species such as wild celery (*Vallisneria americana*) and American bulrush (*Scirpus americanus*), both important food sources for native waterfowl (Knapton and Petrie 1999).

Competition for space and food imposed by mute swans has the potential to reduce the quality and availability of breeding, staging, and wintering habitats for native species of migratory waterfowl in areas where feral populations of swans are established (Cobb and Harlan 1980, Allin 1981, Allin et al. 1987). This could be a particular problem around the coastal Great Lakes, given the already extensive reductions in availability of coastal wetlands in that region and the importance of these wetlands for staging native waterfowl.

Management recommendations

Although we cannot quantify the total extent of the impact of mute swans, there are reasons for concern. It seems prudent to take management action now, given that the species is nonnative and given the history of problems caused by nonnative species in other regions, the particularly large potential impact of this species, the current rapid growth rate of the population, and the lack of any evidence that natural causes will limit the population in the near future. Considering the situation on Chesapeake Bay, it is important to control the growth of this species in the Great Lakes region before the population becomes much larger.

We recommend that the first step be to remove mute swans from the list of protected species in all regions in the United States and Canada. Second, we recommend initiation of a control program. Nonlethal control programs have been implemented in a number of the eastern United States, but their effectiveness has been limited. Rhode Island destroyed 9,378 eggs in 1,629 nests over a period of 22 years, but the population increased by over 500% (C. Allin, Rhode Island Department of Environmental Management, Division of Fish and Wildlife, personal communication). Population models indicate that the most effective way to

reduce population growth for a long-lived species such as the mute swan is to reduce adult survival rates (e.g., Schmutz et al. 1996). This potentially could be done through capture and removal programs or through shooting. Swan capture and removal would be costly, and it is doubtful that a sufficient number of repositories exists for these birds or that captured birds would never be released. Given that populations may be increasing by up to 18% per year, it would be necessary to remove up to 20-30% of the population every year to achieve even a relatively modest decline of 10% per year. With the current population on the Canadian side of the lower Great Lakes probably exceeding 2,000 birds, this would imply capturing and removing several hundred birds per year. It seems doubtful that sufficiently large numbers could be captured in a cost-effective manner.

A simpler and far more effective alternative would be to encourage hunters and managers of refuges to shoot adults. Such a program would be unlikely to eradicate the species but would probably be sufficient to maintain the regional population at no more than a few hundred individuals. In areas where lethal control may not be appropriate, such as city parks, egg oiling could also be implemented to prevent population expansion. Obviously, it would be necessary to maintain current monitoring programs to assess the effectiveness of control measures. If those measures were not sufficient, professional culling programs could be implemented.

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Literature cited

- ALLIN, C. C. 1981. Mute swans in the Atlantic Flyway. Proceedings of the International Waterfowl Symposium 4: 149-154.
- ALLIN, C. C., G. C. CHASKO, AND T. P. HUSBAND. 1987. Mute swans in the Atlantic flyway: A review of the history, population growth, and management needs. Transactions of the Northeastern Section of the Wildlife Society 44:32-47.
- ANDERSON, W. L. 1992. Legislation and lawsuits in the United States and their effects on nontoxic shot regulations. Pages 56-60 in D. J. Pain, editor. Lead poisoning in waterfowl. Proceedings of the International Waterfowl and Wetlands Research Bureau Workshop. International Waterfowl and Wetlands Research Bureau Special Publication 16, Slimbridge, United Kingdom.
- BELLROSE, F. C. 1980. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.
- BIRKHEAD, M. E., AND C. M. PERRINS. 1985. The breeding biology of the mute swan, *Cygnus olor*, on the River Thames with special reference to lead poisoning. Biological Conservation 32:1–11.
- BIRKHEAD, M. E., AND C. M. PERRINS. 1986. The Mute Swan. Croom Helm, London, United Kingdom.
- BROWN, M. J., E. LINTON., AND E. C. REES. 1992. Causes of mortality among wild swans in Britain. Wildfowl 43:70–79.
- BUTCHER, G. S. 1990. Audubon Christmas Bird Counts. Pages 5–13 in J. R. Sauer and S. Droege, editors. Survey designs and statistical methods for the estimation of avian population trends. United States Fish and Wildlife Service Biological Report 90(1).
- CIARANCA, M. 1990. Interactions between mute swans (*Cygnus olor*) and native waterfowl in southeastern Massachusetts on freshwater ponds. Thesis, Northeastern University, Boston, Massachusetts, USA.
- CIARANCA, M. A., C. C. ALLIN, AND G. S. JONES. 1997. Mute swan (*Cygnus olor*). Account No. 273 *in* A. Poole and F. Gill, editors. The Birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologists' Union, Washington, D.C., USA.
- COBB, J. S., AND M. M. HARLAN. 1980. Mute swan (*Cygnus olor*) feeding and territoriality affects diversity and density of rooted aquatic vegetation. American Zoologist 20:882.
- CROWDER, A. A., AND J. M. BRISTOW. 1988. The future of waterfowl habitats in the Canadian lower Great Lakes wetlands. Journal of Great Lakes Research 14:115–127.
- CZAPULAK, A. 1991. Status of the mute swan *Cygnus olor* and the whooper swan *Cygnus cygnus* in Silesia (SW Poland). Wildfowl Supplement No.1:39-43.
- DELANY, D., C. REYES, E. HUBERT, S. PIHL, E. REES, L. HAANSTRA, AND A. VAN STRIEN. 1999. Results from the International Waterbird Census in the western Palearctic and southeast Asia 1995 and 1996. Wetlands International Publication No. 54.
- EASTERLING, D. R., T. C. PETERSON, AND T. R. KARL. 1996. On the development and use of homogenized climate datasets. Journal of Climate 9:1429-1434.
- ENVIRONMENTAL PROTECTION AGENCY. 1997. Climate change and Pennsylvania. United States Environmental Protection Agency 230-F-97-00811.
- ESSELINK, H., AND J. H. BEEKMAN. 1991. Between year variation and causes of mortality in the non-breeding population of the Mute swan *Cygnus olor* in the Netherlands, with special

reference to hunting. Wildfowl Supplement No.1:110-119. FENWICK, G. H. 1983. Feeding behavior of waterfowl in relation

- to changing food resources in the Chesapeake Bay. Dissertation, Johns Hopkins University, Baltimore, Maryland, USA.
- GILLHAM, M. E. 1956. Feeding habits and seasonal movements of mute swans on two south Devon estuaries. Bird Study 3: 205-212.
- HARDMAN, J. A., AND D. R. COOPER. 1980. Mute swans on the Warwickshire Avon—a study of decline. Wildfowl 31:29-36.
- HERDENDORF, C. E. 1987. The ecology of the coastal marshes of western Lake Erie: A community profile. Report 85 (7.a) National Wetlands Research Center, United States Fish and Wildlife Service, Department of the Interior, Washington, D.C., USA.
- HUGHES, B., J. KIRBY, AND J. M. ROWCLIFFE. 1999. Waterbird conflicts in Britain and Ireland: Ruddy Ducks Oxyura jamaicensis, Canada Geese Branta canadensis, and Cormorants *Phalacrocorax carbo*. Wildfowl 50:77-99.
- KNAPTON, R. W., AND S. A. PETRIE. 1999. Changes in distribution and abundance of submerged marcophytes in Long Point's Inner Bay, Lake Erie: implications for foraging waterfowl. Journal of Great Lakes Research 25:783-798.
- KNAPTON, R. W., S. A. PETRIE, AND G. HERRING. 2000. Human disturbance of diving ducks on Long Point Bay, Lake Erie. Wildlife Society Bulletin 28:923–930.
- KRIVONOSOV, G. A. 1991. The status and distribution of the mute swan *Cygnus olor* in the USSR: a review of recent censuses. Wildfowl Supplement No.1:33-38.
- LINK, W. A., AND J. R. SAUER. 1998. Estimating population change from count data: application to the North American Breeding Bird Survey. Ecological Applications 8:258–268.
- LINK, W. A., AND J. R. SAUER. 1999. Controlling for varying effort in count surveys—an analysis of Christmas Bird Count data. Journal of Agricultural, Biological, and Environmental Statistics 4: 116-125.
- MACDONALD, J. W., R. GOATER, N. K. ATKINSON, AND J. SMALL. 1990. Further causes of death in Scottish swans *Cygnus olor*. State Veterinary Journal 44:81–93.
- MATHIASSON, S. 1973. Distribution and behaviour of non-breeding Mute swans of the Swedish west coast. Vittrery 8: 400-452.
- McCRACKEN, J. D., M. S. W. BRADSTREET, AND G. L. HOLROYD. 1981. Breeding birds of Long Point, Lake Erie. Canadian Wildlife Service Report 44.
- MILLS, E. L., J. H. LEACH, J. T. CARLTON, AND C. L. SECOR. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1–54.
- O'HALLORAN, J., A. A. MYERS, AND P. F. DUGGAN. 1988. Lead poisoning in swans and sources of contamination in Ireland. Journal of Zoology London 216:211–223.
- O'HALLORAN, J, A. A. MYERS, AND P. F. DUGGAN. 1991. Lead poisoning in mute swans *Cygnus olor* in Ireland: a review. Wildfowl Supplement No.1:389-395.
- OWEN, M., AND C. J. CADBURY. 1975. The ecology and mortality of mute swans at the Ouses Washes, England. Wildfowl 25: 31-42.
- PENNYCOTT, T. W. 1999. Causes of mortality in mute swans *Cygnus olor* in Scotland 1995–1996. Wildfowl 50:11-20.
- PERRINS, C. M. 1991. Survival rates of young mute swans *Cygnus* olor. Wildfowl Supplement No.1:95–103.
- PERRINS, C. M., AND C. M. REYNOLDS. 1967. A preliminary study

of the mortality of the mute swan, *Cygnus olor*. Wildfowl Trust Annual Report 18:74-84.

- PETRIE, S. A., AND R. W. KNAPTON. 1999. Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie; possible influence of waterfowl predation. Journal of Great Lakes Research 25:772-782.
- PETRIE, S. A., S. BADZINSKI, AND K. L. WILCOX. 2002. Population trends and habitat use of Tundra Swans staging at Long Point, Lake Erie. *In:* E. C. Rees, S. L. Earnst and J. Coulson, editors. Proceedings of the Fourth International Swan Symposium, 2001. Waterbirds 25, Special Publication 1:143–149.
- PETRIE, S. A., AND K. L. WILCOX. 2003. Migration chronology of eastern population tundra swans. Canadian Journal of Zoology 81:861-870.
- PRINCE, H. H., P. I. PADDING, AND R. W. KNAPTON. 1992. Waterfowl use of the Laurentian Great Lakes. Journal of Great Lakes Research 18:673-699.
- REESE, J. G. 1975. Productivity and management of feral mute swans in Chesapeake Bay. Journal of Wildlife Management 39: 280–286.
- RODRIGUE, J., AND A. REED. 1999. Incidence of lead shot in Canada geese taken during the spring subsistence hunt on the eastern shores of James Bay. Canadian Wildlife Service Progress Notes 213.
- SAS INSTITUTE INC. 1999. SAS System for Windows, version 8.0. SAS Institute, Cary, North Carolina, USA.
- SCHMUTZ, J. A., R. F. ROCKWELL, AND M. R. PETERSEN. 1996. Relative effects of survival and reproduction on population dynamics of emperor geese. Journal of Wildlife Management 61:191–200.
- SEARS, J., AND A. HUNT. 1991. Lead poisoning in mute swans, *Cygnus olor*, in England. Wildfowl Supplement No.1: 383-388.
- SMITH, P. G. R., V. GLOOSCHENKO, AND D. A. HAGAN. 1991. Coastal wetlands of three Canadian Great Lakes: inventory, current conservation initiatives, and patterns of variation. Canadian Journal of Fisheries and Aquatic Science 48: 1581–1594.
- WALTER, P. J., P. J. BACON, AND S. SEARS. 1991. An analysis of mute swan, *Cygnus olor*, breeding data. Wildfowl Supplement No.1:151-156.
- WELLER, M. W. 1969. Potential dangers of exotic waterfowl introductions. Wildfowl 20:55–58.
- WHILLANS, T. 1982. Changes in marsh area along the Canadian shore of Lake Ontario. Journal of Great Lakes Research 8: 570–577.
- WIELOCH, M. 1984. Numbers and distribution of the mute swan *Cygnus olor* in Poland against the situation of this species in Europe. Acta Ornithologia 20: 187-240.
- WIELOCH, M. 1991. Population trends of the mute swan *Cygnus olor* in the Palearctic. Wildfowl Supplement No.1:22-32.
- WILLEY, C. H. 1968a. The ecology, distribution and abundance of the mute swan (*Cygnus olor*) in Rhode island. Thesis, University of Rhode Island, West Kingston, USA.
- WILLEY, C. H. 1968b. The ecological significance of the mute swan in Rhode Island. Transactions of the Northeastern Wildlife Conference 25:121-134.

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