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Reproductive Success of Exotic Mute Swans in Connecticut

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Mute Swans (*Cygnus olor*) are native to Eurasia and were introduced to North America, where free-ranging populations have existed since the early 1900s (Allin et al. 1987). Originally observed in New York, breeding populations of Mute Swans have expanded into all of the Atlantic coastal states from Maine to Maryland and also have become established in Michigan, Minnesota, Wisconsin, British Columbia, and Ontario (Willey and Halla 1972; Reese 1975, 1980; Allin et al. 1987; Knapton 1993). Allin et al. (1987) synthesized 33 years of population data on Mute Swans from the Atlantic Flyway and estimated a 1987 population of 5,300, with most of the birds in New York, Connecticut, Rhode Island, and New Jersey. In the southern New England states of Massachusetts, Rhode Island, and Connecticut, Mute Swans constitute a single population with considerable interchange of individuals among states (Willey and Halla 1972).

During the 1960s and 1970s, the Chesapeake Bay population nested mostly on estuaries and tidal rivers (Reese 1975, 1980), as did the southern New England population (Willey and Halla 1972, Kania and Smith 1986). For instance, 90% of the Mute Swans in Rhode Island in 1967 nested on estuaries, and no nests were more than 5 km inland (Willey and Halla 1972). Since then, large numbers of Mute Swans in southern New England have started breeding at inland sites on lakes and ponds.

Expanding Mute Swan populations may have detrimental effects on native biota. One concern is the influence of swan herbivory on aquatic vegetation (Willey and Halla 1972, Reese 1975, Allin et al. 1987, Conover and Kania 1994) and associated macro-invertebrates (Krull 1970); another is that Mute Swans are aggressive toward other waterfowl species (Willey and Halla 1972, Kania and Smith 1986, Allin et al. 1987, Conover and Kania 1994). Because many native species of waterfowl nest at inland sites, Mute Swans may pose more of a threat to native avifauna at inland sites than at estuaries and tidal rivers (Willey and Halla 1972, Kania and Smith 1986, Conover and Kania 1994).

The present study was conducted to measure reproductive success of the portion of the Mute Swan population that nests in Connecticut and to determine whether Mute Swans nesting on lakes and ponds are as successful as those nesting on estuaries and tidal rivers. Despite the increase in Mute Swan numbers in North America, little is known about their reproductive biology. Reese (1975, 1980) recorded population levels and reproductive success of Mute Swans on Chesapeake Bay from 1968 to 1978. To our knowledge, the only subsequent study of Mute Swans in North America was conducted in southern Ontario by Knapton (1993).

Methods.—Mute Swan nesting data were collected in Connecticut from 1982 to 1990. The study area extended from the Housatonic River to the Connecticut River and included most of the nesting Mute Swans in Connecticut. Population trends were monitored using data from Audubon Christmas Bird Counts in Connecticut and from midwinter waterfowl counts conducted by the Connecticut Department of Environmental Protection using observers in fixed-wing aircraft.

Nests were located during coastal flight surveys conducted each spring by the Connecticut Department of Environmental Protection. Mute Swans nests are readily identifiable from the air owing to the large size and bright white plumage of adult swans. Additional nests were located by ground and boat surveys and by reports from local citizens. We believe that coverage of the study area was complete and that nearly all nests were located.

For each nest, we counted the number of eggs or cygnets present and recorded the presence or absence of parents. Most nests were visited every two weeks. Each nest was classified into one of two habitat types: lakes and ponds (hereafter "lakes") or tidal rivers and estuaries (hereafter "estuaries"). We defined clutch size as the maximum number of eggs observed in a nest and brood size as the maximum number of cygnets observed per swan pair. The maximum number of cygnets was always observed on

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the first visit after all cygnets hatched (i.e. we observed no adoptions, "gang" brooding, or creching). Cygnets that survived to 1 September were considered to have fledged.

Nests were incubated constantly; hence, the absence of an adult at the nest indicated that a nest had terminated. To determine a nest's fate, we located the parents in their territory as soon as incubation ceased and checked for the presence of cygnets. We confirmed nest failures by checking the nest to see if any eggs had hatched. We distinguished between hatched and depredated eggs by the presence of detached shell membranes (Klett et al. 1986).

We estimated nesting success, defined as the probability of a nest surviving the incubation period to produce at least one cygnet (Johnson et al. 1992), using both the "apparent" (proportion of nesting attempts that were successful) and the Mayfield (Mayfield 1961, 1975) methods. The Mayfield method is based on estimating daily survival rate (DSR) during the time nests are exposed to risk and ascertaining the outcome of the attempt during the observation period. In most studies, this observation interval (exposure days) for successful nests is the number of days between discovery of the nest and the estimated hatching date. The latter is determined by estimating the age of eggs when found and subtracting this value from the mean number of days in the laying and incubation periods for the species in question (Klett et al. 1986).

The exact date on which a nesting attempt terminates usually is unknown if the nest is not visited daily. Under these conditions, exposure days for successful nests are derived by summing (1) known exposure days (number of days between nest visits when the nest was active), and (2) probable exposure days based on the estimated hatching date (Klett et al. 1986). Exposure days for unsuccessful nests are determined by adding (1) known exposure days, and (2) the number of days between the last visit when the nest was active and the first visit after it failed divided by two. We used this method to determine exposure days for unsuccessful nests, but we did not use the estimated hatching date to determine the exposure period for successful nests because we were unable to age cygnet embryos accurately, and we could not determine hatching dates reliably. Instead, we determined the probable exposure days for successful nests by dividing by two the number of days between our last visit to an active nest and the first visit after the eggs had hatched. Usually, we checked nests every three to four days when hatching was imminent, so that differences in exposure days based on estimated hatching dates and our method were minor.

Bellrose (1980) reported that the incubation period for Mute Swans was 36 to 38 days and that they laid eggs every 36 to 48 h. Willey and Halla (1972) reported that the incubation period for Mute Swans lasted 39 days and that eggs were usually laid daily. Based on these data, we assumed that the incubation period was 38 days and the laying period was 8 days (36 h $\times$ 5.6, which was the mean clutch size minus one). Hence, we raised DSR to the 46th power to determine nesting success.

We defined brood success as the probability of at least one cygnet in a brood surviving to fledge and estimated it using the apparent and the Mayfield methods. For the latter, we calculated a mean DSR for broods and then raised this to the 120th power (120 days equals fledging age in Mute Swans; Willey and Halla 1972, Reese 1975, Bellrose 1980).

All nests were checked after incubation ceased. Egg survival was defined as the proportion of eggs in successful nests that hatched (Johnson et al. 1992). Successful nests were those from which at least one egg hatched. Egg survival is referred to by some authors as hatching rate (Willey and Halla 1972). Eggs left in the nest after incubation ceased were considered abandoned. We opened most of these eggs to check for embryo development. We considered any missing eggs to have been depredated. Cygnet survival was defined as the proportion of cygnets that fledged from successful broods (i.e. at least one cygnet fledged). The probability of an egg surviving to fledging was calculated by multiplying nesting success, egg survival, brood success, and cygnet survival. This method follows Johnson et al. (1992) except that they combined brood success and cygnet survival into a single term called "survival rate of young." Flint et al. (1995) calculated brood success and chick survival separately, and we have followed their approach because it provides more information and symmetry with treatment of losses during the incubation period. Furthermore, the survival rate of young can easily be calculated by multiplying brood success by chick survival.

Results were analyzed by summarizing data for each year to obtain yearly means for each parameter. These means were then used as the sampling unit and also were combined to calculate a grand mean and standard error. To examine the effect of habitat, we used the apparent method as the most accurate estimate of nesting success and brood success, based on the reasoning of Johnson and Shaffer (1990). We compared the yearly means obtained from swans nesting on lakes with those from swans nesting on estuaries using one-way ANOVA (df = 1 and 16). The fate of individual eggs was examined using a Chi-square test of independence to determine whether there was a habitat effect on the number of (1) hatched versus unhatched eggs, (2) abandoned versus unabandoned eggs, (3) depredated versus nondepredated eggs, and (4) on the proportion of abandoned eggs that showed signs of development.

Results.—During this 9-year study, the Mute Swan population in Connecticut increased by more than 50% (Fig. 1). We observed 377 breeding attempts in

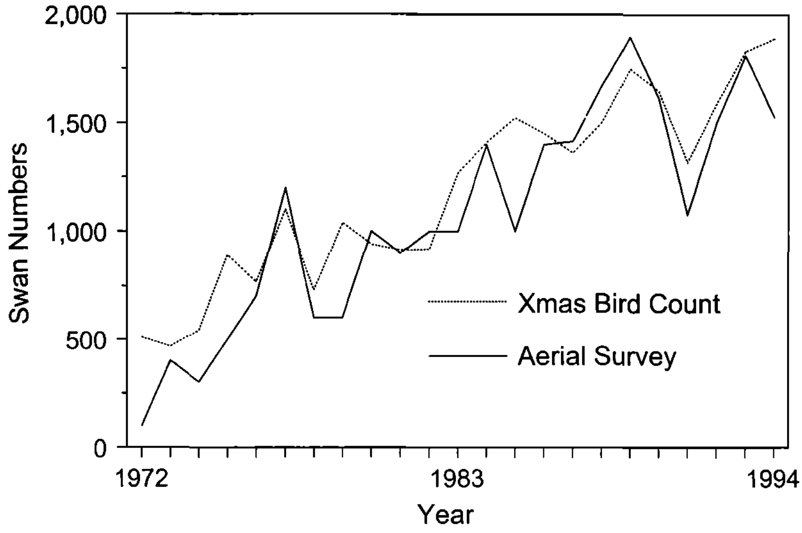

FIG. 1. Numbers of Mute Swans counted in Connecticut during the Audubon Society's Christmas bird count and during midwinter aerial surveys conducted by the Connecticut Department of Environmental Protection.

the study area from 1982 to 1990, with a low of 15 nests in 1982 and a high of 62 nests in 1988. Two renesting attempts were located, one in 1983 and the other in 1984. Both occurred on lakes, and both were successful.

Nesting success of Mute Swans was high throughout the study: all nests hatched during four of nine years (Table 1). Mean nesting success was 0.89 ± SE of 0.04 based on the apparent method and 0.81 ± 0.06 based on the Mayfield method. We determined the cause of failure for 33 nests: 46% were flooded, 27% were abandoned, 15% were disturbed by humans, 6% were lost to predators, and 6% failed after a parent died.

Brood success also was high; all broods succeeded during three years and the lowest brood success rate for any year was 0.78. Mean brood success was 0.94 ± 0.02 based on the apparent method and 0.92 ± 0.02 based on the Mayfield method.

Mean clutch size was 6.6 ± 0.1, initial brood size was 4.5 ± 0.3, and brood size at fledging was 3.2 ± 0.2 (Table 1). Mean egg survival was 0.69 ± 0.04. In successful nests, 71% of the eggs that failed to hatch had been depredated and 29% were abandoned. Most (59%) of the abandoned eggs showed no signs of development. Mean cygnet survival was 0.74 ± 0.03. The probability of an egg surviving to produce a fledged cygnet was 0.41 ± 0.03 based on the apparent method and 0.39 ± 0.02 based on the Mayfield method. Given a mean clutch size of 6.6, each nesting

TABLE 1. Reproductive success of Mute Swans in Connecticut from 1982 to 1990. The first three variables are mean values. Nesting success is the proportion of nests from which at least one egg hatched, egg survival is the proportion of eggs in successful nests that hatched, brood success is the proportion of broods from which at least one cygnet fledged, cygnet survival is the proportion of cygnets from successful broods that fledged, and complete survival is the proportion of eggs that produce fledged cygnets.

	Year									
Variable	1982	1983	1984	1985	1986	1987	1988	1989	1990	Overall[a]
Initial clutch size	6.5	6.8	6.7	6.6	6.9	6.7	6.6	6.2	6.5	6.6 ± 0.1
Brood size at hatching	2.5	5.3	5.1	4.6	5.4	4.3	4.2	5.1	4.2	4.5 ± 0.3
Brood size at fledging	2.5	3.9	3.0	3.0	3.7	3.7	3.0	2.8	3.4	3.2 ± 0.2
Nesting success	1.00	0.83	0.64	1.00	1.00	0.83	0.80	1.00	0.89	0.89 ± 0.04
Egg survival	0.39	0.78	0.76	0.70	0.79	0.64	0.64	0.82	0.66	0.69 ± 0.04
Brood success	0.85	0.94	0.92	1.00	0.92	1.00	0.94	1.00	0.92	0.94 ± 0.02
Cygnet survival	1.00	0.74	0.59	0.66	0.69	0.86	0.70	0.54	0.80	0.74 ± 0.01
Complete survival	0.33	0.45	0.26	0.46	0.50	0.46	0.34	0.44	0.43	0.41 ± 0.03

[a] $\bar{x}$ ± SE.

pair of Mute Swans produced a mean of 2.7 fledged cygnets. This value is lower than the mean brood size at fledging of 3.2 because the latter does not take into account pairs that lost their complete clutch or brood.

Nesting success was identical on lakes and estuaries, with a mean nesting success of 0.89 ± 0.05 in each habitat ($F = 0.00$, $P = 0.96$). Mean clutch size on lakes (6.8 ± 0.1) and on estuaries (6.3 ± 0.2) was similar ($F = 3.43$, $P = 0.08$), as was egg survival on lakes (0.70 ± 0.01) and on estuaries (0.67 ± 0.01; $F = 0.26$, $P = 0.62$). Habitat did not affect the proportions of eggs that were unhatched ($\chi^2 = 0.30$, $P = 0.59$) or abandoned ($\chi^2 = 0.74$, $P = 0.19$), or the proportion of abandoned eggs that exhibited signs of development ($\chi^2 = 0.61$, $P = 0.43$).

Mean brood success also was similar in the two habitats (lakes, $\bar{x} = 0.95 \pm 0.02$; estuaries, $\bar{x} = 0.93 \pm 0.03$; $F = 0.14$, $P = 0.71$). Mean brood size at hatching was 4.8 ± 0.4 on lakes and 4.2 ± 0.3 on estuaries ($F = 2.06$, $P = 0.17$), and mean brood size at fledging was 3.1 ± 0.2 on lakes and 3.2 ± 0.2 on estuaries ($F = 0.33$, $P = 0.57$). Cygnet survival on lakes (0.68 ± 0.01) and estuaries (0.81 ± 0.01) did not differ significantly ($F = 2.87$, $P = 0.11$). The probability of an egg surviving from incubation to fledging was similar ($F = 0.80$, $P = 0.38$) for swans nesting on lakes 0.39 ± 0.04 and estuaries 0.43 ± 0.03.

Discussion.—The apparent method can overestimate nesting success because nests that fail before they are found are not detected. For this reason, most waterfowl studies in North America use the Mayfield method (Mayfield 1961, 1975). However, this method can also result in biased estimates because it assumes that daily survival rate is constant throughout the incubation period, which is rarely the case. Johnson and Shaffer (1990) found that the Mayfield method is the preferred method in most situations but that the apparent method is more accurate when nests are on islands, when nests are conspicuous, or when losses are likely to be catastrophic. Because Mute Swan nests meet all of these conditions (46% of nest failures resulted from floods), we believe that the apparent method provided the most accurate estimate of nesting success. The apparent method also has been used in every Mute Swan study known to us. However, because the Mayfield method is so widely used in other studies, we provided nesting-success estimates from both methods so that our results are comparable with those from other studies.

For most waterfowl species, it is difficult to locate broods and to keep track of individual brood members when several broods occupy the same area. In contrast, Mute Swan broods are easy to locate because the adults are so conspicuous, and it is easy to determine the fate of broods because the parents maintain large territories from which they exclude all other swans (Conover and Kania 1994). For these reasons, we were able to estimate brood success, cygnet survival, and the probability of an egg producing a fledged cygnet.

Based on the apparent method, 89% of Mute Swan nests in Connecticut were successful, which is higher than values reported on Chesapeake Bay or in Europe. In England and Scotland, the greatest losses resulted from human predation (Eltringham 1963, Reynolds 1965, Minton 1968, Coleman and Minton 1980). We confirmed the loss of only six nests to egg predators (0.2% of all nesting attempts) and only five to human disturbance (0.1%), perhaps because many swans nested on marshes and islands where access by mammalian predators and humans was limited. Also, Mute Swans are aggressive nest defenders. The most common mammalian predators on waterfowl eggs in Connecticut (Conover 1990) were striped skunks (*Mephitis mephitis*), opossums (*Didelphis virginiana*), and raccoons (*Procyon lotor*), and swans appeared to be effective in deterring these species. On four occasions, mammalian predators destroyed Canada Goose (*Branta canadensis*) or Mallard (*Anas platyrhynchos*) nests within 10 m of a swan nest without taking any swan eggs.

Flooding was the main cause of nest failure for Mute Swans on Chesapeake Bay (Reese 1980) and during an earlier study in southern New England (Willey and Halla 1972) and accounted for 46% of all nest failures in our study, with most of the losses occurring during one year (1984). The mean clutch size in our study (6.6) tended to be higher than that reported for European populations of Mute Swans (4.9 to 6.6; Campbell 1960, Reynolds 1965, Bacon 1980, Perrins and Ogilvie 1981) and for this same population in 1967 (5.9; Willey and Halla 1972).

The proportion of eggs that hatched (0.61) was higher than that reported in this population earlier (0.50; Willey and Halla 1972) or on Chesapeake Bay (0.49; Reese 1980). The proportion of cygnets that fledged was 0.69, versus 0.82 at both Chesapeake Bay (Reese 1980) and Ontario (Knapton 1993). In Europe, this probability ranged from 0.43 to 0.76 (see references above). We found that 41% of all eggs produced a fledged cygnet; similar figures have been reported on Chesapeake Bay (40%) and in England (39 to 41%; Reynolds 1965, Perrins and Ogilvie 1981).

During the nine years of our study, Mute Swan numbers in Connecticut continued to increase (Fig. 1), and reproductive rates ($\bar{x} = 2.7$ cygnets per nesting pair) were among the highest recorded in Mute Swans, suggesting that the population in southern New England was not close to carrying capacity. Mute Swans that first invaded southern New England nested in estuaries and tidal rivers. In the last 20 years, they have expanded their range into freshwater lakes and ponds. Our results indicate that clutch size does not differ between the two habitats and that swans nesting on lakes and ponds are just as successful and productive as those nesting on tidal rivers and estuaries. The ability of Mute Swans to colonize freshwater sites may lead to further range expansion in North America. Expansion into freshwater habitats also may increase the threat that Mute Swans pose to native waterfowl (Kania and Smith 1986, Allin et al. 1987).

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