DEMOGRAPHY OF EUROPEAN MUTE SWANS
IN CHESAPEAKE BAY

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ABSTRACT.—Reproductive success, population expansion, and individual life histories of European Mute Swans (*Cygnus olor*) were monitored annually in Chesapeake Bay after a pair of mated, pinioned swans escaped confinement and began nesting in the wild there in 1962. Of the females, 4% paired before their first birthday, and 13% nested as 1-yr-olds. No males paired before their first birthday, and only 1.7% nested as 1-yr-olds. In 1969–79, 94% of the nests contained eggs, and young fledged from 58%. The average clutch size was 6.2, with 49% of the eggs hatching. The average brood size was 3.9, and 82% of the hatchlings fledged. An average of 2.2 young fledged from nests with eggs. Data presented indicate that reproductive success improves with both age and nest attempts 1 through 4. Flooding was primarily responsible for nest failure, and marine turtles took many hatchlings. Relaying occurred if nests failed before 10 May. Gray-brown plumage characterized 73% of the hatchlings. Mortality of leucistic young was double that of gray-brown young. Postfledging mortality rates for both sexes were 16–17% before the first birthday, dropped to half that during age 1, and to less than 7% annually thereafter. Females survived slightly better than males. Collision with overhead utility wires was the most important known cause of mortality. Swans 2 yr old or older constituted 52% of the population in 1970–78, but only 35% of the population nested. Males predominated in all age classes. Life table analysis shows that the swan population is experiencing unrestricted growth. Age-specific survival rates indicate that 50% of those born to the entire population will survive through age 7, and about 6% of the females and 1% of the males will reach 50 yr of age. Age-specific birth rates for 1- and 2-yr-old females was less than one young; this rate was 2.0 or better in later age classes, however. The net reproductive rate shows that females will replace themselves by age 4, replace themselves 10 times by age 23, and 14.5 times by age 50. The mean rate of population increase was 42% annually during the first decade and 27% annually during the first 7 yr of the second decade (1973–79). *Received 14 June 1978, accepted 14 January 1980.*

FIVE (3 ♂, 2 ♀) pinioned European Mute Swans (*Cygnus olor*) escaped captivity from impoundments at waterfront estates along the Eastern Bay tributary of east central Chesapeake Bay in 1962. A pair of these swans successfully bred there in the wild that summer, and the flock increased their number to 18 by 1968 and 151 by 1974 (Reese 1969, 1975).

The Chesapeake Bay is one of the primary waterfowl wintering areas in the Atlantic Flyway. A large sedentary population of an aggressive, vegetarian waterfowl, individuals of which are larger than any of our native species, could have a detrimental effect on both the ecology of the Chesapeake Bay and the future of native waterfowl. This study monitored nest success and population expansion of the escaped swans and was later expanded to include distribution, seasonal movements, life histories, molt, feeding habits, social organization, behavior, and population dynamics in view of the species' potential as a nuisance. In this paper I analyze the demography of the Chesapeake population through 1979.

STUDY AREA AND METHODS

All Chesapeake tidal waters north of latitude 38°25'N were surveyed from a 300-m altitude in a Cessna 172 in March, April, July, August, and October of 1975–78 to coincide with the establishment of new territories, peak incubation, prefledging, molting, and fall distribution of the swans. Surveys at other times and in other years were sometimes made to monitor movements, distribution, or feeding areas. Ground surveys were frequently conducted in areas of swan concentrations throughout the year. The

TABLE 1. Age at first pairing (P) and nesting (N) of known-age European Mute Swans.

	0			1			2			3			4			5			6–20			Σn
	n	P	N	n	P	N	n	P	N	n	P	N	n	P	N	n	P	N	n	P	N	
FEMALES																						
1970[a]	3	0	0	1	0	0	2	2	2	1	1	1	1	1	1				3	3	3	11
1971	9	1	0	3	2	0	1	0	0	2	2	2	1	1	1				3	3	3	19
1972	10	2	0	6	2	1	2	2	2	1	1	0	1	1	1	1	1	1	3	3	3	24
1973	7	0	0	10	7	2	6	5	3	2	2	2	1	1	1	1	1	1	4	4	4	31
1974	15	1	0	8	2	0	9	8	5	6	5	5	2	2	2	1	1	1	5	5	5	46
1975	12	0	0	12	4	1	7	4	2	9	8	7	6	6	5	2	2	2	6	6	6	54
1976	27	0	0	8	6	3	11	10	6	8	7	6	9	8	7	5	5	5	8	8	8	76
1977	35	1	0	20	9	1	8	7	5	11	10	8	7	7	7	9	8	7	11	11	11	101
1978	18	0	0	28	6	5	16	9	8	8	7	7	8	8	8	7	7	7	18	17	17	103
Totals	136	5	0	96	38	13	62	47	33	48	43	38	36	35	33	26	25	24	61	60	60	465
Percent of age		4	0		40	14		76	53		90	79		97	92		96	92		98	98	
MALES																						
1970	8	0	0	0	0	0	2	2	2	2	1	1	1	1	1				3	3	3	16
1971	15	0	0	8	2	0	0	0	0	2	2	2	2	1	1	1	1	1	3	3	3	31
1972	5	0	0	16	3	0	4	3	2	2	1	0	1	1	1	1	1	1	4	4	4	33
1973	9	0	0	4	1	0	16	4	4	4	2	2	2	1	1	1	1	1	5	5	5	41
1974	24	0	0	16	0	0	4	2	0	15	4	4	4	4	4	2	1	1	6	6	6	71
1975	8	0	0	19	2	0	15	1	0	4	4	2	13	7	6	4	4	4	8	8	8	71
1976	22	0	0	5	1	0	19	11	7	14	8	6	4	3	2	10	8	8	9	9	9	83
1977	40	0	0	19	6	0	5	2	1	18	14	10	12	7	7	4	3	3	19	17	17	117
1978	29	0	0	28	2	2	16	9	8	3	2	2	14	12	12	10	7	7	18	13	12	118
Totals	160	0	0	115	17	2	81	34	24	64	38	29	53	37	35	33	26	26	75	68	67	581
Percent of age		0	0		15	2		42	30		59	45		70	66		79	79		91	89	

Age (yr)

[a] Calendar years begin on 1 October.

area of study centered in the eastern estuaries of Chester River, Eastern Bay, and Choptank River where swan activity was greatest. All swan territories and nests were visited by boat five or more times each nesting season in 1962–79. Eggs were marked with waterproof ink when first observed, and addled eggs and dead swans were collected for necropsy. Personal observations of swans nesting or feeding were solicited from local residents.

Since 1971, 422 swans have been marked with aluminum USFWS leg bands and auxiliary markers of coded plastic neck and tarsus bands. All nesting pairs and young were banded in 1971, and the progeny of all successful nests were banded each year thereafter. Unmarked swans over 1 yr old were sometimes captured for banding during the mid-1970's, and these swans were believed to be young fledged before 1971. Consequently, it is believed that nearly the entire Chesapeake population is banded. Neck bands were 8 cm wide and engraved in a contrasting color several times around with a 2.5-cm tall, vertical code of 2 letters and 2 numbers, as set forth by Sladen (1976). Tarsus bands were 4 cm wide with 1.5-cm high codes. Coded neck bands could be read as far away as 350 m with a 30–40× spotting scope, which permitted recognition of individual swans without recapture. Most of the data presented here were based on over 12,000 resightings of these marked swans.

The term "young" applies to prefledging swans, and "fledglings" were young with feathers necessary for flight (at least 110 days old) and less than 1 yr past fledging. Mute Swan young require 4 months of growth to fledge; this time was not counted toward their first birthday, so a 1 October anniversary date was used here to correspond to the time when young were capable of leaving the care of their parents and becoming independent members of the population. Ages given signify that the swan has lived past that birthday (x) but has not yet reached birthday $x + 1$. Swans in their first year after fledging are denoted age 0; a 1-yr-old swan is in its second breeding season after hatching, and so on for successive ages. Precaution should be taken throughout the paper not to consider given ages as synonymous with the same number of breeding seasons past hatching. Calculations of the survival and fecundity rate functions follow those set forth by Mertz (1970).

RESULTS

Age at first pairing and nesting.—Table 1 shows that 4% of the female swans paired when less than 1 yr old and 13% nested as 1-yr-olds. Most paired at age 2 and began nesting by their third year. No males paired before their first birthday, and only 1.7% nested as 1-yr-olds, indicating that females begin breeding earlier than males. Nesting did not take place until 4 and 5 yr of age for 3 females and 11 males, while 2 males had not nested by their seventh year. Time between pairing and nesting for 87 swans was 1 yr for 63%, less than a year for 28%, and 2 yr for 9%.

I found incestuous pairing and nesting in 6 of 32 banded pairs in 1972–79. Siblings from the same broods formed two pairs, and three pairs involved siblings from different broods. One male paired and nested with one of his progeny after loss of his mate.

Reproductive success.—There were 53 mated pairs of swans on territories in an area about 800 km² along the shores of eastern Chesapeake Bay in 1979. The land in this area is deeply indented by shallow-water tributaries, forming over 2,000 km of shoreline suitable for supporting a much greater density of nesting swans as the population grows. The breeding season commences in late February with courtship display and increased aggression in defense of territories. The young have all fledged by October. One nesting attempt is made annually, but some pairs relay if the original clutch is lost. A complete nesting chronology was presented in Reese (1975).

A total of 210 nesting attempts was observed during 1969–79 (Table 2). Eggs were found in 94% of these nests, young in 65%, and fledglings in 58%. A few nests without eggs were counted in the total, because pair behavior and nest condition strongly suggested that a clutch had been laid but lost before my visit.

Average clutch size ranged from 4.8 to 8.0 annually and was 6.2 for 151 clutches

TABLE 2. Nest success of European Mute Swans in Chesapeake Bay, 1969–79.

	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	Mean
Number of nests	5	3	7	7	10	10	17	22	38	40	51	
Percent of nests with:												
Eggs	80	100	100	86	100	100	100	96	90	93	96	94(210)[a]
Young	80	100	100	71	50	90	47	82	58	65	59	65
Fledglings	80	100	100	71	50	80	41	73	53	48	55	58
Percent of eggs:												
Hatched	63 (19)	47 (30)	75 (40)	54 (48)	27 (71)	75(61)	35(102)[b]	58(117)	52(196)	44(174)	44(260)	49(1,101)
Fledged	58	37	68	40	23	67	25	53	41	29	39	40
Percent of hatchlings fledged	92(12)	79(14)	90(30)	73(26)	84(19)	89(46)	70(30)	91(68)	79(101)	67(76)	89(113)	82(535)
Average clutch size	4.8(4)	6.3(3)	5.3(7)	8.0(6)	6.6(10)	6.1(10)	5.6(14)	6.9(14)	7.1(22)	5.5(25)	6.1(36)	6.2(151)
Average brood size	3.0(4)	4.7(3)	4.3(7)	5.2(5)	3.8(5)	5.1(9)	3.8(8)	3.8(18)	4.6(22)	2.9(26)	3.8(30)	3.9(137)
Average number fledged per nest with eggs	2.8	3.7	3.9	3.2	1.6	4.1	1.2	3.0	2.4	1.4	2.1	2.2

[a] Figures in parentheses are sample sizes.
[b] Seventeen of these eggs were collected for study and excluded from ratio calculations.

TABLE 3. European Mute Swan egg (E) and young (Y) losses in 1969–79.

	1969		1970		1971		1972		1973		1974		1975		1976		1977		1978		1979		Totals	
	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y	E	Y
Disappeared between nest visits	7	1	2	3	6	2	13	7	16	3	5	5	9	6	21	6	68	16	32	21	80	10	259(44)[a]	80(84)
Flooded by high tides			13		3				13		2		11		5		12		10		16		85(15)	
Found as fragments									5		3		19		2		3		14		14		60(10)	
Found outside nest									2		2		15		8		4		15		7		53(9)	
Abandoned							7		3				1		10		8		15		8		52(9)	
Added			1		1		2		6		3				3						7		23(4)	
Predator																			7	2	15		22(4)	2(2)
Collected for study													17										17(3)	
Dead on nest						1								3						1		2		7(7)
Unknown disease																		5		1				6(6)
Destroyed by humans																			5				5(1)	
Stolen by humans									5														5(1)	
Accidentally broken									2														2	
Totals	7	1	16	3	10	3	22	7	52	3	15	5	72	9	49	6	95	21	98	25	147	12	583	95

[a] Figures in parentheses indicate percent of total.

during 1969–79 (Table 2). The largest clutch I found was 10 eggs. The percentage of eggs that hatched varied from 27% to 75% annually and averaged 49%. The percentage of eggs resulting in fledglings ranged from 23% to 68% annually and averaged 40%. The average brood size ranged from 2.9 to 5.2 annually and averaged 3.9. The largest brood I found was 9 young. Survivorship of young to fledging ranged from 67% to 92% annually and averaged 82%. The average number of fledglings per nest with eggs ranged from 1.2 to 4.1 annually and averaged 2.2.

Losses of eggs and the causes of loss are shown in Table 3. Most notable were eggs that disappeared between nest visits, that were flooded by high tides, and that were found outside the nest or as fragments. Eggs were sometimes found trapped in nearby marsh vegetation, which indicated that some eggs were flooded into tributaries and carried away by tidal actions. Direct predation on swan eggs is rare, because wild predators in the Chesapeake area are smaller than the swans and incapable of breaking the eggshell once they scare the swans away. Losses occur when eggs are knocked about or left outside the nest. Someone stole five eggs for monetary gain, and another person drilled holes in five eggs to control reproductive success. One swan accidentally broke two of its eggs while defending the nest against the investigator.

A second clutch was laid all 13 times a first clutch was lost before 10 May, but relaying did not take place after the loss of four first clutches after that date. Between 11 and 30 days transpired between loss of the first clutch and laying of the first egg in the second clutch. This period averaged 18 days for 11 relayings. The first clutch may have been incomplete in eight relaying incidences, as each one contained less than 4 eggs. The first clutch averaged 6.6 eggs and the second 5.2 eggs, for 5 cases where size of both complete clutches was known. Success of second clutches was 31%, with 29% of the eggs hatching. One pair laid two unsuccessful clutches in its first year as nesters, and another pair produced 16 eggs in two clutches during its fourth year of nesting. Second clutches were included in Table 2, but not counted as additional nests or used for clutch-size calculations.

Table 3 also lists some of the circumstances associated with losses of the Chesapeake young. Most notable were young disappearing between my surveys. People observing swans daily near their waterfront estates reported young swans being preyed upon by marine turtles (Chelydra serpentina, Malaclemys terrapin). Most young swans that disappeared were less than 40 days old; turtles or other predators may be responsible for many of these losses. Several young in two broods appeared injured or sick before disappearing in 1977, and I cannot offer an explanation for these losses. Young found dead on nests were all hatchlings that succumbed to chilling during rainy periods.

Gray-brown plumage characterized 73% of 377 hatchlings. Survivorship to fledging was 87% for the gray-brown young and 73% for white young, a significant difference ($\chi^2 = 10.89, P < 0.01$). I observed four incidences where families including dark young ostracized the only white brood member (all 50+ days old), and two of these white young eventually perished.

Fecundity rates for consecutive annual nest attempts by known-age swans are presented in Table 4, which indicates that success improves with both age and nest attempts 1 through 4. One-way analysis of variance tests between means for each age-nest-attempt combination in Table 4 showed that clutch size differences between 2-, 3-, and 4-yr-olds' second attempt and 4-, 5-, 6-, and 20-yr-olds' fourth attempt were

TABLE 4. Average number of eggs, young, and fledglings per annual nest attempt by known-age female European Mute Swans.

Nest attempt	Age (yr)						Nest attempt means
	1	2	3	4	5	6–20	
1	4.9[a] (10)[b]	4.6 (15)	5.4 (8)	5.0 (2)			4.9 (35)
	1.0 (13)	1.1 (22)	1.7 (11)	3.0 (2)	3.0 (1)		1.2 (49)
	0.77 (13)	0.50 (22)	1.2 (11)	2.0 (2)	3.0 (1)		0.84 (49)
2		3.2 (5)	5.8 (11)	6.2 (5)		3.0 (1)	5.2 (22)
		0.86 (7)	2.8 (13)	3.1 (8)	2.0 (1)	1.0 (1)	2.4 (30)
		0.86 (7)	2.2 (13)	2.4 (8)	2.0 (1)	0.0 (1)	1.9 (30)
3			7.2 (6)	6.4 (10)	6.7 (3)	7.0 (1)	6.7 (20)
			3.7 (6)	3.1 (11)	2.0 (3)	7.0 (1)	3.3 (21)
			2.8 (6)	2.8 (11)	2.0 (3)	7.0 (1)	2.9 (21)
4				7.0 (4)	8.5 (2)	5.0 (3)	6.7 (9)
				3.3 (4)	5.0 (4)	3.0 (3)	3.8 (11)
				3.0 (4)	3.5 (4)	2.3 (3)	3.0 (11)
5–15					6.0 (3)	6.6 (37)	6.7 (40)
					3.7 (3)	3.1 (39)	3.1 (42)
					2.3 (3)	2.4 (39)	2.4 (42)
Age means	4.9 (10)	4.3 (20)	6.0 (25)	6.3 (21)	6.9 (8)	6.4 (42)	5.9 (126)
	1.0 (13)	0.90 (29)	2.6 (30)	3.1 (25)	3.5 (12)	3.1 (44)	2.5 (153)
	0.77 (13)	0.59 (29)	2.0 (30)	2.6 (25)	2.7 (12)	2.4 (44)	1.9 (153)

[a] Triplet columnar listing represents average number of eggs, young, and fledglings, respectively.
[b] Figures in parentheses indicate sample size.

significant ($P < 0.02$ and 0.03, respectively), suggesting possible age effect. The number of young per nest for 2-, 3-, and 4-yr-olds' second attempt approached significance ($P < 0.07$). Variables for ages and nest attempts were then pooled for further ANOVA testing. Age effects were tested with the following comparisons: ages 2 vs. 3 for attempts 1–2, ages 3 vs. 4 for attempts 1–2, ages 3 vs. 4 for attempts 2–3, and ages 4 vs. 5 for attempts 3–4. Nest-attempt effects were tested via the following contrasts: attempts 1 vs. 2 for ages 2–3, attempts 1 vs. 2 for ages 2–4, attempts 1 vs. 2 for ages 3–4, attempts 2 vs. 3 for ages 3–4, and attempts 3 vs. 4 for ages 4–5. The difference between ages 2 vs. 3 for attempts 1–2 was significant for clutch size ($P < 0.01$), young per nest ($P < 0.02$), and fledglings per nest ($P < 0.02$). Differences between nest attempts 1 vs. 2 for ages 2–4 were significant for young per nest ($P < 0.04$) and fledglings per nest ($P < 0.02$), and attempts 1 vs. 2 for ages 2–3 were significant for fledglings per nest ($P < 0.05$). Clutch sizes for attempts 3 vs. 4 for ages 4–5 approached significance ($P < 0.09$). These comparisons indicate an effect associated with experience. A two-way ANOVA test between 2- and 3-yr-old females and nest attempts 1 and 2 showed that age effect was significant for clutch size ($P < 0.005$), young per nest ($P < 0.03$), and approached significance for fledglings per nest ($P < 0.06$). A two-way test between swans 3 and 4 yr of age and attempts 2 and 3 was nonsignificant ($P > 0.05$).

Postfledgling survivorship.—Table 5 gives the number of known-age swans that were marked with auxiliary bands each year and the number resighted in subsequent years. Male survivorship from one age to the next (age x divided by $x - 1$) ranged between 83 and 100% and averaged 90% for the 9-yr period 1970–78, while females ranged between 84 and 100% and averaged 89%.

The oldest swans in the Chesapeake population were the five pinioned birds that gave rise to the present population. Of the 3 males, one lived at least 9 and one 18 years, while one 15-yr-old male was still alive in 1979. Of the two females, one lived

TABLE 5. Resighting of European Mute Swans marked with auxiliary bands.

Year	Number banded	Years resighted								
		1	2	3	4	5	6	7	8	9
FEMALES										
1970[a]	2	2	1	1	1	1	1	1	1	1
1971	9	7	7	7	7	6	6	6	5	
1972	10	9	8	8	8	8	7	7		
1973	7	6	6	6	5	5	5			
1974	15	12	12	12	9	8				
1975	12	10	9	9	8					
1976	27	21	17	17						
1977	35	29	27							
1978	18	18								
Total	135	114	87	60	38	28	19	14	6	1
MALES										
1970	6	6	5	5	5	5	4	4	4	3
1971	15	14	14	13	11	9	9	9	8	
1972	5	4	4	4	4	4	3	3		
1973	9	8	7	7	7	6	5			
1974	23	18	18	17	15	15				
1975	8	6	6	5	3					
1976	22	20	19	16						
1977	40	31	25							
1978	29	23								
Total	157	130	98	67	45	39	21	16	12	3

[a] Calendar years begin on 1 October.

at least 12 and the other 20 yr, and the latter nested for 16 consecutive yr. The oldest flighted swans are a living pair known to be at least 16 yr old; 1979 was their 13th consecutive year of nesting.

Table 6 lists the causes of mortality for 36 postfledging Mute Swans during 1969–79. The most important known cause of mortality was overhead utility cables across tributaries and narrow portions of land. Swans that collided with cables were electrocuted or broke their necks in the collision or fall. Swans surviving collisions were temporarily injured and vulnerable to predation. Of the 10 fatalities found beneath overhead utility cables, 7 were less than 1 yr old and 7 were females. Gross necropsies of other fatalities revealed white nodules coating the respiratory system from the trachea through the thoracic air sacs on one incubating female and on another that was simultaneously molting and brooding young. The infections of both swans

TABLE 6. Causes of mortality for some postfledging European Mute Swans in 1969–79.

Cause	Number	Females	Age (yr)
Unknown	12	3	0–5
Overhead utility cables	10	7	0–5
Dog	3	2	1–2
Respiratory infection	2	2	4–5
Intraspecific fighting	2		3–7
Circulatory infection	1	1	3
Severe weather	1	1	19
Lightning	1	1	3
Drowned	1		0
Alimentary compaction	1		0
Shot	1		3
Lead poison	1		19
Totals	36	17	

TABLE 7. Survival and fecundity rates of female European Mute Swans in Chesapeake Bay.

Age x (yr)	L_x	M_x	$L_x M_x$
0	0.844	0.0	0.0
1	0.765	0.05	0.038
2	0.726	0.16	0.116
3	0.689	0.79	0.544
4	0.653	1.20	0.784
5	0.620	1.24	0.768
6	0.588	1.18	0.694
7	0.558		0.658
8	0.529		0.624
9	0.502		0.592
10	0.476		0.562
11	0.452		0.533
12	0.428		0.505
13	0.406		0.479
14	0.385		0.455
15	0.366		0.431
16	0.347		0.409
17	0.329		0.388
18	0.312		0.368
19	0.296		0.349
20	0.281		0.331
25	0.216		0.255
30	0.166		0.195
35	0.127		0.150
40	0.098		0.115
45	0.075		0.089
50	0.058		0.068
			Total (R_0) = 14.489

were characteristic of *Aspergillosis* and suggested asphyxiation during stress, but confirmation of the fungus species was not made by laboratory examination. A sickly female held captive several days before dying was infested with mallophaga and had microfiliariae in the blood, but the parasite species was not ascertained. One male killed both males in two adjoining territories and seriously injured the male of a third pair nearby while establishing his new territory among the other three established territories. One pinioned swan found dead on a frozen tributary during the severe winter of 1976–77 starved as a result of its limitations. A swimming female was struck by lightning during a thunderstorm, while four young and a mate at her side were unharmed. One swan drowned after suffering a head concussion when a flock resting on a frozen tributary stampeded towards food hand-outs just tossed into a hole cut in the ice near a private pier. One necropsied swan had a small, lead fishingline sinker and several lead shots in the gizzard.

Age and sex ratios.—Swans 2 yr or older constituted 30–61% of the population annually and averaged 52% for 1970–78; only 35% of the population actively engaged in nesting, however, and this portion ranged from 26 to 52% annually (calculated from data in Table 1). Swans 1 yr old or less dominated the population (55%) during 1970–74 but slipped to 46% thereafter as the population rapidly grew.

Males dominated all age classes in nearly all years, having their lowest mean ratio of 54% before the first birthday and increasing to 57% by age 2 and older (Table 1).
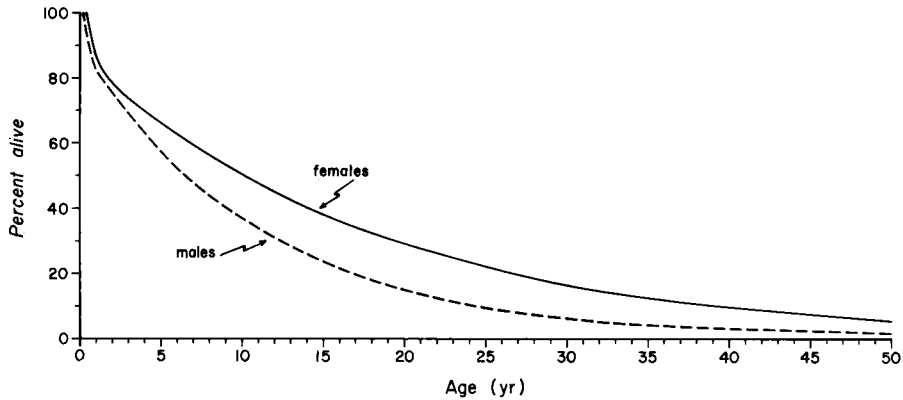
Fig. 1.   Survivorship (L_x) curves for European Mute Swans in Chesapeake Bay.

Life table functions.—Demographic functions of the Chesapeake Bay population of European Mute Swans given in Table 7 show that the population is presently experiencing unrestricted growth.

Age-specific survival rates $(L_x$, which denotes the probability that a newly fledged swan will survive to age x) indicate that about 6% of the females and 1% of the males will reach 50 yr of age (Table 7, Fig. 1). About 50% of those born in the entire population will survive to at least age 7.

Annual age-specific survival rates for both sexes dropped more before the first birthday (16–17% mortality) than at any other period (Table 7, Fig. 1). The survivorship of both sexes dropped an additional 8% during age 1. Age-specific survivorships for both sexes paralleled one another thereafter, with females surviving slightly better than males and both dropping 7% or less annually through age 4, and 2–5% in older age-classes. Sample sizes for ages 3–9 were smaller than desired for individual analysis, so the mean for these years (0.95) was used to calculate L_x after age 2.

Age-specific productivity for females showed that 1- and 2-yr-olds fledged less than 1 young per female while older females fledged 2.0 or better (Table 4). The age-specific birth rates $(M_x$, the expected number of female fledglings produced per female of age x) increased for each age class up to 6 yr old (Table 7). Sample sizes for older age classes were too small for individual analysis, so the mean productivity for ages 6–20 in Table 4 was used to calculate the age-specific birth rate for female swans 6 yr or older in Table 7.

Age-specific survival and birth rates show that new females entering the population contribute nothing to population growth during the first year but make their maximum annual contributions at ages 4–6 (Table 7). The net reproductive rate (R_0) denotes the number of females that a newly fledged female is expected to produce throughout her lifetime. This analysis indicates that nesting females will completely replace themselves by age 4, replace themselves 5 times by age 11, and 10 times by age 23. The net reproductive rate for females decreases considerably after age 20, with a cumulative R_0 of 14.5 by age 50.

The mean rate of population increase (calculated from observed census figures
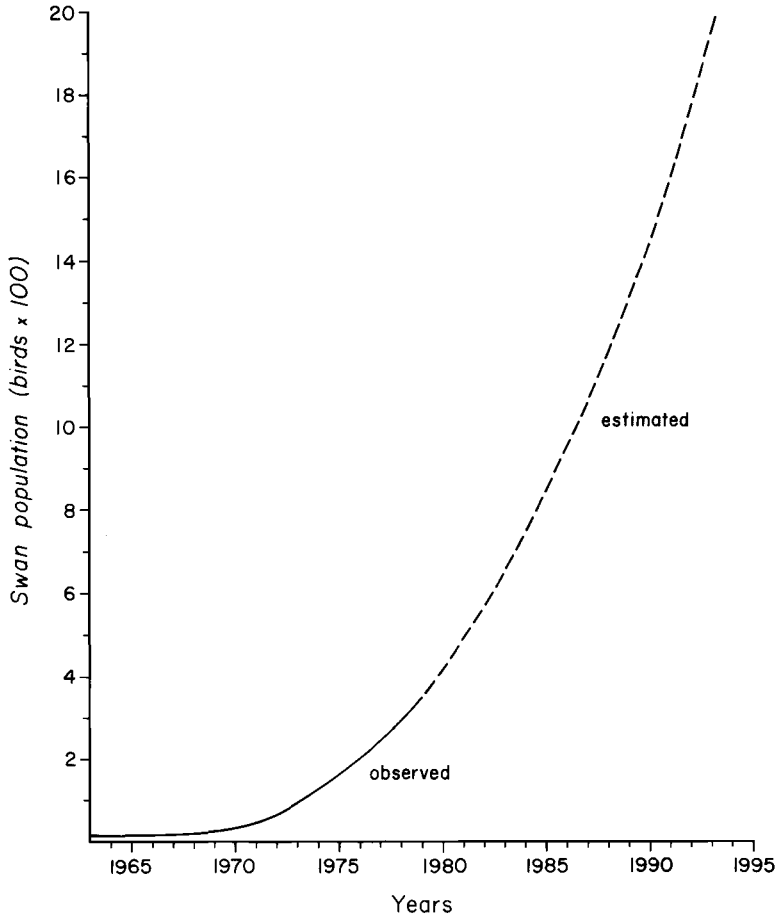
Fig. 2. Growth curve for European Mute Swan population in Chesapeake Bay.

plotted in Fig. 2) was 42% annually during the first decade, 27% during the first 7 yr of the second decade (1973–79), and 36% for the 17 yr since the original swans escaped into the wild.

DISCUSSION

Age at pairing and first nesting.—Age at pairing and first nesting by Mute Swans in Chesapeake Bay was similar to that noted in England. Both Perrins and Reynolds (1967) and Minton (1968) found that many Mute Swans in England paired during the second breeding season after birth (1 yr old) and nested for the first time in the third season, while others in the population had not paired or nested by season 6–7. Minton noted that 1 yr usually separated pairing and nesting but found 7 incidences of a 2-yr lapse. He also presented some pairings that suggested females begin to breed earlier than males.

Reproductive success.—Successes of nests in other studies were below the 1969–79 Chesapeake averages (Table 2). Willey and Halla (1972) found eggs in 76% of 257 nests studied in Rhode Island in 1962–67. Eltringham (1966) observed young

in 62% of 143 English nests in 1961, and Minton (1968) located young in 58% of 456 nests in 1961–67. Jenkins et al. (1976) reported that 45% of 343 Scottish nests in 1971–74 contained fledglings.

Other studies report egg success higher than the 49% hatching and 40% fledging of Chesapeake eggs (Table 2). Willey and Halla (1972) recorded that 87% of 142 eggs hatched in 1967. Reynolds (1965) found that 94% of 103 English eggs hatched and 48% of these eggs resulted in fledglings in 1964. Small sample sizes in some years and high egg or young losses in others caused annual variability in the number of eggs hatching and fledging in the Chesapeake population. Disparity in egg success between this study and others may be due to sample sizes, as Chesapeake averages were based on 11 yr of study and over 1,000 egg histories. The mean of 6.2 eggs for 151 Chesapeake clutches was slightly above the 5.6–6.1 reported in other studies (Paludan and Fog 1956, Campbell 1960, Eltringham 1963, Reynolds 1965, Perrins and Reynolds 1967, Willey and Halla 1972, Feiler 1974, Tenovuo 1975).

The mean of 3.9 young for 137 Chesapeake broods during 1969–79 was above the 3.1 and 3.5 found by Perrins and Reynolds (1967) and Minton (1968) but was well below the 4.3–5.6 reported by Berglund et al. (1963), Zajac (1963), Eltringham (1963), Willey and Halla (1972), and Feiler (1974). The latter studies had either much smaller sample sizes, covered only one season of investigation, or employed aerial surveys to count young. Any or all of these factors could cause an overestimation of the brood size.

In this study 82% of 535 young fledged, which is a better success rate than that reported in most other studies. Jenkins et al. (1976) noted 72% of the young fledged in the Outer Hebrides, Reynolds (1965) and Perrins and Reynolds (1967) found 50–51% success in England, and Willey and Halla (1972) gave 34% for Rhode Island. Berglund et al. (1963) estimated that 91% of the young fledged along coastal Sweden. The Jenkins and Berglund values were based on aerial censuses, while the other studies report a single year and much smaller sample sizes, all of which could add to the broad disparity between cited fledging successes.

The Chesapeake mean productivity of 2.2 young fledged per nest with eggs is comparable with the 2.0–2.5 found in Great Britain during 1955–67 (Rawcliffe 1958, Eltringham 1966, Perrins and Reynolds 1967, Minton 1968) but is considerably above the 1.4 given for Sweden (Berglund et al. 1963), Finland (Tenovuo 1975), and Outer Hebrides (Jenkins et al. 1976).

Perrins and Reynolds (1967) and Willey and Halla (1972) report flooding as the most common cause of nest destruction and failure, while Eltringham (1963) and Minton (1968) found human vandalism more important. Flooding by spring tidal waters was responsible for many egg losses in this study and is thus an important factor inducing relaying after loss of the first clutch. Reynolds (1965) and Willey and Halla (1972) recorded only three instances of relaying in predominantly nontidal nesting habitats. Minton (1968) attributed most losses to human vandalism, inducing 22 instances of relaying observed in largely nontidal nesting habitats; 55% of the relayings were successful. This was considerably above the 31% relaying success in the Chesapeake. Minton also noted that relaying does not normally take place after early June but did observe one pair that laid three clutches in one season.

Most of the studies cited above agreed that losses of young were most frequent during the first few weeks of life. Marine turtles were thought to be the most important factor hampering success of young in Chesapeake Bay and Rhode Island, but other studies offered no explanation for failure of young to survive.

Leucistic plumage characterized 17% of 377 Chesapeake young, which is very close to the 16% Munro et al. (1968) found in 488 Rhode Island swans. Kear (1972) reports that the white phase is rare in Britain and Scandinavia. Feiler (1974) found that the white phase constituted 6% of all young in the German Democratic Republic in 1971. European swan-farmers may be responsible for a higher leucistic ratio in North America because they selectively bred for the white-phase young, which had better sale value to New England estate owners in the early 1900's. Kear (1972) suggested that the usual gray-brown young are better camouflaged and also present a plumage pattern distinctly different from the white plumage of adults. White young lack these safeguards and thus are more susceptible to predation and parental harassment. These points were supported by the Chesapeake observations, which noted that mortality was 14% greater in white than gray-brown young and that white young were indeed sometimes harassed by their parents.

Postfledgling survivorship.—The survivorship values given here are believed to be very accurate, because nearly the entire population was marked with coded neck bands and the history of each individual was compiled by year-round resighting efforts each year. Band loss was not considered important in this study, as each swan had three separate coded bands, so band loss could be detected by resighting either of the remaining bands. Losses were restricted to neck bands, and most of these were quickly replaced through an active banding effort.

Collision with overhead utility cables was the most important mortality factor observed in this and other studies (Ogilvie 1967, Minton 1968, Willey and Halla 1972, Owen and Cadbury 1975). Mortality occurred most frequently in the March–April and October–November periods, which correspond to parental dispersal of fledglings from the natal area, dispersal of paired swans in search of territories, and first flights of fledglings. Ogilvie (1967) noted that most mortality occurred during similar periods in England.

Age and sex ratios.—Willey and Halla (1972) noted that swans 2 yr old or older composed 52% of the Rhode Island population in 1966–67, which is identical with the Chesapeake ratio.

Campbell (1960) found 35% of the British swan population nesting during a 1955 census, Eltringham (1963) noted 29% on a subsequent census in 1961, and Minton (1968) gives 30–39% for swans he studied in England during 1961–66. The proportion of the population that nested in these studies was comparable to the 35% found in the Chesapeake. Feiler (1974) found that 22% of the swan population nested in the German Democratic Republic in 1971.

Willey and Halla (1972) calculated that 58% of the combined age classes were males in Rhode Island in 1962–67, which is close to the 54–57% found among the Chesapeake age classes.

Life table functions.—I subjectively chose to calculate the age-specific survival rates to 50 yr (Table 7, Fig. 1), because that age was near the end of the calculated life expectancy of a female and close to the longevity records of 19- to 50-yr-old swans cited by Kortright (1942), Rydzewski (1962), and Kear (1972). Losses of inexperienced fledglings were responsible for the sharp drop in survival rates of both sexes prior to the first birthday (Table 7, Fig. 1). Of the females, 14% nested as 1-yr-olds, yet their survival rate did not differ from nonnesting males in the same age class. Appreciable numbers of males first began nesting at age 2, when one-third of the males and one-half of the females nested (Table 1). Male survival dropped 3%

below females at that time, and this disparity continued as a larger percentage of the males came into the nesting portion of the population. This suggests that there are greater risks for males than for females newly recruited into the nesting population. This may be true considering that the male swan's principal defense tactics involve making itself as conspicuous as possible to attract the attention of territory intruders, then driving them off with aggressive actions. Sharp annual increases in recreational boat use of tributaries and development of shoreline habitats has surely augmented the stress and risks for male swans defending territories.

Age-specific birth rates in this study were based upon the actual productivity (average number of young fledged per nest with eggs) observed for each age class (Table 4); thus, fecundity rates used in the analysis should be more accurate than those of studies using clutch-size values. Low age-specific birth rates in early age classes occurred because only 14% of the 1-yr-old females, 53% of the 2-yr-olds, and 79% of the 3-yr-olds nested (Table 1). By age 4, 92% of the females were nesting, and the potential for maximum birth rates was first realized.

Delayed maturity is characteristic of many waterbirds, but its significance is not fully understood. Ricklefs (1973) points out the possibility of restricting recruitment of young into the breeding population to a level compatible with adult losses. Female survivorship in this study was 84% by the first birthday, and dropped an additional 7% during age 1, and 5% or less each additional year through age 4. Annual decreases in survivorship never were more than 3% per year after age 4. Age 4 also marked the first time that over 80% of the females nested and overall survivorship dipped below 69%.

Reaching a net reproductive rate of 1.0 by age 4, the unusually high rates of 10.0 by age 23, and 14.5 by age 50, plus a life expectancy beyond that, indicate that the population is rapidly growing. The annual mean rate of population increase for swans during the first decade (1963–72) of nesting was 42% in the Chesapeake (Fig. 2) and 43% in Traverse Bay, Lake Michigan (1949–58, Gelston pers. comm.). In the second decade the rate dropped sharply to 15% (1959–68) in Michigan, while the Chesapeake rate was 27% for the first 7 yr (1973–79) of the second decade. The Chesapeake rate could be more comparable by the end of the second decade in 1982. Willey and Halla (1972) presented population totals that indicated a rate of 12% for the period 1963–67 of the second decade in the Rhode Island population. The Michigan rate dropped to 12% in the first 9 yr (1969–77) of the third decade and has averaged 23% since 1949. These comparisons suggest that under the present conditions, the Chesapeake population will continue substantial increases each year for several more decades.

If the Chesapeake population continued to increase at the overall observed rate of 36% annually, there would be 19,243 swans at the end of the third decade in 1992, which seems an unrealistic estimate. It has taken about three decades for the Michigan population to grow from a single nesting pair to about 1,000 swans. The mean rate of population increase during that time was almost identical to that observed during the first 17 yr of the Chesapeake population. Projecting the second and third decade Michigan rates onto the Chesapeake population after 1979 yields 611 swans at the end of the second decade in 1982 and 1,832 swans at the end of the third decade in 1992, which seems a more realistic estimate for the population at that time (Fig. 2).

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