

NEST SITE SELECTION BY MUTE SWANS
IN THE GRAND TRAVERSE BAY AREA,
MICHIGAN

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ABSTRACT

NEST SITE SELECTION BY MUTE SWANS IN THE GRAND TRAVERSE BAY AREA, MICHIGAN

By

Alan L. Koechlein

The reproductive characteristics and nesting habitat associated with a feral population of Mute Swans in the Grand Traverse Bay area of Michigan was evaluated. The nesting activity began approximately the same time swans left the wintering area and open water became available along rivers and lake habitat adjacent to moving water. These areas provided the first available nesting areas.

Nests were located and observed at least every two weeks. Forty-seven broods were observed at least every two weeks until flight age. Physical and vegetative characteristics were described in 24 quadrates systematically placed around 72 nests.

At least 96 nest sites were present on the study area and 69 percent of the nesting pairs successfully hatched one or more cygnets. Cygnet mortality was highest during their first four weeks of life and survival was related to the date nest sites were initiated. The

most cygnets produced to flight age in relation to total eggs produced occurred during the period of 18 to 21 April. The sex ratio among cygnets was not significantly different from an expected 50:50 ratio. The weight of male and female cygnets increased linearly between 59 and 122 days but were not significantly different.

Mute Swans returned to the vicinity of breeding areas occupied during the previous year and defended an average of 2.6 hectares from other swans. Following the hatch of young, a family increased their range of activity often forcing adjacent pairs to abandon their nest.

The majority of Mute Swans constructed nests on muskrat lodges and islands as compared to constructing their own nest base. Nest sites were located adjacent to shallow water and vegetation accessible for their construction. Submergent vegetation was not a significant factor in the selection of nest sites. Cattail, sedge, and bulrush were the three most important species utilized by Mute Swans and associated with nest sites. Nest success tended to be greater at sites with more than 71 percent of the quadrates containing vegetation.

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INTRODUCTION

The Mute Swan (Cygnus olor) is endemic to portions of East and West Asia, Europe, Scandinavia, and the British Isles (Delacour 1954). Feral populations have developed in North America along the Atlantic coast from Delaware to the coastal and inland water-ways of Massachusetts (Willey 1968) and in the northern half of the lower peninsula of Michigan. The Michigan population resulted from a pair of Mute Swans introduced from England in 1919 to the south arm of Lake Charlevoix near East Jordan, Michigan (Gelston 1970a). A small flock began developing from the original pair. During the winter of 1948, a pair of Mute Swans were reported for the first time in the west arm of Grand Traverse Bay, about 45 miles from the East Jordan area. Since 1948, there has been a steady increase in the wintering swan population on Grand Traverse Bay with 100 recorded in 1959, 200 in 1966, 300 in 1969, and approximately 400 swans in December of 1970 (from Gelston 1970b) (Fig. 1). Similar increases in Mute Swan populations have been reported on the Atlantic coast of North America (Halla 1966, Willey 1968), the British Isles (Eltringham 1963, Boase

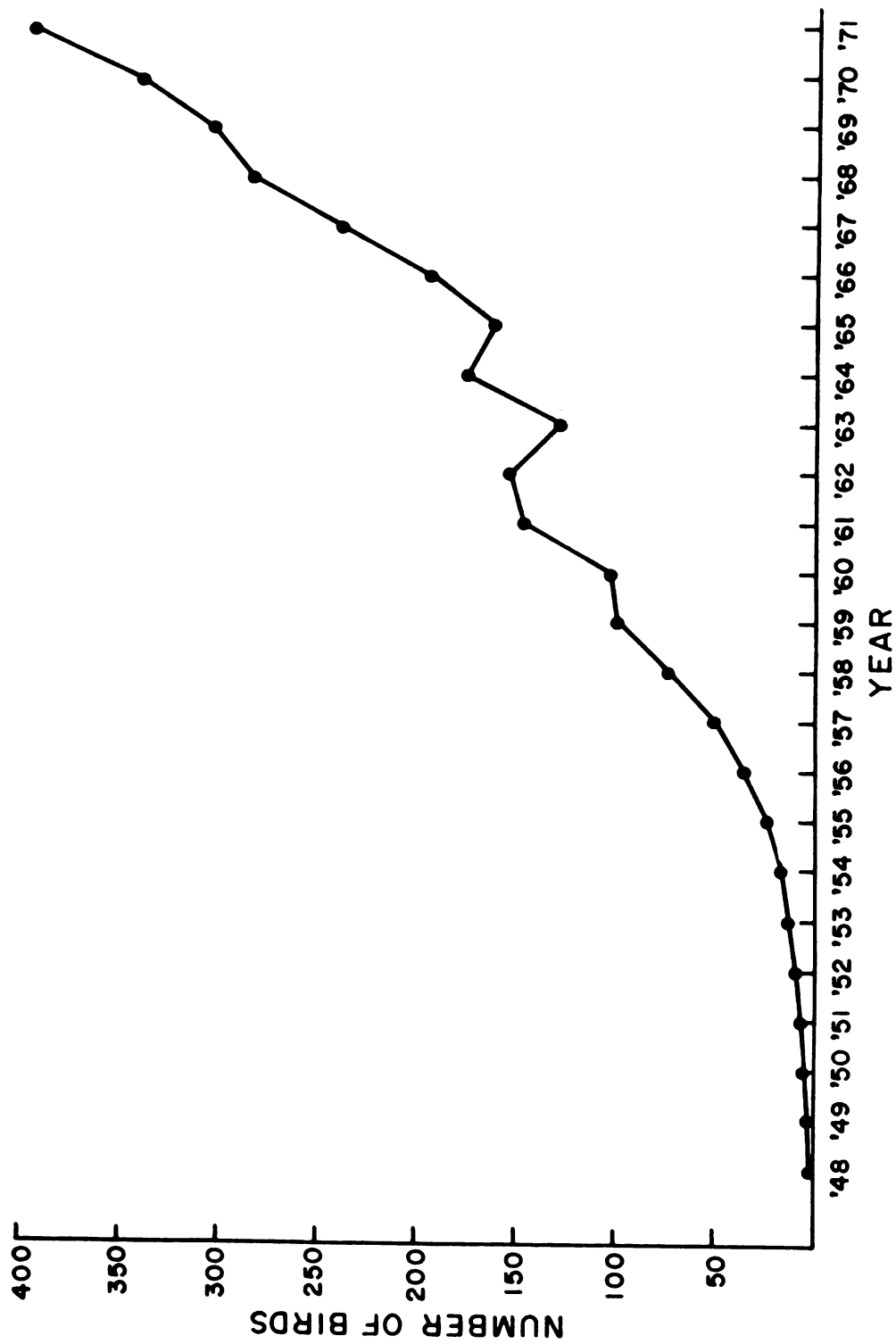


Figure 1. Winter counts of Mute Swans in the Grand Traverse Bay area
(from Gelston 1970b).

1965), in Sweden (Berglund et al. 1963), and in Denmark (Bloch 1971).

The success of this exotic species in Michigan is due primarily to two factors; a winter feeding program in Traverse City that has grown in proportion to the number of wintering swans, and the successful adaptation to the habitat in northern Michigan for nesting and brood rearing. The purpose of this study is to describe the breeding habitat and reproductive characteristics of the Mute Swan in the Grand Traverse Bay area of Michigan.

The Mute Swans wintering near Traverse City frequent the ice free areas at Grand Traverse Bay and Boardman Lake, south of Traverse City. In 1970, 275 to 300 birds utilized this area during January, February, and March, with about 160 birds moving out of the wintering area during late March and early April to begin nesting (Gelston 1971) (Fig. 2). Nests were located during 1969 and 1970 in the following Michigan counties: Alpena, Antrim, Benzie, Charlevoix, Cheboygan, Emmet, Grand Traverse, Kalkaska, Leelenau, Manistee, Montmorency, and Otsego (Gelston 1970b and 1971).

A typical Mute Swan nest consists of vegetative material assembled until the top is 20 to 50 cm above the water level. The female accepts vegetation from the male and lays it around herself to form a nest bowl for the eggs. A typical nest will measure about 2 meters in

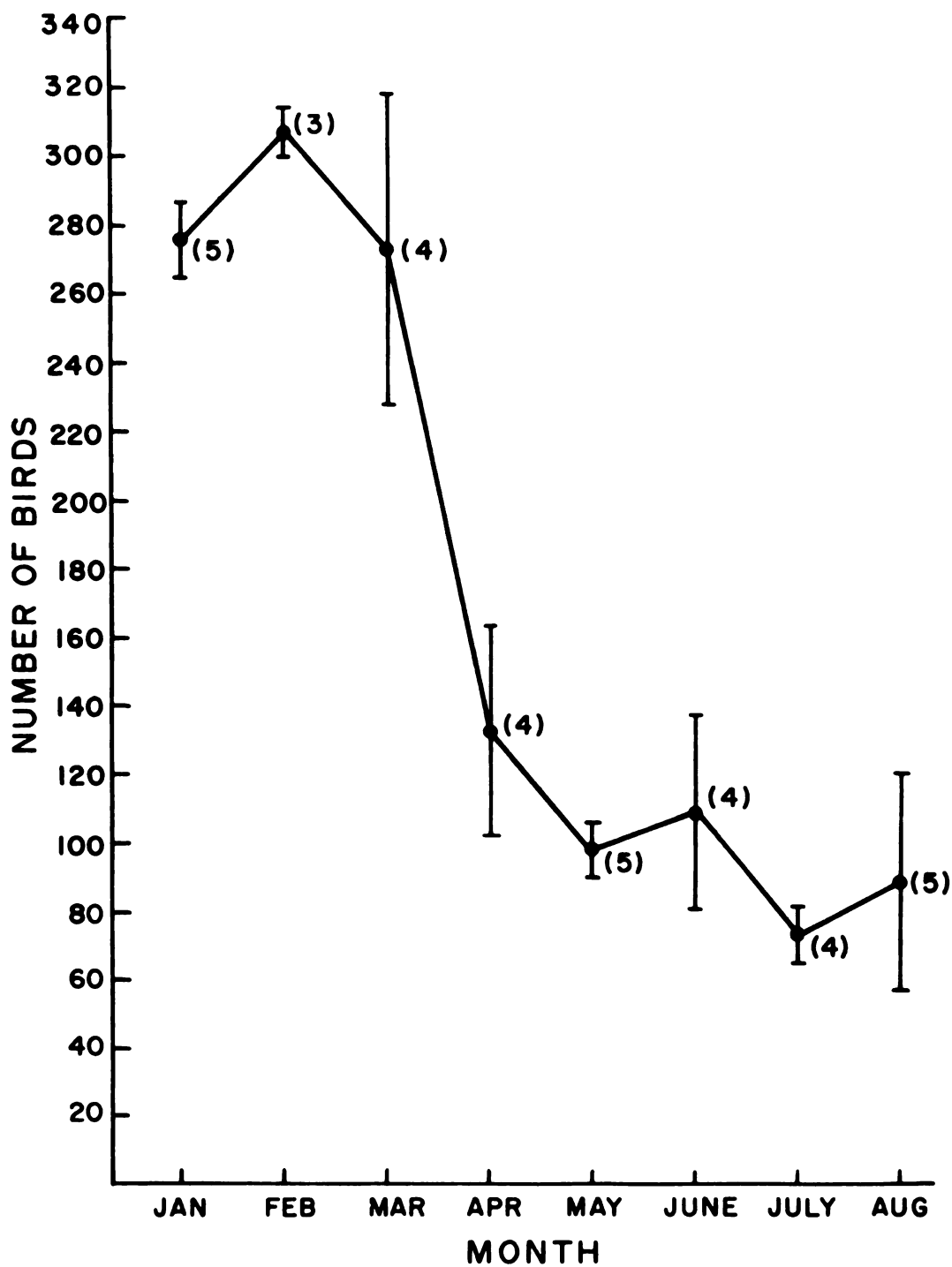


Figure 2. Average number of Mute Swans ($\bar{X} \pm \text{S.D.}$) (n) on Grand Traverse Bay and Boardman Lake by months during January through August 1970 (from Gelston 1971).

diameter at the base with a bowl about 38 cm in diameter that contains the eggs (Halla 1966). Only the nest bowl needs construction when the female selects a muskrat lodge or island for nesting. Nests have been found on islands (Berglund et al. 1963, Halla 1966), on top of muskrat lodges (Gelston 1970b), among emergent vegetation on shores of lakes and coastal water (Berglund et al. 1963, Willey 1968, Gelston 1970b) and along rivers (Eltringham 1966, Perrins and Reynolds 1967, Gelston 1970b, Campbell 1960).

A survey was initiated in April 1969 to determine the distribution and reproductive characteristics of the Mute Swans in the northern half of the lower peninsula of Michigan. A total of 52 nest sites were found (Gelston 1970b). The reproductive success of 40 of these pairs of swans as well as seven other Mute Swan populations are summarized in Table 1. The mean clutch size found in the four European populations ranged from 5.4 to 6.1 eggs with the number of eggs per clutch ranging from 1 to 11 eggs. The Michigan population of Mute Swans had a lower average clutch size (4.0 eggs) and clutches with greater than seven eggs were not found by Gelston (1970b) (Table 1). The Mute Swans of Rhode Island had a higher mean clutch size (6.4 eggs) and the range was similar to that found among the European populations. The nest success is relatively constant for all studies ranging from 67 to

Table 1. Summary of nesting and brood rearing success of Mute Swans in Europe and North America.

Location of Study	Number		Clutch Size		Percent Nest Success	Mean Brood Size	Percent Fall Cygnet Mortality	Reference
	Years	Nests	Mean	Range				
Great Britain	1	57	6.0	2-10	88	4.4	12.4	Eltringham (1963-1966)
Great Britain	1	18	6.1	3-10	89	6.0	50.0	Reynolds (1965)
Great Britain	3	102	5.8	1-11	67			Perrins et al. (1967)
Sweden	2	84			85	4.1	15.4	Berglund et al. (1963)
Poland	1	353			88	3.9		Zajac (1963)
Denmark	1	435	5.4	1-11	77	3.6	13.0	Bloch (1971)
Rhode Island	4	77	6.4	2-11			13.0	Halla (1966)
Rhode Island	1	61				5.5	56.0	Willey (1968)
Michigan	1	40	4.0	1-7	75	3.4	37.0	Gelston (1970b)

89 percent. The average brood sizes at hatch range from 3.4 to 6.0 young per female. The Michigan population of Mute Swans had the smallest mean clutch size and brood size reported. Cygnet mortality is not only highly variable between studies but between years as well. Halla (1966) observed an average of 13 percent cygnet mortality from 1962 through 1965. Willey (1968) observed a 56 percent cygnet mortality from hatch to flight during 1967 in Rhode Island (Table 1).

STUDY AREA

The center of winter activity of the Mute Swan population is Grand Traverse Bay in the northwest corner of the lower peninsula of Michigan. Nesting activity occurred along the bay shore and on inland rivers and lakes. This study was conducted on six major watersheds that flow into Lake Michigan within Antrim, Leelanau, and portions of Benzie, Grand Traverse, Kalkaska, and Charlevoix counties (Fig. 3). The major watersheds include Lake Leelanau; Glen Lake-Crystal River; Platte River-Platte Lake; Boardman River; the chain of lakes from Intermediate River through Six Mile, Ellsworth, Intermediate, Bellaire, Torch, and Elk lakes; and Jordan River-Lake Charlevoix.

The majority of the Mute Swans utilize Grand Traverse Bay and Boardman Lake during the winter from December through February. In March and April the breeding pairs select lakes and rivers where territories and next sites are established. Typical nesting habitat varies from river and lake areas to marsh communities where both nesting and brood rearing of young takes place in the same general vicinity. The more common genera of

Figure 3. The study area, Grand Traverse Bay.

plants associated with nesting areas are cattail (Typha spp.), burreed (Sparganium spp.), bulrush (Scirpus spp.), water-willow (Decodon verticillatus), sedge (Carex spp.), grasses, spikerush (Eleocharis spp.), and woody species such as willow (Salix spp.), sweet gale (Myrica gale), black alder (Alnus rugosa), and dogwood (Cornus stolonifera). Brood rearing usually centers around the nest site and quiet waters of river and lake areas. The more common genera of floating and submergent vegetation associated with the brood areas are Nymphaea spp., Nuphar spp., Potamogeton spp., Chara spp., Utricularia spp., and Myriophyllum spp.

MATERIALS AND METHODS

A search for nest sites was conducted from 4 April until 1 June 1970. Nests were located by visiting 1969 nest sites reported by Gelston (1970b), a systematic search of the watersheds in the five county study area (Fig. 3), and an aerial search on 20 May over portions of Grand Traverse, Antrim, and Charlevoix counties.

When a nest was found, its location was recorded on a county map and it was revisited at least once every two weeks until the eggs hatched or 45 days had elapsed from the date of the initial observations. During each visit, the location of the male was recorded with a corresponding point placed on a map of each area. A record was made of the number of eggs in the nest and physical characteristics of each nest. Physical characteristics include the proximity of water, vegetation, and whether the base was a muskrat lodge or constructed by the swan. The nest sites were photographed and the habitat surrounding each site was described in relation to standing water and shorelines. The proximity of other swan nests in contiguous habitat was measured by the use of the plane table and aerial photographs.

The number of cygnets that hatched at each nest was recorded and each brood was observed at least every two weeks until August. During each visit, the location of the family was recorded on a map in a similar manner as done for the male after each nest had been found. During August and September, when cygnets were between 9 and 16 weeks of age, as many cygnets as possible in each brood were captured, banded, sexed, and weighed.

A more detailed analysis of vegetation and other physical characteristics around 72 nest sites was made between 13 June and 30 July, after the nesting activity was completed at each site. Four lines from each nest were extended 30 meters in the cardinal directions with 30 x 66 cm quadrates (0.2 m^2) placed every 5 meters along each of the lines. Qualitative estimates were made of the percent cover of submergent vegetation in each quadrate. The depth of water, maximum height of dead and perennial vegetation, and the species composition and number of main stems of each species of live vegetation (density) were recorded in a total of 24 quadrates around each nest site. Samples of each species of vegetation recorded in the quadrates were collected in August from the vicinity of several nests to obtain an average wet weight value per stem. The mean weights per stem for each species were then multiplied by the density of each species in the quadrates to facilitate dominance estimates

(total weight of each species of plant in the quadrates). The relative percent of the three phytosociological measurements of frequency, density, and dominance were added to obtain an importance value for each species found in the quadrates (Curtis 1959).

RESULTS

Nest Distribution

Eighty-six Mute Swan nest sites were located in 1970. Eighty (93 percent) were original nests and 6 (7 percent) were renests. The nest sites of 10 additional successful pairs with broods were not found, hence a total of at least 96 nest sites occurred within the Grand Traverse Bay study area (Fig. 3). Seventy-four percent (69) of the sites were located between the principle wintering area of Boardman Lake-Grand Traverse Bay and East Jordan where the population originated (Fig. 3). Twenty-eight percent of 89 sites were located beside water without a current while 72 percent were located on or adjacent to running water, either a river (19 percent) or a portion of a lake or pond near inlets or outlets (53 percent). Fifty-five percent of 60 sites were selected adjacent to moving water before 17 April and all the sites near still water were initiated after 17 April (Fig. 4).

Nesting Activity

Chronology

The departure of swans from the Grand Traverse wintering area to breeding areas in 1970 began the third

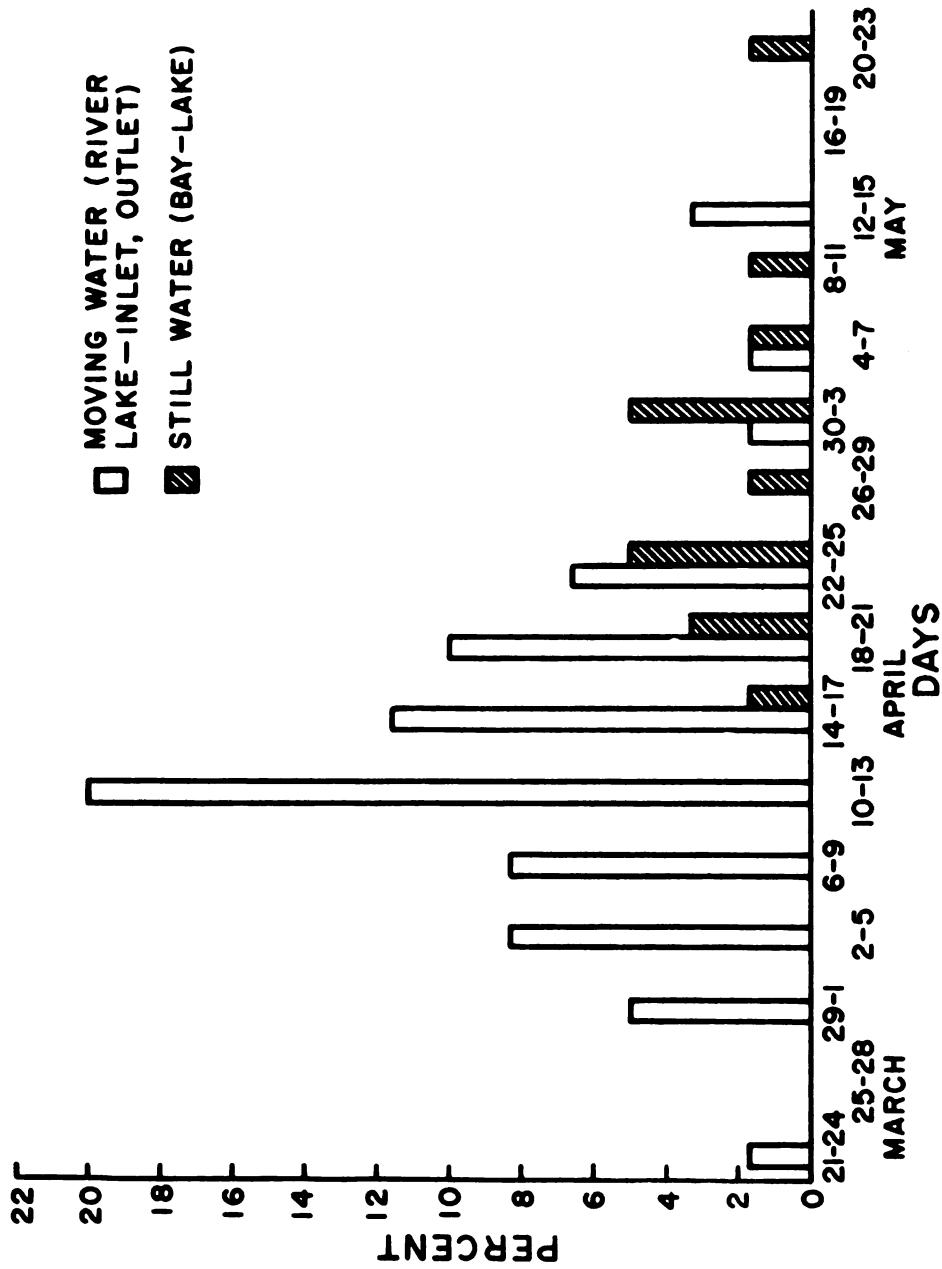


Figure 4. The relationship between the date of nest initiation by Mute Swans and the presence and absence of moving water near the site.

week in March with about 66 percent of the wintering population having left by the last week of April (Fig. 2). The chronology of the reproductive season is presented in Figure 5. Nests were initiated between 21 March and 22 May with 70 percent of the nest attempts being started between 4 and 24 April. The eggs were laid at a rate of an egg per 1.5 days ($n = 7$). The number of eggs in a completed clutch ranged from 1 to 8 with a mean of 4.8 ± 0.2 eggs. The dates females began incubating ranged from 28 March to 30 May with 68 percent beginning between 11 April and 1 May (Fig. 5). Cygnets began hatching from 10 May to 27 June with 78 percent hatching between 17 May and 6 June (Fig. 5). Sixty-nine percent (62) of the 90 pairs of swans observed during this study produced one or more cygnets. The mean number of cygnets that hatched in 62 nests was 3.4 ± 0.1 . Among 47 broods with complete records that were observed at least once every two weeks, 15 percent of the mortality among cygnets and a 11 percent reduction in the mean brood size occurred within the first four weeks (Table 2). Although 89 percent of the breeding pairs reared at least one or more cygnets to 18 weeks of age, only 76 percent of the cygnets survived (Table 2). Cygnets began flying in 129 ± 1.1 days or about 18 weeks ($n = 32$).

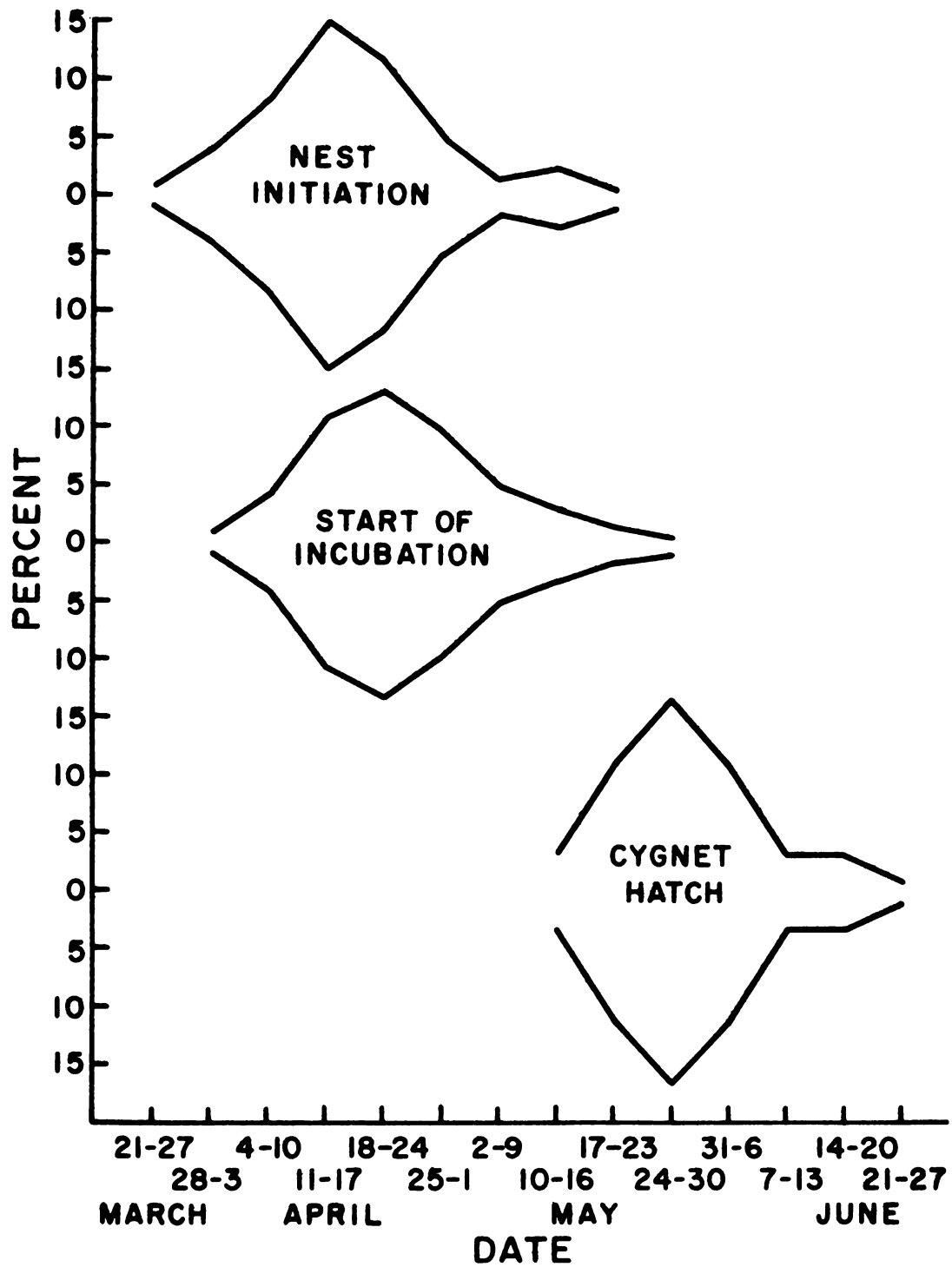


Figure 5. The chronology of nesting activity by Mute Swans during 1970 in the Grand Traverse Bay study area, Michigan.

Table 2. Cygnet survival by two-week intervals until the mean flight age of 18 weeks.

	Hatch	Age Class (Week)						
		1-2	3-4	5-6	7-8	9-10	11-12	13-18
Number of broods	47	45	45	43	43	42	42	42
Number of broods lost during interval	0	2	0	2	0	1	0	0
Number of cygnets	171	159	145	136	133	131	130	130
Percent cumulative loss of cygnets	0	7.1	15.2	20.5	22.2	23.4	24.0	24.0
Mean brood size ($\bar{x} \pm \text{SD}$)	3.6 $\pm$ 0.2	3.5 $\pm$ 0.2	3.2 $\pm$ 0.2	3.2 $\pm$ 0.2	3.1 $\pm$ 0.2	3.0 $\pm$ 0.2	3.1 $\pm$ 0.2	3.1 $\pm$ 0.2
Percent cumulative loss in mean brood	0	2.8	11.1	11.1	13.9	16.7	13.9	13.9

Nest Success

The relationship of nest success and cygnet survival with the date of nest initiation was adjusted to a base of 1000 eggs from 208 breeding pairs of swans laying an average clutch of 4.8 eggs with 69 percent of the nests being successful (Fig. 6). Fifty-eight percent (581 eggs) of the eggs were laid between 10 and 25 April (Fig. 6). Nest sites initiated between 10 and 13 April contributed 106 cygnets from a total of 203 eggs for 53 percent success. Sites initiated between 18 and 21 April contributed 91 cygnets from a total of 124 eggs for 73 percent success. Among the cygnets that hatched from nest sites initiated during 10 to 13 April, 61 (53 percent) survived to flight age. Ninety-three percent (85) out of the 91 cygnets that hatched from sites initiated between 18 and 21 April were successfully reared to flight age (Fig. 6).

Sex Ratio and Weight of Cygnets

Among 131 cygnets captured during their ninth to sixteenth week of age, the sex ratio was 58.8 percent males to 41.2 percent females which was not significantly different from the expected 50:50 ratio. There was no significant difference between the growth rate of 0.20 kilograms for males per day and 0.15 kilograms per day for females during the ninth to sixteenth week (Fig. 7).

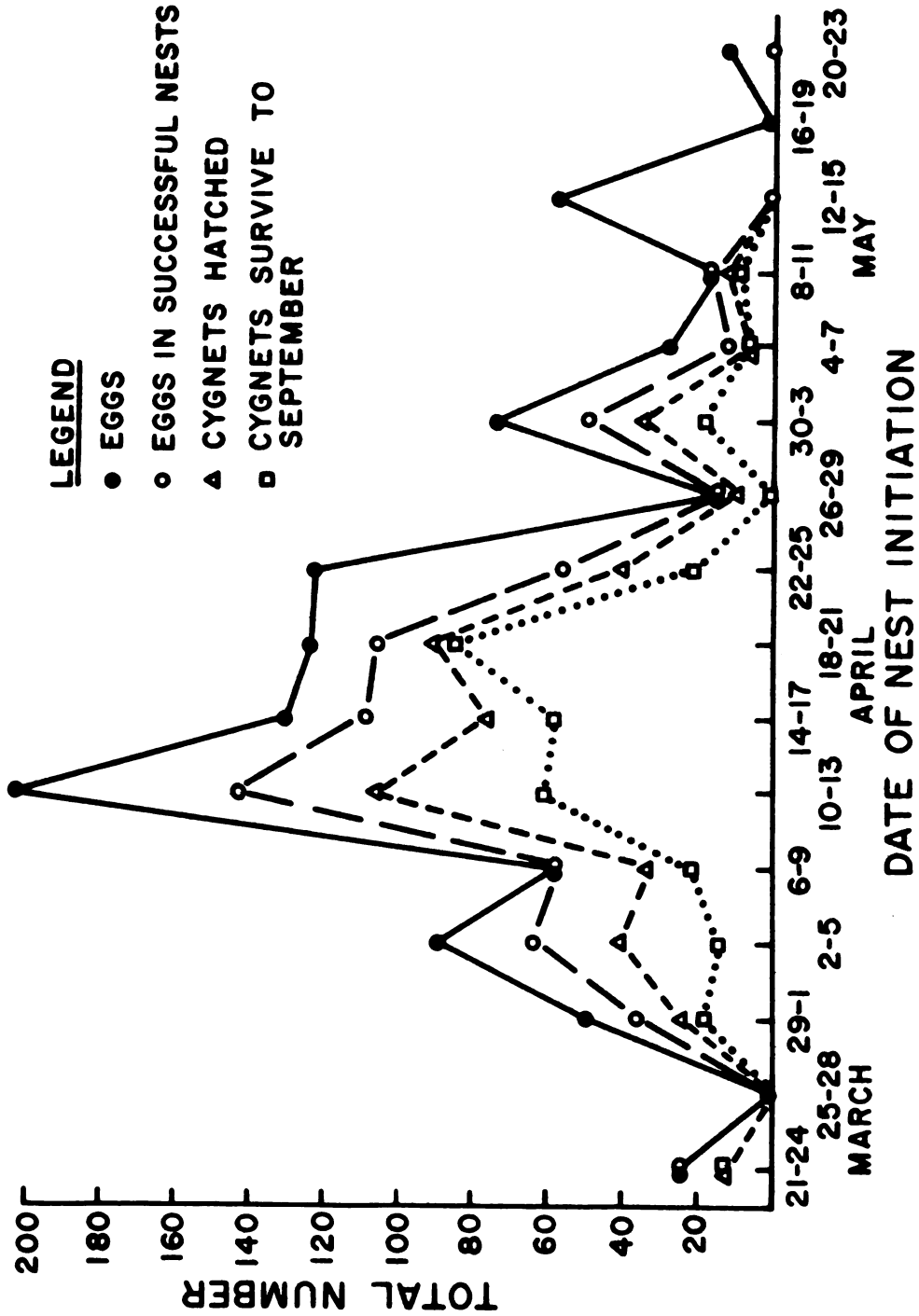


Figure 6. The relationship of successful nests and cygnet survival with the date of nest initiation. Data are based on 1000 eggs from 208 pairs at 4.8 eggs per pair.

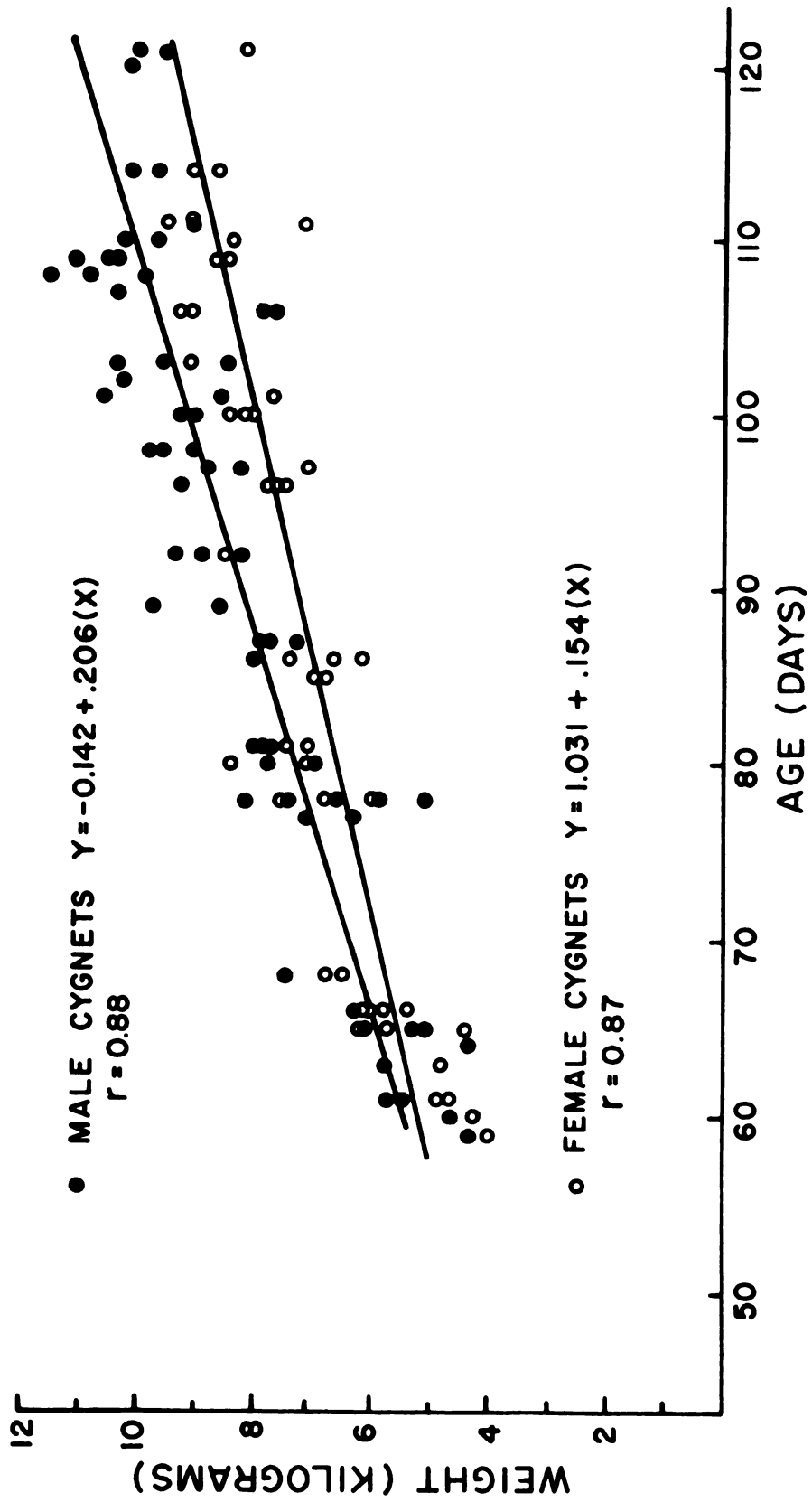


Figure 7. Weights of known age male and female Mute Swan cygnets captured between 59 and 122 days of age.

Use of Habitat

Forty-seven nest sites were located by Gelston (1970b) in 1969 within the area of this study. In 1970, 85 percent of the swans returned to nest in the vicinity of the 1969 nest sites. Nine of the 47 nest bases were still present in April 1970 and seven of these were used again.

The area that was defended around the nest site by six pairs of Mute Swans was measured by observing the points where confrontations occurred between males in contiguous habitat. The points of confrontation were placed on maps of each nesting area and connected by straight lines. The size of the territories ranged from 1.7 to 4.0 hectares with an average of 2.6 ± 0.3 hectares.

The location of the male was plotted on a map of the area during each visit while the female was incubating the eggs. Following hatch, the location of the family was similarly plotted during the first 5 weeks on a map during each visit. Straight lines were drawn between the points that circumscribed the largest area (hectares). There was a significant correlation ($r = .84$, 4 d.f.) between the area used by the males and the families. For every hectare used by the parent male, the area used by the family increased by a factor of 1.72 (Fig. 8). The area defended by three males was identical to the area used during their daily activities before the cygnets hatched.

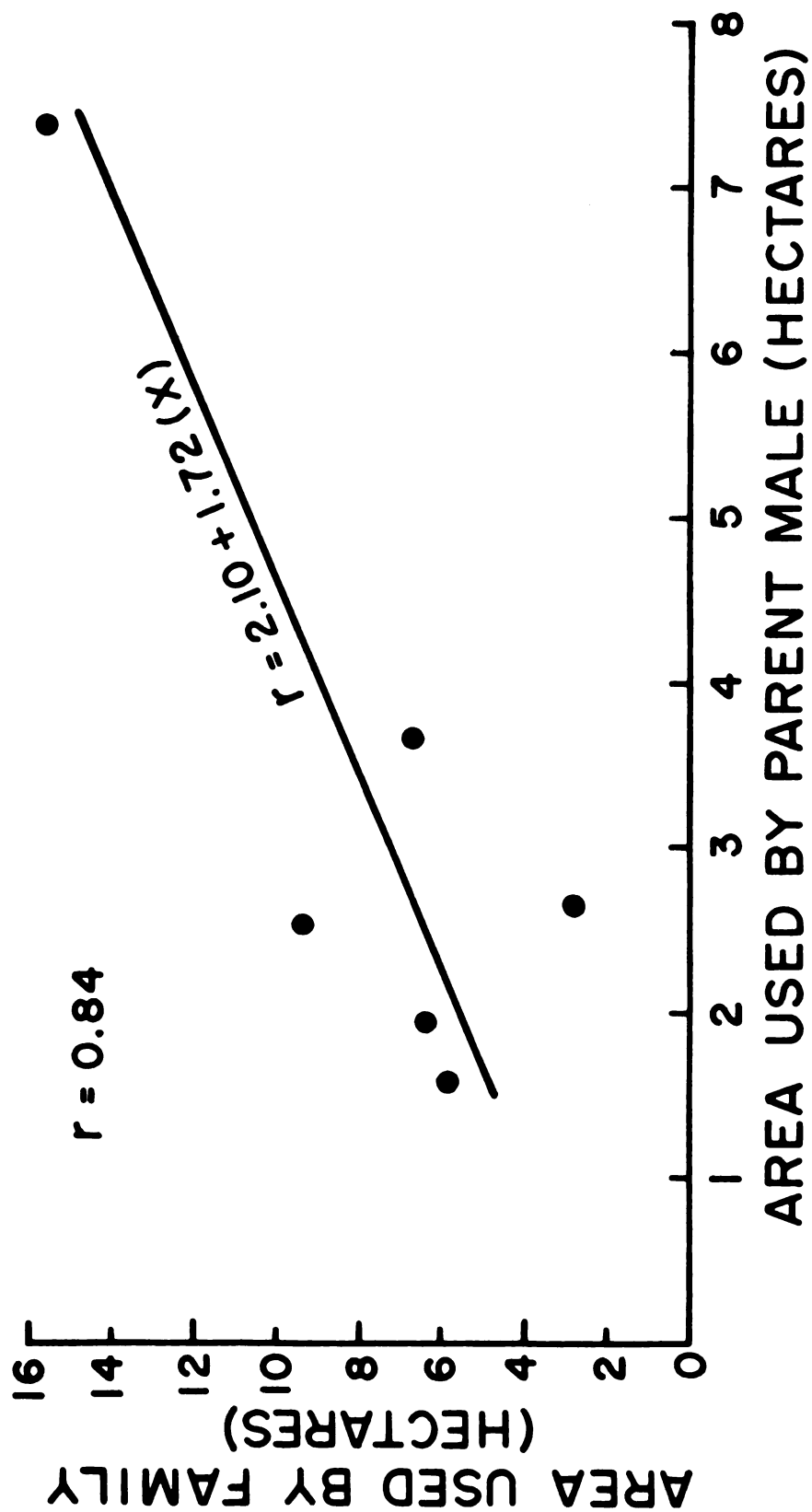


Figure 8. The relationship of the area used by the parent male during incubation to the area used by the family during the first 5 weeks after hatching.

The shortest distance between any two nests was 8 meters. The mean distance between 36 nests in contiguous habitat ranged from 8 to 528 meters with a mean of 197 ± 23.8 meters.

Analysis of Nest Sites

Physical Characteristics

Water completely surrounded 75 percent of the nest sites and 25 percent were established along a shore line (Table 3). The majority of nests (70 percent) were constructed on pre-existing bases above the water level; either an island (26 percent) or a muskrat lodge (44 percent). Thirty percent constructed their own nest base (Table 3). Nest success was similar for all types of nest bases.

The area surrounding 67 nest sites occupied by swans in 1970 and five sites occupied exclusively in 1969 were analyzed for vegetative and other physical characteristics. The physical characteristics measured during this study were grouped by each of the six sampling intervals (5-30 m) for analysis.

Fifty-one percent of the nest sites were located five meters or less from open water (Fig. 9). Water was present in at least one of the four quadrates at the 5 meter sampling interval around all but two of the 72 nest sites. When considering the total sample area around the

Table 3. Relationship of 81 Mute Swan nests to water and the structure upon which each nest was constructed.

Relationship	Number		Percent	
Nest surrounded by water	61		75.3	
on a muskrat lodge		29		35.8
on materials assembled by swans		11		13.6
on islands		21		26.0
Nest along shore line	20		24.7	
on muskrat lodge		7		8.6
on materials assembled by swans		13		16.0
Total	81	81	100.0	100.0

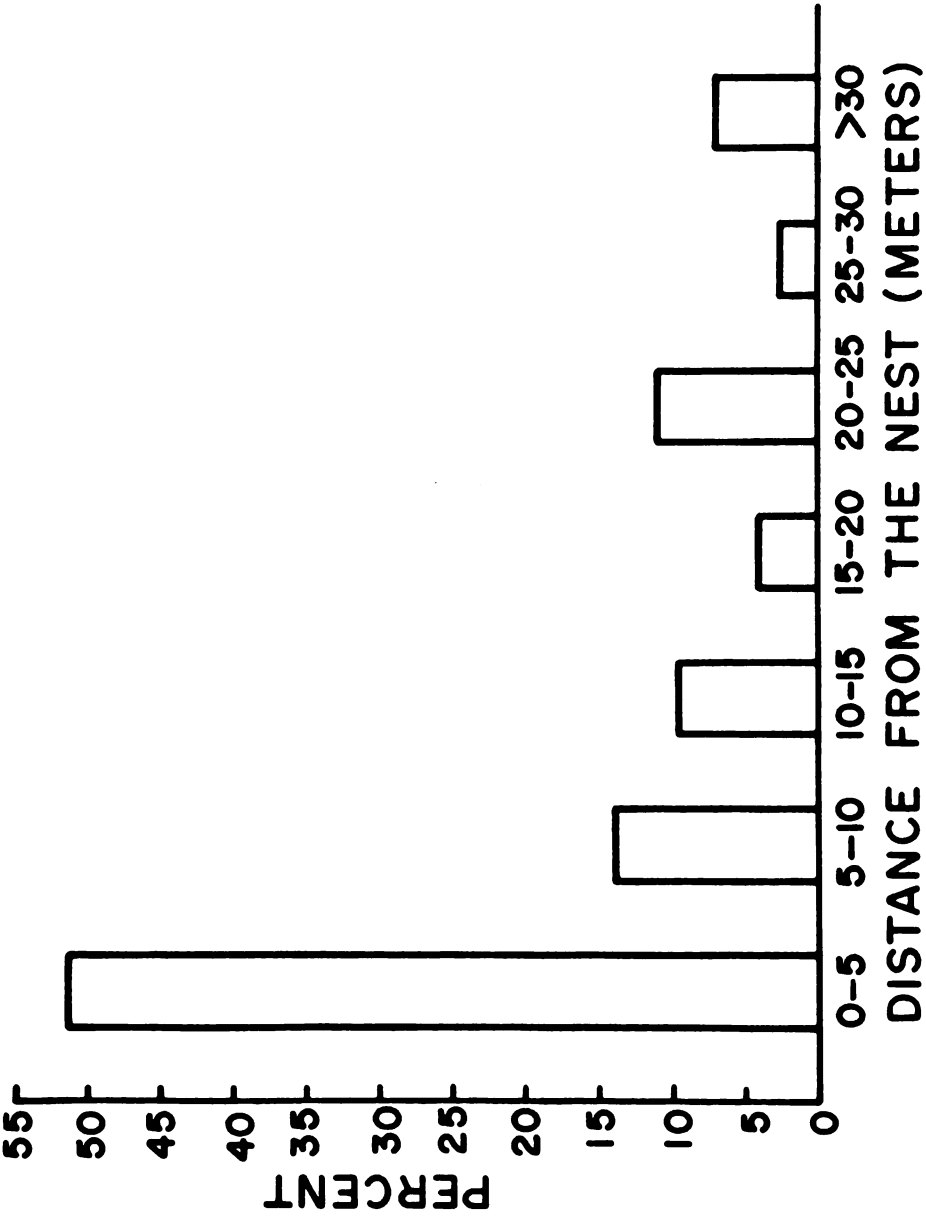


Figure 9. The distance of 72 Mute Swan nest sites to open water.

nests, approximately 80 percent of the quadrates at each interval from 5 to 30 meters from the nest site contained water (Fig. 10). The mean water depth of the quadrates containing water increased from 27 ± 1 cm at the 5 meter interval to 59 ± 3 cm at the 30 meter interval (Fig. 10).

Vegetative Characteristics

The percent cover of submergent vegetation on the bottom of the lakes and rivers in water between 12 and 150 cm deep was recorded in the following categories: 0, 25, 50, 75, and 100 percent. Submergent vegetation was absent from over 80 percent of the quadrates in each sampling interval from 5 to 30 meters.

Emergent vegetation was present within one of the four quadrates placed 5 meters from each nest site 91 percent (66) of the time. Although four of the remaining sites (6 percent) had vegetation (water-willow or sedge) less than 5 meters from the nest that were not recorded in any of the quadrates, only two nest sites (3 percent) constructed of sticks had no vegetation in the immediate vicinity of the nest. When all four quadrates are considered collectively by sampling interval, 60 percent of the quadrates contained standing vegetation at the 5 meter sampling interval and this declined progressively as the distance from the nest increased to 40 percent of the quadrates containing standing vegetation 30 meters from the nest site (Fig. 10).

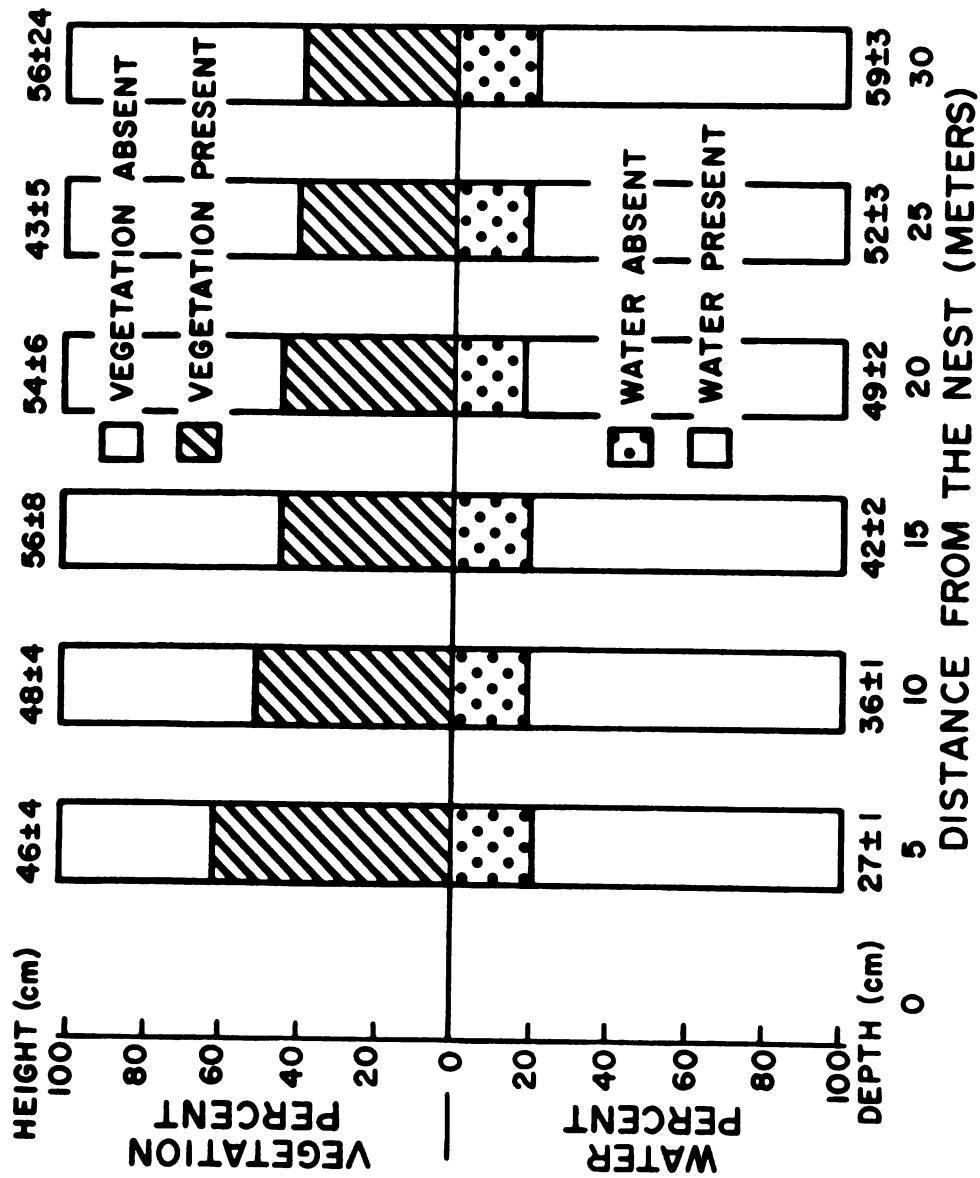


Figure 10. The percentage of 30 x 66 cm quadrates around 72 Mute Swan nest sites containing vegetation and water 5 to 30 m from the nest with mean maximum height of dead vegetation and mean water depth by interval ($\bar{x} \pm S.E.$).

The height of the vegetation present in each quadrate was not significantly different between intervals and the means ranged from 43 ± 5 cm to 56 ± 24 cm (Fig. 10).

The vegetation sampled 5 meters from each nest best represents the vegetation present from which plant material was obtained to construct each nest. The common genera of emergent vegetation were bulrush, cattail, sedge, burreed, and water-willow (Table 4). Bulrush and cattail occurred most frequently among all the quadrates 5 meters from the nest sites. The two most frequent associations were cattail with sedge and bulrush with burreed (Table 4). Sedge, burreed, and water-willow were found more frequently with one of the other four genera (Table 4).

Cattail, bulrush, burreed, and water-willow decreased in occurrence among quadrates from the 5 to 30 meter sampling interval. Sedge increased in occurrence to a peak at the 25 meter sampling interval. The mean density for cattail, bulrush, sedge, burreed, and water-willow at the 5 meter interval are 15.0 ± 5.0 , 61.5 ± 10.0 , 179.0 ± 19.5 , 22.0 ± 1.0 , and 47.0 ± 8.0 stems per square meter, respectively. No significant difference was found by an analysis of variance among the mean density of all five genera between the six sampling intervals (5 to 30 m).

An importance value for the species of vegetation sampled within all the quadrates from 5 to 30 meters was obtained by adding the relative frequency, relative

Table 4. Frequency of association of each of five species (bulrush, cattail, sedge, burreed, and water-willow) in 288 quadrates located 5 meters from 72 Mute Swan nest sites.

Genera	Frequency	Associated With
Bulrush	10.8	None
Cattail	9.7	None
Sedge	7.6	None
Cattail	6.9	Sedge
Bulrush	4.2	Burreed
Burreed	3.8	None
Water-willow	2.4	None
Bulrush	1.4	Cattail
Cattail	1.4	Water-willow
Bulrush	1.1	Water-willow
Sedge	1.1	Water-willow
Bulrush	0.7	Sedge
Sedge	0.7	Burreed
Cattail	0.3	Burreed
Total	52.1	
Quadrates with other vegetation	9.4	
Quadrates without vegetation	38.5	
Total quadrate samples	100.0	

density, and relative dominance which is based on a total of 300 (Curtis 1959). Table 5 shows those genera with an importance value greater than 10. Cattail had the highest importance value of 70 at the 5 meter interval and declined to a value of 25 at 30 meters (Table 5). Bulrush declined from 32 to 20 in importance from 5 to 30 meters. The highest importance value of water-willow was 21 at the 10 meter sampling interval. The lowest and highest importance values for sedge were at the 15 and 25 meter sampling intervals, respectively. The importance of Kentucky blue grass increased from 38 to 52 from the 5 to the 20 meter sampling interval (Table 5) primarily from the contribution of cultivated lawns near five nest sites. Sedge, willow, grass, spikerush, sweet gale, red osier dogwood, black alder and other species show higher importance values among the sampling intervals beyond 5 meters (Table 5). The distribution of importance values of these species show an increase in frequency in locations where quadrates reached the shore of lakes, ponds, and rivers. This reflects the greater frequency of nest sites surrounded by water (75 percent) (Table 3) rather than the few quadrates (20 percent) where standing water was absent from 5 to 30 meters from the nest sites (Fig. 10).

Nest success seemed to be related to the vegetation in 24 quadrates around the nest sites. Nests surrounded with vegetation in 0-4 out of 24 quadrates showed the

Table 5. The importance values of vegetation observed in each of six sampling intervals (5 to 30 m) from 72 Mute Swan nest sites.

Taxon	Sampling Interval					
	5	10	15	20	25	30
Cattail (<u>Typha</u> spp.)	70.4	55.7	37.4	36.0	35.3	25.0
Sedge (<u>Carex</u> spp.)	52.5	54.6	38.9	49.9	60.6	40.9
Kentucky Blue Grass (<u>Poa pratensis</u>)	38.5	34.0	46.4	52.7	44.8	50.5
Bulrush (<u>Scirpus</u> spp.)	32.7	25.9	25.2	24.1	21.4	20.7
Burreed (<u>Sparganium</u> spp.)	18.7	19.3	13.2	22.0	18.8	11.1
Grasses (Gramineae)	18.2	25.3	23.8	20.6	25.5	32.6
Willow (<u>Salix</u> spp.)	16.1	12.8	34.2	18.9	7.8	30.6
Water-willow (<u>Decodon verticillatus</u>)	14.5	21.1	9.7	10.2	5.9	7.4
Spikerush (<u>Eleocharis</u> spp.)	13.4	15.0	11.8	4.5	13.9	10.7
Sweet gale (<u>Myrica gale</u>)	5.6	6.5	17.6	17.6	13.0	11.4
Dogwood (<u>Cornus stolonifera</u>)	4.8	11.1	6.8	8.2	9.3	10.6
Others	14.6	18.7	35.0	35.3	43.7	48.5
Total	300.0	300.0	300.0	300.0	300.0	300.0

lowest nest success (32.8 percent of the eggs hatched), the lowest mean clutch size (4.5 ± 0.4 eggs), and the smallest mean brood size of 3.2 ± 0.5 cygnets (Table 6). Nest sites surrounded by vegetation in 17 to 20 and 21 to 24 quadrates show the greatest nest success with 71 and 59 percent of the eggs hatching, respectively (Table 6). Nest sites surrounded with vegetation in 21 to 24 quadrates contained the largest mean brood size at hatch of 3.8 ± 0.3 cygnets (Table 6).

Table 6. The relationship of nest success to the presence of vegetation in 24 quadrates (0.2 m²) around each of 67 Mute Swan nest sites.

	Number of Quadrates with Vegetation				
	0-4	5-8	9-12	13-16	17-20 21-24
Number of nests	13	12	13	7	14 8
Mean clutch size	4.5 ± 0.4	4.9 ± 0.4	5.2 ± 0.4	5.6 ± 0.3	4.7 ± 0.3 4.9 ± 0.6
Percent hatch	32.8	45.8	41.2	35.8	71.2 59.0
Mean brood size at hatch	3.2 ± 0.5	3.4 ± 0.3	3.7 ± 0.2	3.5 ± 0.5	3.6 ± 0.3 3.8 ± 0.3

DISCUSSION

Population

The Mute Swan population appears to be increasing in an exponential manner at the present time. The range of all breeding pairs between Manistee County in the West and Alpena County in the East during 1970 (Gelston 1971) suggests the number of swans will continue to increase by range expansion. However, a large proportion of the nesting pairs were located between the place of origin and the principle wintering areas of Boardman Lake-Grand Traverse Bay. This area includes three watersheds. The largest (Intermediate River through Elk Lake) is located between the Boardman River and the East Jordan watershed.

The first opportunities to nest occurred prior to the complete breakup of ice on rivers and portions of lakes close to inlets and outlets. The majority of the nest sites found in the Grand Traverse Bay study area of Michigan were located near running water. Eighty percent of the nests examined by Halla (1966) were located on rivers, on brackish ponds, and along the coast of Rhode Island. Ninety-eight percent of the breeding pairs observed by Berglund et al. (1963) were found along the coast as

opposed to inland lakes near Blekinge Sweden. It is probable that these areas were available prior to freshwater lakes and ponds. Mute Swans returned to breeding places in Sweden immediately after the breakup of ice (Berglund et al. 1963). In Rhode Island the pairs of Mute Swans returned to nest sites as soon as weather permitted (Halla 1966).

A partial life equation representing 50 pairs and 50 nests is presented in Table 7. During 1970 the Mute Swan had an average clutch size of 4.8 ± 0.2 eggs per nest which represents an increase of 17 percent over 1969. However, this is lower than the mean clutch size reported among other populations which ranged from 5.4 to 6.4 eggs (Bloch 1971, Campbell 1960, Church 1956, Eltringham 1963 and 1966, Halla 1966, Ogilvie 1967, Perrins and Reynolds 1967, and Reynolds 1965). Fifty nesting pairs were unsuccessful which represented a potential of 240 eggs which was reduced by 30 percent. The loss was primarily due to unknown factors (10 percent) and nest sites being abandoned by females (13 percent) as the result of territorial aggression from neighboring pairs. During 1970 an average of 69 percent of the nesting pairs successfully hatched young. This was similar to the 75 percent nest success observed in 1969 (Gelston 1970b) and within the range of success observed among six European populations of Mute Swans (Table 1). Thirty percent of the eggs in successful

Table 7. A partial life equation for a breeding population of 50 Mute Swan pairs in the Grand Traverse Bay area, Michigan.

x	lx	dx F	dx	100 qx
Age Interval	No. Alive at Beginning of x	Factor Responsible for dx	Number Dying During x	dx as Percentage of lx
Nests				
Eggs 4.8 eggs per nest	240			
Unsuccessful nests 31%		Abandoned by female	31	12.9
		Nest flooded	7	2.9
		Human disturbance	12	5.0
		Unknown	24	10.0
		Total	<u>74</u>	<u>30.8</u>
Successful nests 69%	166	Unknown	50	30.1
Broods				
2 weeks	116	Cygnets stepped on by female	2	1.7
		Cygnets drowned	3	2.8
		Unknown	3	2.8
4 weeks	108	Unknown	10	9.2
8 weeks	98	Unknown	8	8.1
12 weeks	90	Dog predation	1	1.6
		Unknown	1	1.6
16 weeks	88		0	
20 weeks			0	
Nesting and brood period			152	63.3

nests failed to hatch from unknown causes. A total of 116 cygnets were produced of which 7 percent of the cygnets died during the first two weeks and 9 percent during the second two weeks due primarily to unknown factors.

Reynolds (1965) observed 31 percent loss of cygnets during the first two weeks and 8 percent mortality in the second two weeks of life. Reynolds reported 50.5 percent survival in 13 weeks, whereas, survival at the end of 13 weeks was 76 percent in this study. Snapping turtles caused a large proportion of cygnet loss before flight age in Rhode Island (Halla 1966, Willey 1968). Men and dogs were the only mammals known to affect nest success and cygnet survival, respectively in this study which is similar to mortalities reported in Rhode Island (Halla 1966), Mammalian predators were of little consequence as a limiting factor among Mute Swans in Britain (Ogilvie 1967) and Trumpeter Swans in the Red Rock Lakes Wildlife Refuge of Montana (Banko 1960).

There was a 63 percent mortality from the biotic potential of 240 eggs to the age cygnets began to fly. Cygnets in the Grand Traverse Bay study area began flying in an average of 129 ± 6 days or 18 weeks. Berglund et al. (1963) reports a time period of approximately 136 days.

Breeding pairs initiating nest sites between 10 and 21 April contributed 63 percent of the total cygnets to

flight age than Mute Swans initiating nest sites during any other period of time. However, the greatest nest success occurred among breeding pairs initiating nest sites between 18 and 21 April in the study area. During this four-day period, the still waters of lake shores and the Grand Traverse Bay were available for the selection of nest sites (see Fig. 4). Based upon a laying rate of an egg per 1.5 days and an average incubation period of 37 days (Gelston 1971), a pair initiating their nest site on 18 April would hatch cygnets on approximately the first of June. Cygnets hatching during the early part of June appear to have a higher rate of survival than any earlier period of time.

The sex ratio among cygnets captured in 1970 between 59 and 122 days of age was 58.8 percent male to 41.2 percent female. In 1969 the ratio was 60.4 percent male to 39.6 percent female (Gelston per com.) which was not significant from an expected 50:50 ratio. Over a six-year period, the average sex ratio of cygnets captured in Rhode Island was 53.6 to 46.4 percent male to female (Willey 1968). Adult Mute Swans three years of age and older contained a significant proportion of males suggesting differential mortality favoring males had occurred in Rhode Island (Willey 1968).

There was no difference in weight gain between male and female cygnets. A linear increase occurred in the

weight of cygnets from 60 to 122 days of age. Weighing cygnets from hatch to 151 days, Portmann (1950) showed a similar linear increase from 60 to 120 days. Cygnets gained 23 percent of their weight between 60 and 120 days, whereas, 32 percent of the weight gained by the cygnets occurred from 120 to 151 days of age (Portmann 1950).

Use of Habitat

The swans tended to return to the vicinity where nests had been located in 1969. Mute Swans will often re-use the same nest site if available. Of the 80 observed nest sites during this study, 9 (11.2 percent) were still available from among the sites used during 1969 and 7 (78 percent) of these were used during both 1969 and 1970.

The size and defense of the territory varied considerably between nesting pairs on the study area. This is similar to the observations by Willey (1968) where through the use of the aggressive response by Mute Swans toward other swans, other waterfowl, and man; 12 territories were measured averaging 1.7 hectares and ranging from 0.2 to 4.8 hectares. This was comparable to a mean of 2.6 ± 0.8 hectares ranging from 1.7 to 4.0 hectares in this study. Willey (1968) recognized a considerable variability among pairs in their response to waterfowl and man. During this study, only the aggressive response directed toward other swans was deemed a reliable indicator

of the boundary to the territory. Aggression toward other waterfowl was not observed and the swans consistently responded to me while on land but not while wading or in a boat.

The distance between nest sites in contiguous habitat was 197 ± 23.8 meters. The area of a circle with a radius of 98 meters (one-half the mean distance) will enclose 2.4 hectares around a nest, which was slightly larger than the mean size of the six territories. The increase in area, by a factor of 1.72 utilized by the swans following hatch of the young could have a detrimental effect on the nest success of adjacent pairs spaced at a mean distance of 197 meters.

Habitat Selection

Habitat selection among birds has been reviewed by Lack (1933), Svardson (1949), Hilden (1965), Klopfer (1969), and Klopfer and Hailman (1965). Their reviews show that habitat selection is a combination of innate and learned reactions to stimuli from components of the habitat, members of their own species, and other species. As a result, each species shows a characteristic preference for a substrate in the habitat that supplies most of the favorable stimuli. Similarly, the selection of sites for the location of nests depends on stimuli-specific components of the habitat that have some regularity and predictability.

Water was an integral part of the swans' habitat. Banko (1960) reported that the most suitable water conditions in the breeding habitat of Trumpeter Swans are: stable levels, low wave action, and a depth shallow enough for some emergent vegetation. These same criteria are applicable to the selection of breeding habitat by 71 percent of the Mute Swans in the Grand Traverse Bay study area of Michigan. Nineteen percent of the nest sites were on rivers where current was continually present and 10 percent were susceptible to wave action along Grand Traverse Bay. Seventy-five percent of the sites were surrounded by water rather than located on a shore line. This may be important in providing protection for the nest and female from predatory mammals. The lack of cryptic coloration would make the swan a susceptible prey if it were not a large bird and highly aggressive. Mammalian predators were of little consequence as a limiting factor among Mute Swans in Great Britain (Ogilvie 1967) and Trumpeter Swans in Montana (Banko 1960).

The mean depth of water from 5 to 30 meters of the nest sites permitted an adult Mute Swan to probe on the lake or river bottom for vegetative parts used for nest construction or food. According to Berglund et al. (1963) the adult sized birds commonly grazed on underwater vegetation in a depth ranging between 50 and 120 cm and in water of greater depths if the tops of aquatic plants

were accessible. The occurrence of submergent vegetation was apparently not a significant factor in nest site selection.

Nests were frequently constructed on existing physical bases such as muskrat lodges and islands. Nest success was not affected by the use of an existing base. The use of muskrat lodges by the Mute Swan for nest sites apparently is restricted to Michigan. The presence of muskrat lodges enhanced the successful breeding of Trumpeter Swans in Montana (Banko 1960) and South Dakota (Monnie 1966).

Emergent vegetation occurred within the first 5 meters of the majority of nests. The frequency of vegetation considered collectively in all quadrats showed a decline from 5 to 30 meters. This corresponded to the increase in mean depth in water away from the nest. Swans assembling vegetative material for a nest required a site with shallow water and sufficient emergent vegetation for nest construction. Nest success was greatest from nest sites surrounded with 17 to 24 quadrates in which vegetation occurred.

Habitat selection among birds has been described according to plant communities rather than specific plant species (Beecher 1942, Weller and Spatcher 1965). The use of a variety of vegetative species for nest support within the geographic range of an avian species reflect

its plasticity and adaptability to various suitable nesting substrates. Beecher (1942) refers to the variety of substrates used for nest site support and construction among marsh birds as their life-form. Specific sites that are chosen contain components of the birds' life-form in the habitat with some regularity.

The Mute Swan will select a base to support the nest (islands and muskrat lodges) and a plant community that will contribute to nest construction and permit visual surveillance of the surrounding habitat. Habitat containing aquatic forms of emergent vegetation were selected for the location of nest sites by the majority of breeding pairs. The plant species with the greatest regularity and predictability and contributing to the life-form of the Mute Swan are: bulrush, cattail, sedge, and the associations of sedge with cattail, and bulrush, with burreed within the 5 meter interval. Sedge, burreed, and water-willow were more frequently associated with one of the other four genera.

Cattail, sedge, and bulrush were the three most important genera found in the habitat selected by the Mute Swan. The decline in the importance value of cattail and bulrush from 5 to 30 meters reflected the importance of these species in the vicinity of the nest. These species of plants probably provided both protection and material for nest construction. Sedge was observed more frequently

in quadrates placed over locations where water saturated the soil. The importance of woody species (willow, sweet gale, and dogwood) was greater beyond 10 meters from the nest sites confirming the greater frequency of nest sites surrounded by aquatic vegetation and water.

The Mute Swans in Rhode Island selected plants of a similar life-form using reed (Phragmites sp.), cattail, cordgrass (Spartina spp.), and bulrush as the most common nesting materials (Halla 1966). Near Blekinge Sweden, Mute Swans showed a preference for a shallow shore zone with emergent vegetation or islands inaccessible from shore and formed their nest with reeds or bulrushes (Berglund et al. 1963). An increase in breeding adults resulted in the exploitation of exposed shore line for nesting habitat. Nest materials were algae, grass wack (Zosteria marina), Bulrush, and/or grass (Berglund et al. 1963). As an alien species to the North American continent, the Mute Swans have adapted well by exploiting habitat similar to their ancestral areas.

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