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ASSESSMENT OF THE STOCK OF GREEN TURTLES NESTING AT EAST ISLAND, FRENCH FRIGATE SHOALS

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INTRODUCTION

This report assesses the status of green turtles, Chelonia mydas, nesting at East Island, French Frigate Shoals, a key breeding ground of this species in the Hawaiian Archipelago. Although observations of green turtle occurrence and habits have been recorded throughout the Hawaiian Islands over many years, for the most part these are sporadic and unsuitable for a rigorous quantitative analysis. However, at East Island, Balazs (1980 and elsewhere) has studied the turtle population intensively since 1973. His studies have ranged over many aspects of green turtle biology and ecology, and his observations provide a reasonably solid basis for partial assessment of the East Island stock. The analysis reported here, relying entirely on Balazs' data over the period 1973-82, focuses specifically on the dynamics of the nesting females. Males are not considered, nor are immature animals. The primary questions posed are:

- How large is the stock of mature females in the East Island colony?
- How many of these can be expected to be nesting in any year?
- How many females reach maturity each year, i.e., how many recruits (neophytes) are added to the population each year?
- What can be said about trends in these variables over recent years?

The following sections describe the models and methods used, indicate the data sources employed, and present the basic findings relative to the major questions. While many of the key assumptions are discussed, some of the more obvious ones are omitted. Further, mathematical details are not given and many of the finer analytical points are glossed over; these will be the subject of another report.

MODELS AND METHODS

Basic Population Model

To evaluate changes in the number of nesting females on East Island, we first need a conceptual model which relates the actual number of females observed nesting there each year to the basic underlying population processes. The model used here states that the number of nesters during the current season depends on four factors:

(1) The sequence of recruitments of first-time nesters joining the mature female population. One such year class is added each year;

(2) the probabilities that members of each existing year class will still be alive during the current breeding season (survival rates);

(3) the probabilities that survivors from each year class will actually be hauling out to nest at sometime during the current breeding season (remigration probabilities); and

(4) the probability that any turtle hauling out to nest during the current season will be observed and counted during the specified survey period on East Island (coverage rate).

For this analysis there were 10 basic observations, i.e., each year's sample count of nesting females during 1973-82. Unfortunately, the number of unknown parameters greatly exceeded 10, so some simplifying assumptions were required and some of the parameters had to be estimated from other data.

Analytical Procedure

Specifically, the following approach was adopted:

(1) Coverage rates and estimated nesting populations.--Coverage rates for each year were estimated from a stochastic model of turtle residence at East Island. The model is based on probability distributions for (a) the within-season time of arrival and commencement of nesting activity for individual females, (b) the number of nesting episodes (potential clutches of eggs deposited) per female, (c) the time interval between successive nesting episodes (during these intervals a female is temporarily absent from the nesting population), and (d) the duration of each nesting episode. A nesting episode is defined as the sum of nocturnal activity of hauling out and digging associated with the laying of a particular clutch of eggs, or the ultimately unsuccessful attempts to deposit the eggs.

Each of these probability distributions was estimated empirically using Balazs' detailed observations for the 1974 and 1975 breeding seasons. Assuming the same distributions were applicable to each year 1973-82, the coverage rate for a specified year was estimated, given the survey period (or set of periods) for that year. The coverage rates were then divided into the actual counts of turtles nesting during the survey periods to estimate the total numbers of turtles nesting during the full breeding seasons.

(2) Annual survival rates and remigration rates.--Annual survival rate for mature females was assumed to be constant during 1977-82, and this rate, together with two parameters of a theoretical probability distribution of remigration intervals, were then estimated from tag

recapture statistics gathered by Balazs during this 6-year period. The analysis was based on the numbers of turtles resighted on East Island during the survey periods of 1978-82 from cohorts of nesting females tagged during the 1977-81 seasons (Table 1). The observed numbers of recaptures each year were adjusted upward to correct for tag shedding (Table 2; tag shedding probabilities were estimated from double-tagging data), and were increased further by applying the appropriate coverage rates.

The theoretical remigration model assumed that during any breeding season the probability that a mature female hauls out to nest depends only on the number of years elapsed since her last nesting, and that this probability increases asymptotically from some minimum value for an interval of 1 year to unity as the time interval increases.

When survival rate and remigration parameters were estimated jointly and no constraints were placed on the estimation, the analysis suggested a high survival rate. However, because the estimates of survival rate and remigration parameters are statistically confounded in the tag recapture model, they are not as reliable as we might like. Accordingly, three different sets of remigration parameters were computed, each conditional on a different assumed level of annual survival during the 1977-82 period when the tagged females were at large. In each case the combination of survival rate and remigration parameters was consistent with the adjusted tag resighting data.

(3) Annual recruitment.--Annual recruitment to the mature female population was assumed to be a function of time. The form of the relationship depends on a set of coefficients estimated from the sequence

of adjusted annual counts of nesting females, and a matrix of "contribution" factors computed from survival and remigration probabilities. Estimating a single coefficient in this model is equivalent to assuming constant recruitment; the estimate of the coefficient is the estimate of this constant recruitment level. Estimating two coefficients is equivalent to assuming a linear trend in recruitment during the relevant time period; the estimates of the coefficients indicate the time-specific values of recruitment and, most important, the direction of the assumed trend. Models with three or more coefficients could be fit to the data, but with only 10 years of observations in the analysis, the higher-order recruitment functions are not informative.

In computing the "contribution" factors, we considered two kinds of scenarios regarding survival rates among adult females: (a) Annual survival rate was constant over all relevant years at one of the three levels assumed in estimating remigration rates, and (b) annual survival rate was lower in the years prior to 1978, when the harvesting of green turtles was outlawed. For each of the three levels of survival rate assumed above for the 1978-82 period, three lower levels of constant annual survival rate were assumed to apply during the pre-ban period.

A total of 12 scenarios resulted from this scheme, defined as follows:

	Annual survival rate (%)	
Scenario	Pre-ban	Post-ban
1	95	95
2	90	90
3	80	80
4	90	95
5	80	95
6	70	95
7	85	90
8	75	90
9	65	90
10	75	80
11	65	80
12	55	80

For each scenario, recruitment coefficients were estimated, average recruitment level was determined and the trend in recruitment was assessed.

(4) Population size.--The estimates of annual recruitment were combined with assumed survival rates to compute, for each scenario, the average number of mature females in the East Island population during both the pre-ban and post-ban periods.

RESULTS

Coverage Rates and Estimated Nesting Populations

Coverage rates ranged from 25% in 1977 to 84% in 1974 (Table 3). These were applied to the observed number of turtles nesting during the survey periods to estimate the total yearly nesting populations (Table 3 and Figure 1). Nesting populations varied from 81 in 1973 to 220 in 1981, and showed an increasing trend during the 10-year period. The average annual nesting population increased from 126 turtles during 1973-77 to 161 during the following 5-year period. However, the increase in size of the nesting population is not statistically significant.

Survival Rate and Remigration Parameters

The estimates of remigration parameters were relatively insensitive to the assumed annual survival rate during the tag-recapture period. Regardless of whether survival rate was assumed to be 95, 90, or 80%, the probability that a nesting female will, if still live, nest again during the following breeding season was judged to be virtually nil (Table 4). The probability of nesting increases each year thereafter as the "dormant" years accumulate, as shown for a representative case in Figure 2. The associated probability distribution of the remigration interval for this case is shown in Figure 3. In all three cases examined, the most frequent interval between breeding seasons for a female was 3 years (34-37%), followed by 2 years (28-34%), and 4 years (20-23%). The average remigration interval is about 3 years (Table 4).

Considering both survival rates and the sequence of annual nesting probabilities associated with any particular female's mature life, the average female with a possible mature life of 20 years will remigrate an average of 3.8 times if annual survival is 95%, 2.4 times if survival is 90%, and only once if annual survival rate is 80% (Table 4). The chances of remigrating at least once are 86, 74, and 51%, respectively. When survival rate is 95% each year, the most probable number of remigrations during a mature female's life is 6, followed by 7, then 1, 5, 2, 3, 4, 8, and 9. These distributions change markedly with changes in basic remigration parameters and survival rates (Table 4).

Recruitment

Estimates of the average annual recruitment of neophytes to the nesting population at East Island range from 30 turtles under the uniformly high survival rate of scenario 1, to 104 turtles under scenario 12 (Table 5). As expected, the recruitment estimates are inversely related to the assumed average survival rate. The actual average recruitment is probably between 40 and 70 turtles per year.

In 11 of the 12 scenarios, the estimated trend in recruitment over the relevant time period (mid-1960's through 1982) was upward. This result is not necessarily expected. The total nesting population was judged to be increasing over 1973-82, and such a trend might be attributed either to increasing survival rates or to greater recruitments, or both. However, in each scenario the increasing trend in recruitment was statistically insignificant, and the hypothesis of constant recruitment could not be rejected. This was especially so for those scenarios which assumed a dramatic increase in survival; only when a constant survival rate was assumed did the upward trend in recruitment approach significance. Because the two factors are highly confounded, without some independent measures of survival rates or recruitment it will be difficult to evaluate trends in the nesting population.

Population Size

Estimates of the total number of mature females in the East Island population, averaged over 1973-77 and 1978-82, are given in Table 6. In the scenarios with constant survival rate and steady recruitment, population size is also constant, and is estimated to be between about 360 and 400 turtles. Estimates computed under other scenarios are not very useful, because neither the increases in nesting population nor the estimated upward trend in recruitment were statistically significant.

Steady State Characteristics

Assuming constant annual recruitment, we can compute a variety of steady state characteristics of the mature female population under the fixed survival rate scenarios. In particular, it may be shown, using the statistics in Tables 4 and 7, that the expected egg and hatchling production by a single female over her entire mature life is equal to the total annual egg and hatchling production per recruit. Maintenance of this hypothetical equilibrium would require total survival rates from hatchling (entering sea) to neophyte nesters ranging from about 0.4% under scenario 1 to 1.0% under scenario 3. Given an average nesting population of 144 turtles, together with the estimated average recruitment and total mature female population, we can compute the expected number of veteran females in the population and the number of remigrants nesting each year (Table 7). Depending on the assumed survival rate for mature females, the fraction of veterans remigrating each year ranges from 25 to 31%. Under the 80% survival rate, 50% of the nesting population each year would be neophytes. If annual survival rate is 95%, this figure is reduced to 21%.

SUMMARY AND CONCLUSIONS

The average nesting population at East Island during 1973-82 was 144 turtles. There was an upward trend in the yearly number of nesters, but this was not statistically significant.

The average number of neophyte turtles recruiting to the mature female population each year was estimated to be between 30 and 72, depending on the assumed adult female survival rate. The corresponding range in the estimated average total population of mature females was from 397 to 358 turtles. Apparent upward trends in recruitment and the total female population were also statistically insignificant.

Assessment of the adult female stock is complicated by several factors:

(1) While the analysis of tag recapture statistics indicated that annual survival of adult females is high, survival rate and remigration parameters are highly confounded in the estimation model. As a result, a unique and reliable estimate of survival rate was not possible, and further analyses were carried out conditionally, given a variety of assumed survival scenarios.

(2) In the analysis of recruitment and total mature female population, results were weakened by the confounding of survival rate and recruitment, and the absence of a reliable, independent estimate of the survival rate.

(3) In estimating the total nesting population each year, sample counts made during the limited survey periods were adjusted upwards to correct for incomplete coverage. The estimated coverage rates were based on the assumption that the distributions of arrival time, internesting interval, and other factors were the same each year as they were in 1974 and 1975. The same assumption was necessary when the coverage rates were applied to the tag recapture data. Year-to-year variation in the overall residence time distribution could alter the results substantially.

At this juncture, it is apparent that a definitive understanding of the population dynamics of mature females in the East Island breeding colony would require some independent determination of either survival rate or recruitment. Of these, only recruitment could be estimated directly. This would require intensive "saturation tagging" of the entire nesting population each breeding season for many years, and the counting of all untagged and unscarred turtles arriving to nest each year. This is an approach used in other green turtle colonies where access costs are much lower than in the Northwestern Hawaiian Islands. Complete censuses of this type also obviate the need for coverage rate adjustments.

If the primary assessment strategy is to judge the trends in the East Island nesting population on the basis of sample surveys, more work should be done to bolster our understanding of variations in the arrival time distribution and other factors affecting coverage rate. In addition, other types of assessment techniques should be investigated, possibly involving observations on basking turtles as well as nesters. Balazs' excellent program of tagging and recapture should be continued.

Extrapolation of the findings for the mature female population at East Island to other segments of the turtle stock, or to other islands, should obviously be done circumspectly. Balazs estimates that the East Island nesters make up roughly 55% of all females nesting at French Frigate Shoals. On the average, the total nesting female population at French Frigate might then be on the order of 300 turtles, of which perhaps 80-100 are neophytes and the remainder remigrants. The total mature female population associated with French Frigate Shoals is probably about 750 turtles. Speculating further, each year roughly 100 of these die.

With assumptions on sex ratios and comparative survival rates, estimates of the adult male population could be generated based on the figures for females. Alternatively, independent estimates for males might be feasible from analysis of tag returns and basking data, but this seems unlikely.

The analysis here excluded consideration of some major phases in the life cycle. For example, all events associated with the immature stages, and with the "dormant" periods for mature females, were conspicuously neglected. The simple stock-and-recruitment approach adopted treats these other phases as a black box whose inner workings are poorly understood or unimportant. At best, this focusing of attention on the inputs (recruits) and outputs (egg production) of the nesting female population might lead eventually to a predictive relationship between the two variables, as in salmon management. At least, it permits a rough monitoring of the stock. But a genuine understanding of turtle ecology and population dynamics, and the capacity to reliably evaluate management policies, will clearly require concentrated and expensive research on other life stages as well.

LITERATURE CITED

Balazs, George H.

1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-7, 141 p.

Table 1.--Numbers of nesting females tagged on East Island and sighted as remigrants in subsequent years. Data from G. Balazs.

Yearly data

Year of tagging	Number nesting females tagged	Year of resighting				
		1978	1979	1980	1981	1982
1977	38	0	9	8	6	1
1978	52	--	0	3	18	6
1979	52	--	--	0	13	13
1980	45	--	--	--	0	15
1981	120	--	--	--	--	1

Aggregate data

Years after tagging	Total initial release	Total tagged females resighted
1	307	1
2	187	40
3	142	39
4	90	12
5	38	1

Table 2.--Estimated average probabilities of tag retention (at least one tag still attached) for nesting females tagged and resighted at East Island. Based on double-tagging data collected by G. Balazs.

Year of tagging	Year of resighting				
	1978	1979	1980	1981	1982
1977	0.99	0.97	0.95	0.92	0.89
1978	--	0.97	0.94	0.90	0.87
1979	--	--	0.98	0.96	0.94
1980	--	--	--	0.98	0.96
1981	--	--	--	--	0.99

Table 3.--Dates of surveys of nesting female population at East Island, number of turtles seen during these periods, estimated coverage rates, and estimated total nesting populations. Based on data of G. Balazs.

Year	Period	Survey dates From	Survey dates To	Number of nights	Estimated coverage rate	Number of turtles seen	Estimated nesting population
1973	1	1 June	19 July	43	0.81	66	81
1974	1	1 June	19 June	19			
	2	27 June	17 July	21	0.84	104	124
	3	27 July	14 Aug.	19			
1975	1	21 May	21 May	1			
	2	6 June	24 June	19	0.65	104	161
	3	19 July	27 July	19			
1976	1	28 June	11 July	14	0.32	28	88
1977	1	24 June	2 July	9	0.25	44	175
1978	1	9 June	19 June	11	0.39	66	167
1979	1	16 June	28 June	13	0.40	55	136
1980	1	10 June	29 June	20	0.54	45	84
1981	1	26 May	17 June	23	0.58	127	220
1982	1	6 June	24 June	19	0.56	111	199

Table 4.--Various characteristics of hypothetical steady state East Island green turtle population, under three different scenarios. Sources: (1) Assumed value; (2) Estimated by author; (3) Estimated by G. Balazs; (4) Combination of (2) and (3).

Characteristic	Source	Scenario 1	Scenario 2	Scenario 3
• Annual instantaneous mortality rate	1	0.05	0.10	0.22
• Annual survival rate (%)	1	95	90	80
• Remigration parameter α	2	0.4182	0.3863	0.3308
• Remigration parameter θ	2	0.9931	0.9926	0.9912
• Average remigration interval (years)	2	3.0	3.1	3.2
• Probability distribution of remigration interval (%)	2			
1 year		0.7	0.7	0.9
2 years		34.4	32.3	28.5
3 years		37.0	36.3	34.5
4 years		20.0	21.1	22.8
5 years		6.4	7.5	9.8
6 years		1.3	1.7	2.8
7 years		0.2	0.3	0.6
8 years		0.0	0.0	0.1
• Probability of remigrating at lease once during mature life (%)	2	86	74	51
• Probability of never remigrating (%)	2	14	26	49
• Probability distribution of number of remigrations (%)	2			
1 time		12.0	19.3	25.0
2 times		10.3	14.3	12.6
3 times		8.9	10.5	6.4
4 times		8.0	8.0	3.3
5 times		11.5	7.8	1.8
6 times		18.7	8.3	1.0
7 times		13.3	4.5	0.3
8 times		3.2	0.9	0.0
9 times		0.2	0.0	0.0
10 times		0.0	0.0	0.0
• Average number of remigrations	2	3.8	2.4	1.0
• Average number of reproductive seasons	2	4.8	3.4	2.0
• Average number of egg clutches per season	3	1.8	1.8	1.8
• Average number of eggs per clutch	3	104	104	104
• Total egg production during life	4	898	636	374
• Probability of hatching (%)	3	77	77	77
• Probability of emerging (%)	3	71	71	71
• Probability of surviving scramble to sea (%)	3	95	95	95
• Total hatchlings entering sea	4	466	330	194
• Total female hatchlings entering sea (50:50 sex ratio)	4	233	165	97
• Precruit replacement survival rate (%)	4	0.43	0.61	1.03

Table 5.--Estimated average annual recruitments to nesting female population at East Island under different survival scenarios, sign of estimated trend in recruitment and statistical significance of trend (n.s. = not significant, m = marginally significant at 10% significance level). Based on data of G. Balazs.

Scenario	Survival rate (%)		Estimated average recruitment	Sign of trend	Significance of trend
	Pre-ban	Post-ban			
1	95	95	30	+	m
2	90	90	43	+	m
3	80	80	72	+	m
4	90	95	41	+	m
5	80	95	60	+	n.s.
6	70	95	74	-	n.s.
7	85	90	54	+	m
8	75	90	72	+	n.s.
9	65	90	85	+	n.s.
10	75	80	82	+	m
11	65	80	95	+	n.s.
12	55	80	104	+	n.s.

Table 6.--Estimated average mature female population during two time periods, under two recruitment assumptions and 12 survival scenarios. Based on data of G. Balazs.

	Constant recruitment Average mature female population		Linear recruitment Average mature female population	
Scenario	1973-77	1978-82	1973-77	1978-82
1	397	397	317	441
2	387	387	306	426
3	358	358	280	392
4	362	411	305	434
5	296	420	280	424
6	246	418	254	416
7	352	397	294	421
8	290	404	267	411
9	243	402	240	402
10	326	363	266	387
11	272	367	240	381
12	232	366	215	374

Table 7.--Numbers of recruits, veteran females, remigrants and total nesting females for three steady state scenarios. Based on data of G. Balazs.

	Scenario		
Characteristics	1	2	3
•Neophytes recruited per year	30	43	72
•Total mature female population	397	358	358
•Number of veteran females	367	344	286
•Average remigration fraction (%)	31	29	25
•Number of remigrants	114	101	72
•Total nesting population	144	144	144

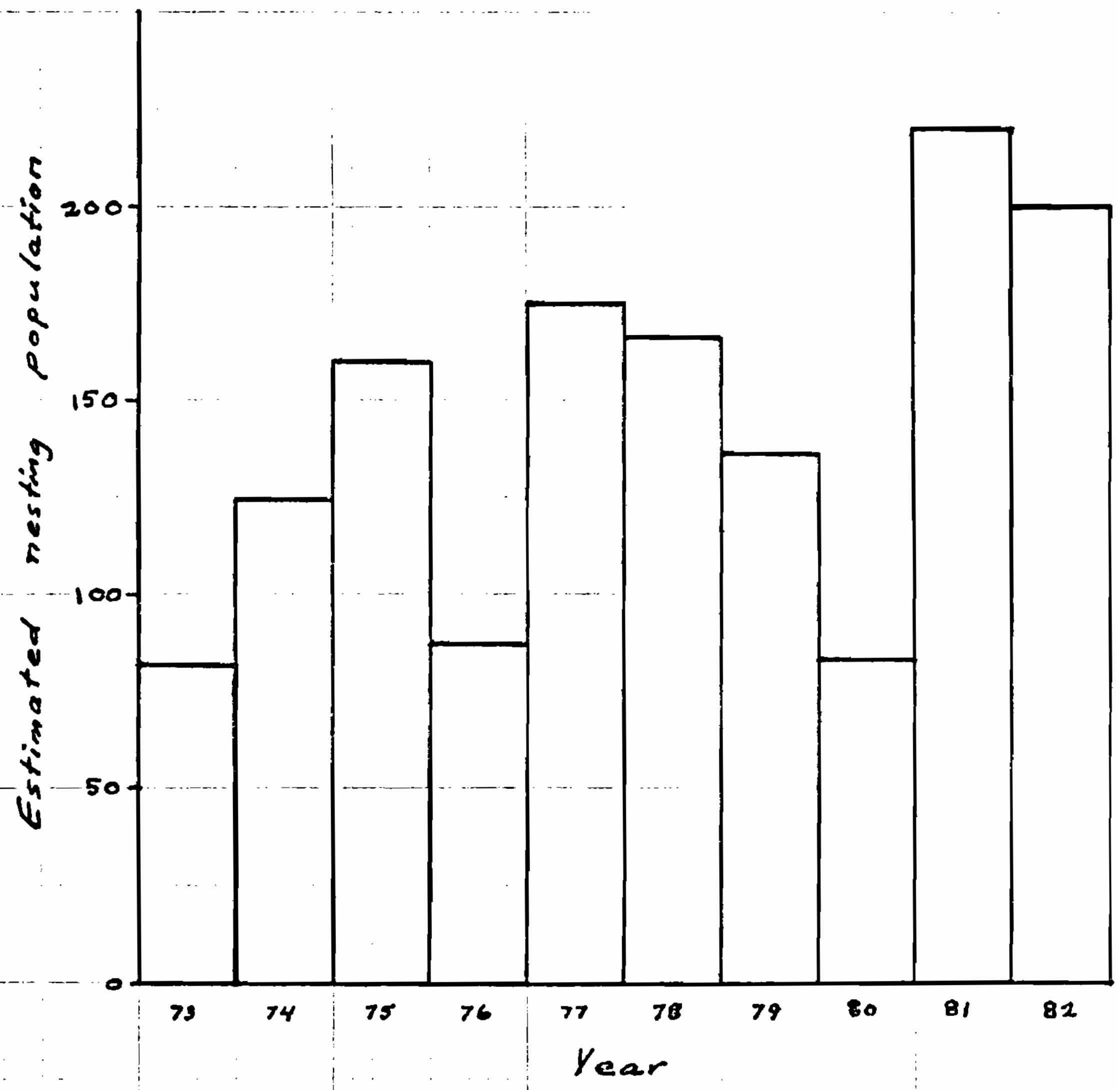

Figure 1.--Estimated nesting population at East Island, 1973-82.
Based on data of G. Balazs.

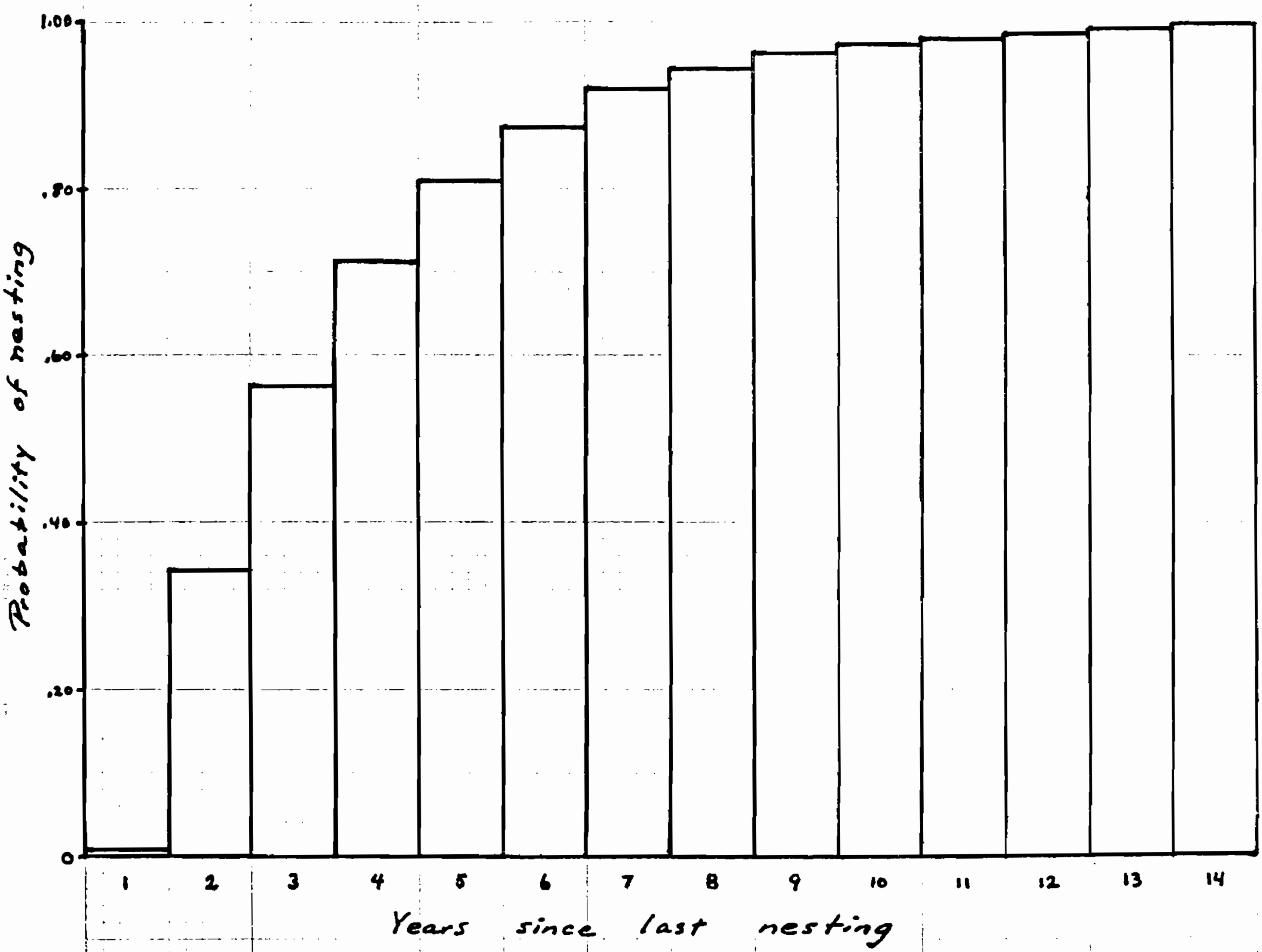

Figure 2.--Probability of hauling out and nesting as a function of years elapsed since last nesting, for females at East Island. (α = 0.42, θ = 0.99)

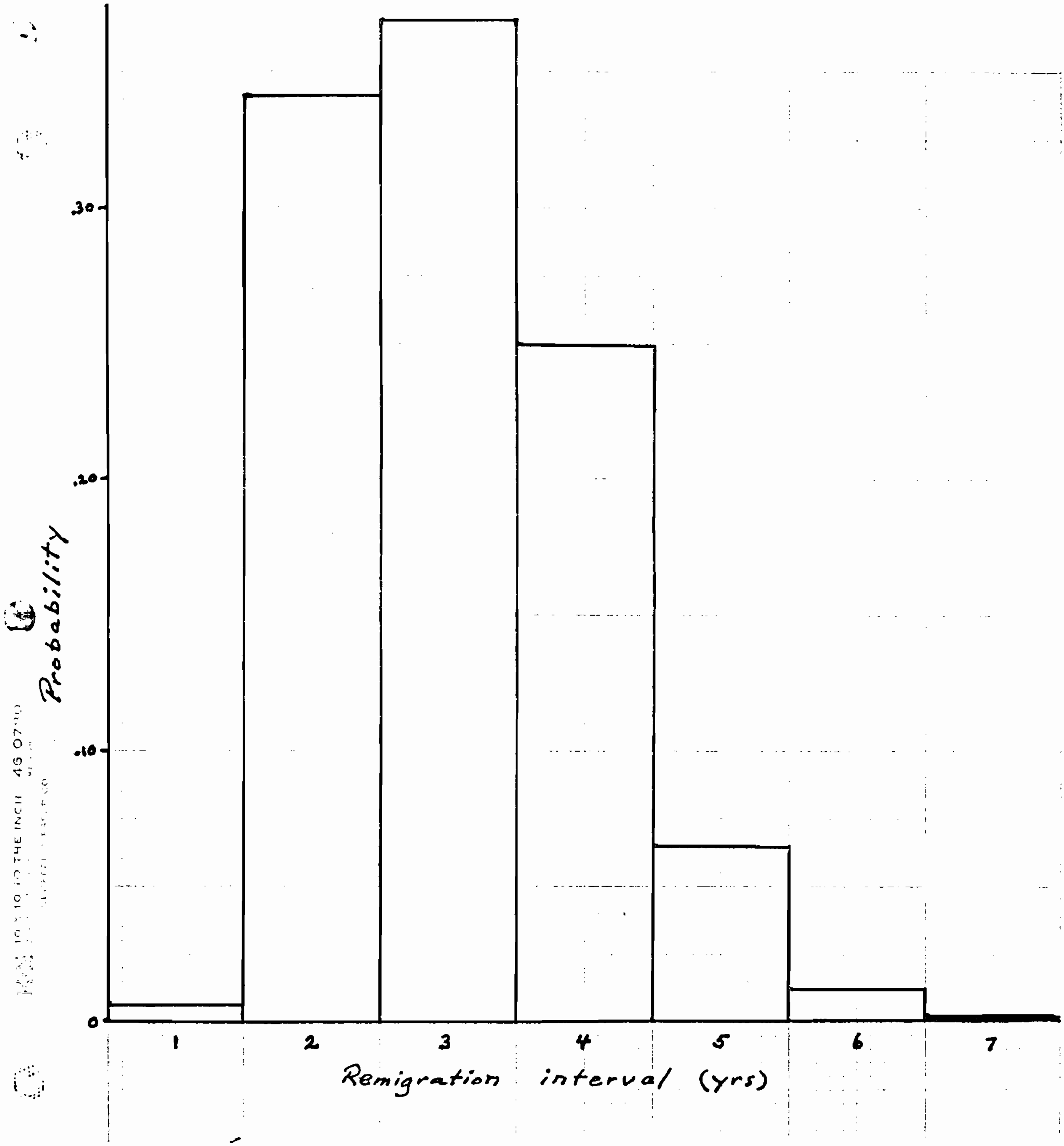

Figure 3.--Probability distribution of the remigration interval (years between successive nestings) for females at East Island. (α = 0.42, θ = 0.99)