AN ABSTRACT OF THE THESIS OF

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Title: AN ANALYSIS OF THE POPULATION DYNAMICS OF SELECTED AVIAN SPECIES

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The impact that pesticides may have had on the mortality rates and productivity rates of non-game birds during the last 25 years was evaluated by studying the population dynamics of 16 species. A mathematical model showing the relationships between population parameters that yielded stable populations was developed. The information needed for the model included: (1) mortality rate schedule (obtained from recoveries of banded birds), (2) productivity rates, and (3) the age of sexual maturity. Production requirements for a stable population and annual rate of change (increase or decrease) in population levels were estimated. Population parameters were compared to determine if changes had occurred between time periods (i.e., 1925-1945 vs. 1946-1965). The great horned owl, red-shouldered hawk, sparrow hawk, osprey, barn owl, Cooper's hawk, red-tailed hawk, great blue heron, black-crowned night heron, brown pelican, barn owl, chimney swift, blue jay, black-capped chickadee,

cardinal, and robin were subjected to this analysis.

No increase in post-fledging mortality rates in any of the species has occurred since 1945. Therefore, accelerated decline in the species studied must have resulted from lowered reproductive rates. Mortality rates have decreased in the Cooper's hawk, sparrow hawk, great blue heron, and brown pelican. A decrease in shooting pressure was associated with decreased mortality rates.

Evidence of declining reproductive rates were found in the brown pelican, osprey, Cooper's hawk, red-shouldered hawk, and sparrow hawk. No changes in reproductive rates were noted in the red-tailed hawk, great horned owl, or barn owl. Information on productivity rates was not available for comparison with the other species although rates of productivity essential for a stable population were estimated. This work will provide the basis for making comparisons in future studies.

No change in reproductive rates was apparent among species feeding primarily on mammals. Species exhibiting a lowered reproductive success since 1945 were those whose major food items consisted of fish, reptiles, amphibians, or birds. Lowered reproductive success was accompanied by a decrease in eggshell thickness. Other investigators have reported that sparrow hawks and mallard ducks fed a diet of DDE and dieldrin have produced thin eggshells under laboratory conditions, and exhibited a lower reproductive success. Many bird species which consume food in which chlorinated hydrocarbon pesticides have been concentrated through a series of transfers along food chains have declined. The chlorinated hydrocarbon pesticides are believed responsible.

An Analysis of the Population Dynamics of Selected Avian Species

by

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INTRODUCTION

This study was designed to evaluate the impact of pesticides on the mortality rates and productivity rates of non-game birds. It is known that applications of DDT and other pesticides can cause high mortality among songbirds. Initial appraisals of effects of DDT on songbirds during the songbirds' nesting season (Hotchkiss and Pough 1946, George and Stickel 1949, Robbins and Stewart 1949, among others) centered on folior applications that were carried out by aerial spray or by hydraulic equipment. Various workers (cited in Bernard 1963) have shown that robin (Turdus migratorius) populations are reduced, sometimes catastrophically, in areas heavily treated with DDT for control of Dutch Elm Disease. Robins dying on one area were estimated at not less than 86 to 88 percent of the population (Hickey and Hunt 1960).

Leopold (1933) presented two general approaches to assess the condition or status of wild populations almost 40 years ago. The approaches were (1) to measure the populations on hand by census, and (2) to measure the productivity of a species and compare it with a standard.

The first approach required less information about the birds and has been in general use on a localized scale since the early 1930's.

Numbers of birds are easily estimated by a census based on sight and sound during the nesting season (Rudd 1964). The magnitude of loss of a bird population resulting from pesticide use on small areas has been determined by making inventory counts before and after applications of the pesticides. Counts of dead birds on study areas following applications of chemicals have also been used. The ability to detect losses among bird populations was tested in an experimental study on a 100-acre area at the Patuxent Wildlife Research Center in Maryland. When approximately 50 percent of the population of certain species was removed artificially, standard census techniques indicated a reduction in the population, but estimates of the loss were only one-fourth of the actual reduction. Repopulation had obscured much of the reduction in a very few days (Buckley 1963). The high degree of mobility of birds makes their absence from a study area inconclusive evidence of mortality, and rapid re-entry to vacated ecological niches by others of the same or similar species further compounds the difficulties in determining the mortality resulting from application of chemicals. Breeding bird surveys which may be able to detect changes in numbers at a regional level have been conducted only since 1966 (Robbins and Van Velzen 1967).

A method of measuring mortality that is not completely dependent on the capability of a research worker to identify pesticide-caused deaths in the field is desirable. Measurement of the productivity of a species (Leopold's second approach) coupled with a production standard was the only alternative available. This approach was utilized in this study. The following were basic to this approach: (1) a source of data which will provide mortality rates for the various species, (2) basic information on the life history of the species of interest, e.g., age of sexual maturity, annual productivity, etc., and (3) a model for relating the mortality rates of the species to the productivity rates necessary for maintaining a stable population, in addition to estimating the rate of change in the populations (stable, increasing, or decreasing).

Fortunately, a bird banding program has been conducted in North America since approximately 1920. These banding data may be used for estimating annual mortality rates of the species. Pioneer banders were interested principally in describing migration routes, but Lincoln (1926) anticipated many additional uses for the collection of banding data. He cautioned that time would be required for sufficient bandings and recoveries to accumulate before conclusions could be reached for any one species. Approximately 20 million birds have been banded since the early 1920's and three-fourths of the bandings occurred on non-game species. The steadily increasing records of banding recoveries has led Davis (1951) to discuss the potentials in these random samples accumulated from wide geographic areas over long periods of time. These records have the potential to provide a continuous monitoring system for avian populations. Hickey (1952) used banding data as the basis for his noteworthy paper on the mortality rates of waterfowl and other American birds.

In this study, it was concluded the quantities of band recoveries were sufficient to provide information on the mortality rates for the 16 species. In addition, I have found that many of the techniques for analyzing band recoveries developed for game species during the last 20 years were equally applicable to the non-game species.

Information available on the life histories of the 16 species was somewhat variable in quality. Therefore, several of the estimated population parameters must be regarded as tentative, since complete nesting studies are lacking for several of the species. Numerous authors have made pleas for continuation of studies of life histories and Harper (1967) has called the strategy of the life cycle itself an ecologically fascinating but neglected subject of study.

The relationships between the life history elements automatically lead to a theoretical approach to population phenomena, because such relationships are often nothing more than interconnections of various aspects of the same process. Henry (1957:106) presented the following five reasons why the theoretical approach to population phenomena is necessary:

> (1) some phenomena cannot be understood without the help of a model. . . , (2) results obtained may be difficult to interpret without proceeding to their mathematical analysis, (3) inconsistent results are observed, (4) only fragmentary data may be available but the population concerned belongs . . .

> to a certain type . . . , and (5) . . . it is necessary to make a synthesis.

A mathematical model (Henny _et al._ 1970 in press) was used for estimating the parameters necessary to maintain stable populations. The use of this model was dependent upon knowing the schedule of mortality rates for the population, the age at which the species breeds, and the recruitment rates or age ratios in the population. Computations based on the model and estimates of the parameters for the population yield production requirements per breeding female that are necessary to maintain a stable population. These computations, for the purposeses of this thesis, will be known as the _modeling approach_ and the production required to assure a stable population will be known as the _production standard._ Thus, ornithologists conducting nesting studies will have a production standard for comparison with their observed results. An additional advantage of the modeling approach is that it quickly makes the investigator aware of information that is needed--thus pointing out possible topics for future research.

The objectives of the research were: (1) to estimate mortality and productivity rates of each species during different time periods (e.g., 1920-1945, 1946-1956, 1957-1965), (2) to compare mortality and productivity rates within subpopulations in various geographical locations, (3) to compare changes in mortality and productivity rates of birds with similar and dissimilar food habits within geographical locations, and (4) to estimate annual rates of change (increase or decrease) in population numbers. Observed changes in population parameters will be discussed in terms of the biology and ecology of the species. This study emphasized determination of the status and population dynamics of the species. However, causes for changes in population parameters are discussed when pertinent literature is available.

Demographic information collected during the last 50 years for 16 bird species is summarized and compared in this report. The results for 4 of the 16 species (osprey (Pandion haliaetus), barn owl (Tyto alba), red-tailed hawk (Buteo jamaicensis), and Cooper's hawk (Accipiter cooperii)) have been published (Henny 1969, Henny and Wight 1969, Henny and Ogden 1970, Henny and Wight 1970, in press); results will be discussed and summarized but the actual data will not appear. Other species in this study include: great horned owl (Bubo virginianus), red-shouldered hawk (Buteo lineatus), sparrow hawk (Falco sparverius), great blue heron (Ardea herodias), black-crowned night heron (Nycticorax nycticorax), brown pelican (Pelecanus occidentalis), barn swallow (Hirundo rustica), chimney swift, blue jay (Cyanocitta cristata), black-capped chickadee (Parus atricapillus), cardinal (Richmondena cardinalis), and robin.

Breeding surveys at the regional level for non-game birds were not conducted in North America until 1966 (Robbins and Van Velzen

1967); thus changes in population levels (by a census index) prior to this date could not be made. I am hopeful that the population dynamics approach used in this study will be combined with the breeding bird survey in the future to determine the status of our avifauna. The two approaches should complement each other.

METHODS

Sources of Data

Records of birds banded in North America during the last 50 years were the major source of data. These records were stored at the Bird Banding Laboratory of the Migratory Bird Populations Station in Laurel, Maryland. Duplicate computer tapes containing banding and recovery records for all species were obtained from the Bird Banding Laboratory the summer of 1967. Records of bandings prior to December 31, 1965 and recoveries prior to December 31, 1966 were used. Analysis was made with the aid of the Oregon State University Computer Center.

Analyses of mortality rates alone (based on the band recovery data) would not provide enough information to determine the status of any population. In fact, in an osprey population that was rapidly declining during the last 20 years, no apparent changes in post-fledging mortality rates could be detected (Henny and Wight 1969). Information on productivity rates was needed. To obtain this information, a questionnaire was sent to approximately 200 persons banding hawks and owls. Included was a standardized data form which requested information concerning time and place of banding, clutch size, and the number of young that were banded per nest. Correspondence with these banders provided substantial numbers of unpublished nesting records from many locations in the United States and Canada which were used as an index to productivity. When the bander was unable to supply the information requested, the original banding schedules were checked. Some banders identified the young birds banded from each nest on their banding schedules. Additional clutch size data were obtained from museums, egg collectors, and nest record schemes. A list of these cooperators is included in the appendix.

Procedures for Analyzing Population Data

Three computer programs and data from 54 species of birds were used in this study. Quantity of the data available for each species was determined in the first program. North America was divided into eight geographical regions (nearly equal in size) and data were analyzed for each region. Sex and age designations for each month of banding were compiled and reviewed by Mr. Chandler S. Robbins, Chief of the Non-Game Bird Section of the Migratory Bird Populations Station, and Mr. Willet T. Van Velzen of the same Section. When plumage characteristics were such that the average bander could not be expected to determine accurately the sex or age of a species, the birds' records were reclassified as to either sex unknown or age unknown. Movements of the migratory species were analyzed with the aid of the second computer program. The regional scheme for analysis was used, and the extent of mixing of populations between regions was noted. Recovery data were compiled into life tables and age-specific mortality rates were computed for the various species in a third computer program.

Sources of Error

Hickey (1952) has discussed the sources of error and the accuracy of bird banding data. Clerical errors in the records are present; however, the sample sizes from each species studied are large and these errors appear unimportant in the overall conclusions. Loss of bands has been discussed by Hickey 1952, Farner 1955, Berger and Mueller 1960, Paynter 1966, Martinson and Henny 1967, and Ludwig 1967. Loss of bands resulting from wear after the band has been on the bird for several years would cause the mortality rates to be over-estimated. "Initial loss" within a few days of the date of banding would have little or no effect on mortality estimates made from the life table approach. Plotting the number of birds alive at the beginning of each year (obtained from the life tables) on a semi-logarithmic scale will indicate if loss of bands is occurring. Loss of bands at a gradually increasing rate would cause the plotted points to deviate from a straight line if annual mortality among adults is constant. Loss of bands was negligible in the species studied (Figure 1).

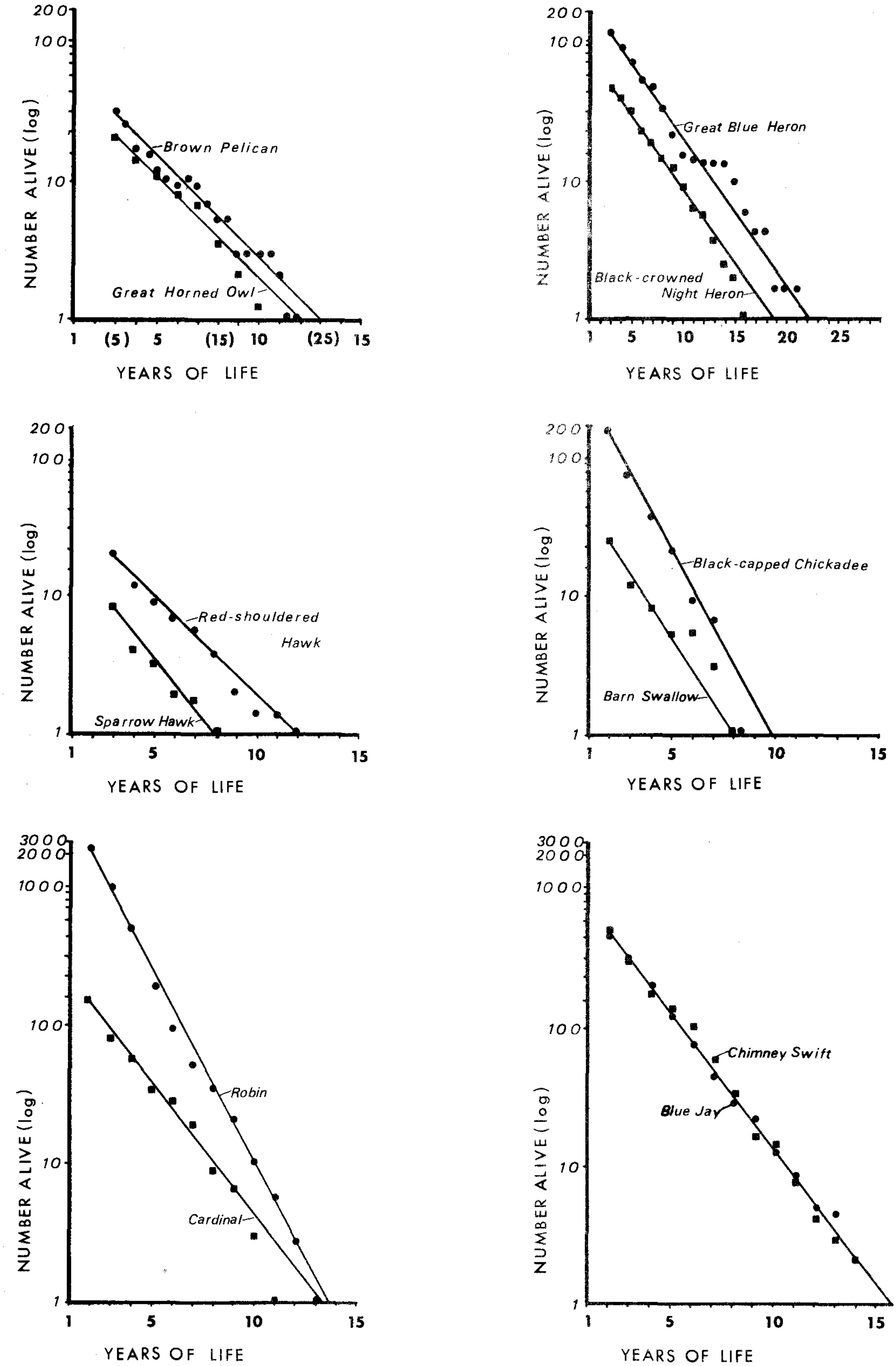

Figure 1. A semi-logarithmic plotting of the number of birds from banded cohorts alive at the beginning of each year. The years of life for the brown pelican are in parentheses.

Life Tables

The composite dynamic life table (Hickey 1952) was used for estimating mortality rates. Haldane's (1955) method was used to calculate the standard error of the mean for the mortality rates. The recoveries used in the life tables were subdivided into four groups depending on the ways recoveries were obtained: (1) birds shot, (2) birds found dead, (3) unsure recoveries (not sure if bird was dead, or alive and subsequently released), and (4) all birds combined. If no significant differences in the mortality rate estimates were detected between the results of the four methods of obtaining recoveries, they were all grouped together. All recoveries except those of brown pelicans were combined. A large percentage of band recoveries from pelicans were obtained by "entanglement in fishing gear" or "caught by hand." Many of these birds were alive at a later date (recaptured again). Therefore, information about these recoveries and other birds that were not known to be positively dead (example, "no information") was omitted from the life table for brown pelicans. This problem was not apparent in the other species.

Many non-game birds have very low recovery rates but relatively high return rates. A bird dead at the time of discovery is considered a recovery; a bird alive and subsequently released is identified as a return. Returns are usually obtained from banders who retrap birds in the same population over a period of years. The large number of returns was not grouped with the recoveries in the life tables as mortality rates calculated from trapped samples were higher than those from samples of birds recovered dead (Plattner and Sutter 1947). However, an attempt was made to use the large number of returns in life tables for the chimney swift.

Initial Date

An initial date for recoveries used in life tables must be selected before beginning to use data on birds banded (Farner 1949, 1955, Hickey 1952). The initial date is critical in this study since all mortality must be accounted for, either directly by observation at the nest, or indirectly from the banding data. Life tables based on banding of nestlings should start with the mean date on which the nestlings were banded (Paynter 1947, Deevey 1947). However, Hickey (1952) believes such a date would introduce sampling variables of unknown influence. Total mortality might be accurately recorded by the investigators if a research station were located at or near the nesting colony; however, reports from the public constitute an entirely different type of sampling after birds disperse. Very young birds are less evident to the casual observer than those of larger adult birds, therefore, estimates of first-year mortality rate based on band recoveries would tend to be underestimated (Hickey 1952). Hickey concluded that the two types of mortality data could be mixed for computing a first-year mortality rate.

With the exception of the colonial nesting brown pelican, I have used the date of banding as the initial date for the species banding as nestlings. Prefledging mortality of the brown pelican was estimated from direct observation by individuals in South Carolina, and the initial date for the life table analysis corresponded to the date the birds left the area. Most species banded as nestlings and analyzed during this study were large birds except the barn swallow. When birds were banded as adults or of unknown age, an initial date of January 1 generally was used. This date was suggested by Farner (1949) since most birds have an adult mortality rate schedule by the first January 1 after banding. Therefore, even though the actual age of the bird is unknown, all can be classified as adults due to their similar mortality rate schedules. The exceptions are noted and discussed in the text.

The Model

Evaluation of the balance between observed recruitment to the population and estimated mortality in the population is basic to this study. The recruitment data may be obtained from nesting studies or from estimates of the populations' sex and age ratios. Status of the population (rate of annual change) may be estimated with a mathematical model that was developed for this study (Henny *et al*. 1970 in press).

when recruitment rates, mortality rates, and age of sexual maturity are given. The usefulness of the model is increased when it can be used for species which begin breeding at any given age. Four modifications of the model may be used to provide information about the status of the population: (1) necessary production for a stable population, (2) allowable mortality for a stable population, (3) annual rate of change in population size, and (4) age ratios in the population which yield a stable condition. The formulas for production necessary for a stable population are as follows:

(1) A proportion of the population reaches maturity at the end of the first year of life, and all older birds breed.

$$\bar{m} = \frac{1 - s}{s_o(s_1 + p_1(1-s))}$$

(2) All of the population reaches maturity at the end of the first year of life, and all older birds breed.

$$\bar{m} = \frac{1 - s}{s_o(1-s+s_1)}$$

(3) A proportion of the population reaches maturity at the end of the second year of life, and all older birds breed.

$$\bar{m} = \frac{1 - s}{s_o s_1(s + p_2(1 - s))}$$

(4) All of the population reaches maturity at the end of the second year of life, and all older birds breed.

$$\bar{m} = \frac{1 - s}{s_o s_1}$$

(5) All of the population reaches maturity at the end of the third year of life, and all older birds breed.

$$\bar{m} = \frac{1 - s}{s_o s_1 s}$$

where,

$\bar{m}$ = the average number of female fledglings produced per breeding age female ($2\bar{m}$ = the total number of young produced per breeding female assuming an equal sex ratio of fledglings).

s = 3rd-year and later survival rate.

s_o = 1st-year survival rate.

s_1 = 2nd-year survival rate.

p_1 = proportion of 1-year-olds attempting to nest.

p_2 = proportion of 2-year-olds attempting to nest.

A similar family of formulas was used to calculate the annual rate of population change:

(1) All of the population reaches maturity at the end of the first year of life, and all older birds breed.

$$\bar{m}* = \frac{(1+u-s)(1+u)}{s_o(1+u-s+s_1)}$$

(2) All of the population reaches maturity at the end of the

second year of life, and all older birds breed.

$$(1 + u)(1 + u - s) = \overline{m}^* s_o s_1$$

(3) All of the population reaches maturity at the end of the third year of life, and all older birds breed.

$$(1 + u)^2(1 + u - s) = \overline{m}^* s_o s_1 s$$

where,

u = the proportion change per year in the population.

$\overline{m}^*$ = the observed productivity rate per breeding bird.

This modeling approach was particularly useful in evaluating the recent impact of environmental contamination on the mortality and recruitment rates of the species studied. Research on pesticides, or any other ecological work, traditionally has taken one of three approaches: (1) the laboratory experiment, (2) the field experiment, or (3) a combination of the first two. Ideally, these experiments have controls. However, controls in field experiments involving pesticides are usually lacking, since essentially no area today is pesticide-free. I have attempted to substitute for the lack of controls by using information gathered prior to 1945 as a "substitute control group." I believe these data represent populations with little or no exposure to modern pesticides.

Statistical Tests

Mortality rate estimates were compared between time periods and geographical locations by the students' t-Test:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{(se_1^2 + se_2^2)^{\frac{1}{2}}}$$

where,

$\bar{x}_i$ = mean mortality rate estimate.

se_i = standard error of the mean.

The probability level of 0.05 was used throughout the study as the value for significant difference.

In summary, the population dynamics approach used in this study involved the determination of six parameters: (1) a tabulation of clutch-size information by time period, (2) a tabulation of the number of young banded per successful nest by time period (index to productivity), (3) calculation of mortality rates by time period, (4) determination of the age at which the species attains sexual maturity, (5) determination of the recruitment schedule required to balance the mortality schedule, and (6) calculation of the annual rate of increase or decrease of the population (based on observed recruitment schedule and observed mortality schedule).

Density-dependent or environmental factors may influence any of the population parameters mentioned above; however, since the information used in this paper was obtained over a long period of time, the average values may be used effectively. Therefore, the parameters estimated from these models do not measure annual fluctuations but refer to the long-term (average) characteristics. Therefore, I would caution against comparing the production requirement for a stable population with observed production rates obtained from localized, short-term studies.

GREAT HORNED OWL

The great horned owl occurs in America, exclusive of the West Indies, from the limit of trees in the Arctic to the Straits of Magellan (AOU 1957). Ten subspecies have been recognized in North America. The North American breeding range has been subdivided into eight geographical regions for this study (Figure 2). The subdivisions were based principally on the amount of nesting data available.

Breeding Cycle and Migration

Great horned owls are nonmigratory as they do not make regular seasonal journeys between breeding and wintering grounds (Bent 1938). Of 434 band recovery records, 405 (93 percent) were from birds taken within 50 miles of the banding sites which indicates very little movement (Stewart 1969). Stewart also found that fewer southern than northern birds made long distance travels; he believed that most of the movement was made by young birds. The large number of subspecies (10) recognized in North America (AOU 1957) further indicates that the birds are relatively sedentary. Baumgartner (1939) found that great horned owls in Kansas remained at their nesting sites throughout the year, except possibly for a few months in late summer and fall. Craighead and Craighead (1956) observed paired birds in the fall and early winter that remained at their nesting sites throughout the

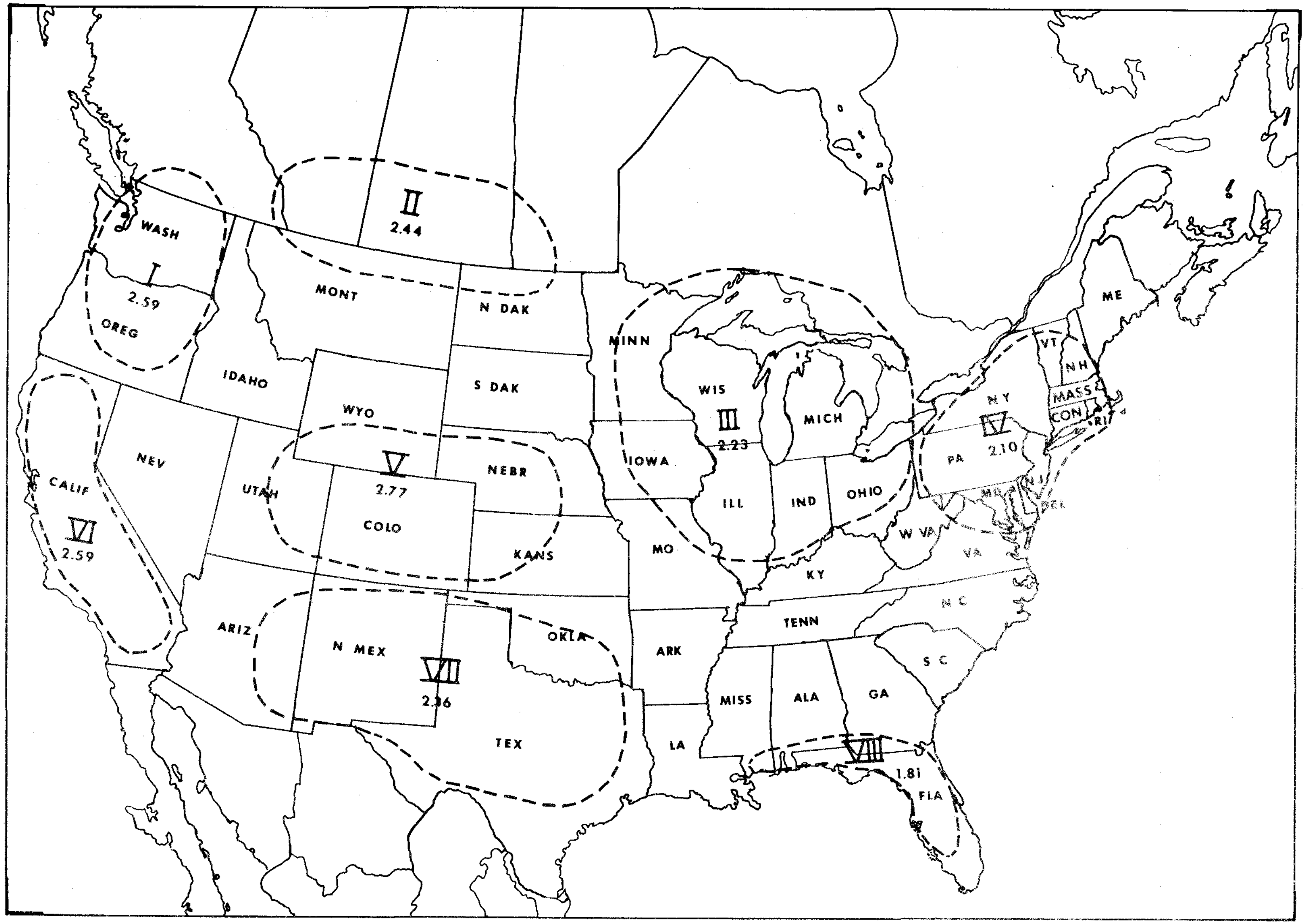

Figure 2. The eight subdivisions used for the productivity analysis of the great horned owl. The numbers indicate the clutch size.

prenesting period.

The great horned owls are one of the first North American species to begin nesting. Their eggs have been taken in late November and early December in Florida (Forbush 1927). A direct correlation can be made between latitude and date of laying. In Labrador sets often are not completed until after the first of April (see Baumgartner 1938 for details).

Nesting Parameters

Clutch Size

Clutch size of great horned owls in the United States and Canada generally increased from south to north and from east to west. The exception to this was in the Rocky Mountain states (Region V), where the largest average clutch size occurred (Table 1).

Annual variations in clutch size of great horned owls have been reported. Dixon (1914) noted that horned owls tend to lay larger clutches of eggs during wet seasons than during dry seasons. He suggested these differences may be related to food availability. Randall (after Baumgartner 1938) commonly found clutch sizes of two or three eggs in his region, but in 1932 all nests that he examined contained four eggs or young. Randall also felt that clutch size was related to food availability. Houston (1960) reported 1960 as "the year of the

Table 1. Clutch size and number of young banded per successful nest for great horned owls in the United States and Canada.

REGION I[a]

Clutch size Classes	Clutch size Obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	0	0	--	3	3
2	7	2	--	4	6
3	10	0	--	2	2
4	0	0	--	0	0
Mean	(2.59)±0.58[b]	(2.00)±0.00		(1.89)±0.78	(1.91)±0.70
Sample size	17	2	--	9	11

REGION II

Classes	Clutch size obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	1	5	16	57	78
2	9	5	18	98	121
3	7	6	18	60	84
4	1	0	2	4	6
Mean	(2.44)±0.70	(2.06)±0.85	2.11±0.88	2.05±0.77	2.06±0.80
Sample size	18	16	54	219	289

REGION III

Clutch size Classes	Clutch size Obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	1	15	76	24	115
2	41	33	107	64	204
3	14	7	10	7	24
4	0	0	0	0	0
Mean	2.23±0.47	1.85±0.62	1.66±0.57	1.82±0.55	1.73±0.58
Sample size	56	55	193	95	343

REGION IV

Classes	Clutch size obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	1	9	15	5	29
2	25	15	13	6	34
3	4	0	3	1	4
4	0	0	0	0	0
Mean	2.10±0.40	1.63±0.49	1.61±0.67	(1.67)±0.65	1.63±0.60
Sample size	30	24	31	12	67

Table 1. (Continued)

REGION V

Clutch size Classes	Clutch size Obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	0	2	4	7	13
2	11	7	7	12	26
3	15	3	6	7	16
4	4	0	0	1	1
Mean	2.77±0.68	(2.08)±0.67	(2.12)±0.78	2.07±0.83	2.09±0.77
Sample size	30	12	17	27	56

REGION VI

Clutch size Classes	Clutch size obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	1	3	3	1	7
2	43	7	13	2	22
3	39	1	5	0	6
4	8	0	0	0	0
Mean	2.59±0.67	(1.82)±0.60	2.10±0.62	(1.67)±0.58	1.97±0.62
Sample size	91	11	21	3	35

REGION VII

Clutch size Classes	Clutch size Obs.	No. banded (obs.) 1925-1945	1946-1959	1960-1968	Totals
1	0	0	4	8	12
2	17	1	21	17	39
3	7	1	5	2	8
4	1	0	0	0	0
Mean	2.36±0.57	(2.50)±0.70	2.03±0.56	1.78±0.58	1.93±0.58
Sample size	25	2	30	27	59

REGION VIII

Clutch size Classes	Clutch size obs.	No. banded (obs.) 1925-1945	1945-1959	1960-1968	Totals
1	7	2	1	0	3
2	13	2	7	1	10
3	2	1	0	0	1
4	1	0	0	0	0
Mean	1.87±0.76	(1.80)±0.84	(1.88)±0.39	(2.00)±0.00	(1.86)±0.53
Sample size	23	5	8	1	14

[a]Regions refer to those shown in Figure 2.

[b]Sample size $<$ 20 enclosed in parentheses, and the standard deviation.

owls" in Saskatchewan. He banded an average of 2.48 young per nest from 44 nests which is slightly higher than the average clutch size previously reported in the region (2.44). Increases in clutch size have been reported for other species of owls in years when the food supply was abundant. Short-eared owls (Asio flammeus) generally lay four eggs but may lay as many as nine when voles are abundant (Lack 1968). Similarly, the number of nestling barn owls banded per brood in southern California was highly variable from year to year and ranged from a high of 4.71 to a low of 2.75 (Henny 1969).

Fledging Rate and Nest Success

The number of young per successful nest that reached a size large enough to be banded was used as an index to the fledging rate. Of primary concern in this study was the comparison between the number of young banded per successful nest prior to 1946 (the "pre-pesticide" era) with subsequent information (1946-1959 and 1960-1968). Chi-square tests indicated no significant change in the number of young banded per successful nest between these time periods (Table 1).

In the regions with 20 or more nesting records available, an estimated 75 to 82 percent of the eggs in successful nests yielded young large enough to band (Table 2). The highest percentage of the eggs that produced banded young occurred in the regions with smaller average clutch sizes. In Region II which includes Saskatchewan, the average number of young fledged per successful nest is probably overestimated because a large percentage of the data were taken in 1960 when productivity was exceptionally high (Houston, personal communication).

Table 2. The relationship between the number of young great horned owls banded per successful nest and the average clutch size in each region.

Location	Clutch size	No. banded[a]	Percentage of eggs yielding bandable young
Region I	(2.59)[b]	(1.91)	(74)
Region II	(2.44)	2.06	(84)
Region III	2.23	1.73	78
Region IV	2.10	1.63	78
Region V	2.77	2.09	75
Region VI	2.59	1.97	76
Region VII	2.36	1.93	82
Region VIII	1.87	(1.86)	(99)

[a] An average for the complete time span (1925-1968) since no significant differences between time periods were detected.

[b] Sample size < 20 enclosed in parentheses.

Nesting studies (Table 3) provided information to indicate that 78 percent of the nesting attempts were successful.

Table 3. Nesting success of the great horned owl.

Location	Years	No. active nests	No. successful nests[a]	Source
California	1939	5	2	Fitch 1940
New York	1949-1952	18	16	Hagar 1957
Wisconsin	1953-1955	41	33	Orians and Kuhlman 1956
Totals		64	50 (78%)	

[a]A successful nest has one or more young fledged from it.

Population Dynamics

Mortality Rates

Band recovery data have been previously used to estimate mortality rates for great horned owls (Hickey 1952, Stewart 1969). Hickey used recovery records available on July 30, 1946 for the development of a life table. However, he considered the analysis to be preliminary and indicated that further analysis should be made when more data have been accumulated. Stewart (1969) used recoveries of birds banded as nestlings prior to 1951 and recovered prior to November 30, 1962. His estimate of first-year mortality rate was 0.464 (refers to percent of that age class which dies the first year), second-year 0.404, and the adult mortality rate 0.290. The overall annual mortality rate was 0.379 ± 0.049 (recalculated from Stewart's data). In following the normal procedure for these analyses, a mortality estimate was made for the period 1946-1965 so that comparisons could be made with Stewart's earlier information (Table 4). No significant difference in the overall annual mortality rates was detected (t = 0.99).

Because of the relatively low first-year mortality rates (0.464 and 0.525), the comments of two authors regarding the early breeding season are mentioned. Orians and Kuhlman (1956:383) stated, "... the breeding season may be early because postfledging survival is better in early broods which learn to hunt and disperse in the early autumn when hunting is easy." The authors mentioned the possibility of a low first-year mortality rate long before the band recovery records were analysed.

Age of Sexual Maturity

Non-breeding individuals have been observed in populations of great horned owls by Craighead and Craighead (1956), Orians and Kuhlman (1956), and Hagar (1957). Results of above studies showed little variation in the percent of the population not nesting (Table 5). The proportion of non-nesting birds in the population led Craighead and Craighead (1956) and Orians and Kuhlman (1956) to suggest that great horned owls do not nest until the second year. Weller (1965) studied bursa depths and the gonad cycle in an effort to determine the age of sexual maturity of the great horned owl. He found that the bursa of Fabricius regresses at approximately two years of age and serves as a fair method of determining age. Weller (1965:111)

Table 4. Estimates of mortality rates for great horned owls banded as nestlings in the United States and Canada between 1946 and 1965.

Year	No. banded	Years survived										First year recovery rate
		1	2	3	4	5	6	7	8	9	10	
1946-1950	319[a]	16	4	1	3	1	0	1	1	0	1	---
1951	54	3	1	0	0	0	0	0	0	0	0	.056
1952	83	7	1	2	0	0	1	2	0	0	0	.084
1953	104	6	3	0	0	1	0	0	0	0	0	.058
1954	81	2	0	1	1	0	0	0	0	0	0	.025
1955	119	1	2	0	0	0	0	0	0	0	0	.008
1956	91	6	5	2	0	0	0	0	1	1	0	.066
1957	103	5	1	1	0	0	0	0	0	0		.049
1958	124	9	3	0	1	0	0	0	0			.073
1959	185	12	4	2	1	1	1	1				.065
1960	227	12	5	6	1	2	1					.053
1961	143	5	2	0	0	1						.035
1962	75	2	2	1	1							.027
1963	99	4	0	0								.040
1964	264	13	6									.049
1965	144	8										.056
Totals	2215	111	39	16	8	6	3	4	2	1	1	.050
No. available		2215	2071	1807	1708	1633	1490	1263	1078	954	851	
Rec/1000		50.11	18.83	8.85	4.68	3.67	2.01	3.17	1.86	1.05	1.18	
Alive at beginning		95.41	45.30	26.47	17.62	12.94	9.27	7.26	4.09	2.23	1.18	
Mortality rates	1st year = 0.525		2nd year = 0.416		3rd and later = 0.327 ± 0.026			overall = 0.430 ± 0.017				

[a]Obtained by assuming the same recovery rate as the average for the years 1951-1965.

concluded, "This rate of disappearance suggests that most individuals do not breed until two years old, although some yearling females may breed." The age of first breeding may vary with time of hatching, population density or location of territories.

Table 5. A summary of the non-breeding portion of the great horned owl populations.

Number of birds present	Number nesting	Percent not nesting	Years and location	Source
22	16	27	New York, 1952	Hagar (1957)
100	74	26	Wisconsin, 1953-1955	Orians and Kuhlman (1956)
38	28	26	Michigan, 1942 Wyoming, 1947, 1948	Craighead and Craighead (1956)
Totals 160	118	26.3		

The percentage of 1-year-olds in the population nesting may be obtained indirectly from the literature (percent of population not nesting) and the age distribution of the population (from life tables). One-year-olds comprised 34.3 percent of the population. However, the non-breeding segment of the population was found to be 26.3 percent (Table 5). If one assumes that all non-breeding birds were counted in the published studies, a portion of 1-year-old birds must be nesting. The percentage of nesting 1-year-olds in the population may be determined by the following formula:

$$\frac{a - b}{a} = c$$

where a = percentage of 1-year-olds in the population.

b = percentage of observed non-breeders in the population (assumed to be all 1-year-olds).

c = percentage of 1-year-olds in population nesting.

An estimated average of 23.3 percent of the 1-year-olds in the population attempted to nest.

Fate of the Population

The special case of the mathematical model in which only a proportion of the 1-year-olds reproduce was used to determine the status of the population. It was assumed that 23.3 percent of the 1-year-olds and all of the older birds attempted to nest. Since no significant change in survival rates was detected between periods (see p. 28), the band recovery data were combined; and the average survival rates for the period 1925-1965 were used in the model ($s_o = 0.508$, $s_1 = 0.592$, $s = 0.704$).

It was estimated that 1.46 young fledged per nesting attempt (including unsuccessful attempts) were necessary to maintain a stable population. The observed production per successful nest in each region, as weighted by the amount of recovery data from each region in the life tables (estimates of mortality rate), yielded an overall productivity rate of 1.85 young per successful nest (Table 6). Nesting success in these studies averaged 78 percent (Table 3), thus the production per nesting attempt was estimated to be 1.44 during the years 1925-1968. Therefore, it appears that over the last 40 years the great horned owl population has remained relatively stable since there has been no significant change in the mortality rates or productivity rates, and recruitment is balanced with mortality.

Table 6. A weighted productivity estimate for great horned owls in North America.

Location[a]	x Percentage of recoveries in life table	y No. banded per successful nest	$x \times y$ Mean production[b]
Region I	0.31	1.91	.005921
Region II	25.86	2.06	.532716
Region III	38.63	1.73	.668299
Region IV	17.13	1.63	.279219
Region V	10.28	2.09	.214852
Region VI	2.49	1.97	.049053
Region VII	4.67	1.93	.090131
Region VIII	0.62	1.86	.011532
		Mean	1.85

[a]Shown in Figure 2.

[b]The number of young banded per successful nest in each region is weighted according to the amount of recovery data in the life table (mortality rates) from each region (1925-1965).

RED-SHOULDERED HAWK

Red-shouldered hawks occur in two distinct locations in North America. One race breeds from northern California south to northwestern Baja California, while four other races occupy various portions of eastern North America from Minnesota and southern Quebec south to central Mexico and the Floriday Keys. The species inhabits moist woodlands such as those found along lowland rivers (Peterson 1961, Stewart 1949, Grinnell and Miller 1944, and Bent 1937). The breeding range was subdivided into six geographical areas (Figure 3) to facilitate analysis of the nesting characteristics of the species.

Migration and Breeding Cycle

The red-shouldered hawk has been called the "winter hawk," although in New England it is much less hardy than the red-tailed hawk and is seldom seen in winter (Bent 1937). It is mainly migratory in the northern portions of the breeding range, although it is usually listed as a permanent resident. According to the distribution of recoveries of banded birds (Table 7), the populations nesting below 40° N. latitude are generally non-migratory.

Fourteen birds (four 1-year-olds and ten adults) have been recovered during the May through July nesting season. All had

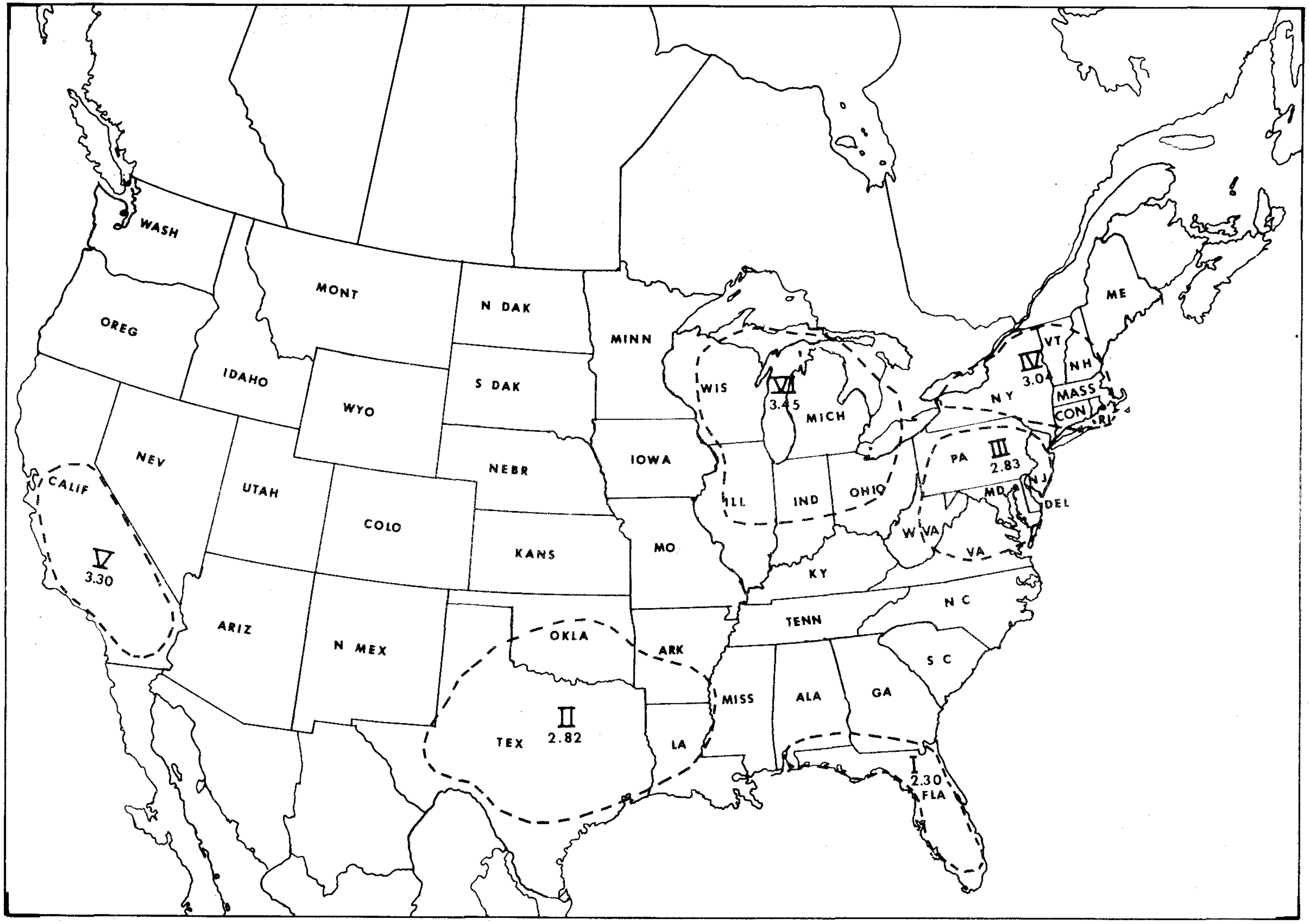

Figure 3. The six subdivisions used for the productivity analysis of the red-shouldered hawk. The numbers refer to the clutch size.

returned to the general location where they were hatched. This information together with the fact that the birds remain in juvenile plumage for about 18 months (Bent 1937) indicates that the percentage of 1-year-olds in the population which nest may be estimated from counts on the breeding areas. Red-shouldered hawks begin repairing old nests or building new ones about the first week of March in Massachusetts, and eggs are laid approximately one month later.

Table 7. A comparison of the non-migratory characteristics of red-shouldered hawks at different degrees of latitude.

Latitude of banding	Total recoveries[a]	Percent recovered at latitude of banding (non-migratory)
⩾ 44	1	0
42-43	45	27
40-41	26	69
36-39	21	95
< 36	9	100

[a]Only recoveries from birds banded in May, June, and July and recovered from October through March (wintering grounds) were included. Also, only "exact dates" of recovery were used.

Nesting Parameters

Clutch Size

The number of eggs laid per nest by red-shouldered hawks throughout the range has been tabulated in Table 8. These data agree with the clutch size reported by Bent (1937). The clutch size of the

Table 8. Clutch size and the number of young banded per successful nest for red-shouldered hawks in the United States and Canada.

	REGION I[a]				REGION II		
Clutch size Classes	Clutch size Obs.	Number banded (obs.) 1900-1945	Number banded (obs.) 1946-1968	Clutch size (obs.)	Number banded (obs.) 1900-1945	Number banded (obs.) 1946-1968
1	1	0	--	0	3	--
2	30	2	--	22	8	--
3	19	0	--	41	7	--
4	0	0	--	9	0	--
5	0	0	--	0	0	--
6	0	0	--	0	0	--
Mean	2.36 ± 0.52[b]	2.00 ± 0.00	--	2.82 ± 0.64	2.22 ± 0.73	--
Sample size	50	2	--	72	18	--

	REGION III				REGION IV		
Clutch size Classes	Clutch size Obs.	Number banded (obs.) 1900-1945	Number banded (obs.) 1946-1968	Clutch size (obs.)	Number banded (obs.) 1900-1945	Number banded (obs.) 1946-1968
1	1	4	10	1	1	11
2	20	10	15	22	9	17
3	39	13	20	95	8	23
4	10	3	3	26	2	2
5	0	0	0	2	0	0
6	0	0	0	0	0	0
Mean	2.83 ± 0.68	2.50 ± 0.86	2.33 ± 0.88	3.04 ± 0.64	2.52 ± 0.76[c]	2.30 ± 0.85
Sample size	70	30	48	146	25	53

	REGION V				REGION VI		
Clutch size Classes	Clutch size Obs.	Number banded (obs.) 1900-1945	Number banded (obs.) 1956-1968	Clutch size (obs.)	Number banded (obs.) 1900-1945	Number banded (obs.) 1946-1968
1	0	0	4	0	8	17
2	10	1	2	3	11	25
3	39	2	5	20	20	32
4	32	0	1	16	8	11
5	0	0	0	3	3	0
6	1	0	0	0	0	0
Mean	3.30 ± 0.73	2.67 ± 0.60	2.25 ± 1.05	3.45 ± 0.74	2.74 ± 1.10	2.44 ± 0.96
Sample size	82	3	12	42	50	85

[a]The regions refer to those shown in Figure 3.

[b]Standard deviation.

[c]Includes 5 nests with a total of 12 birds banded.

red-shouldered hawk, like that of the red-tailed hawk (Henny and Wight 1970 in press), increased from south to north and from east to west (Figure 3). The smallest average clutch size was reported from Florida (2.36); the largest was reported from the Great Lakes region (3.45). Most of the information on clutch size was collected prior to 1930; therefore, no determination could be made whether clutch size had changed in recent years. Craighead and Craighead (1956) reported an average clutch size of 3.43 from 40 nests in Michigan. This value is in agreement with the average for the Great Lakes Region (Region VI).

Fledging Rate and Nest Success

The number of young per successful nest that reach banding size was used as an index to the fledging rate. The number of young banded per successful nest prior to 1946 was compared with later information (1946-1968) to determine if recruitment rates had changed in recent years. A comparison between the two time periods could be made in four of the six regions (Table 9). A decline ranging from 6.8 percent to 15.7 percent in production was noted in all regions compared.

Published data on nesting parameters other than clutch size for the red-shouldered hawk is rare in the literature. Stewart (1949) studied 52 red-shouldered hawk nests in Maryland and found an average of 2.7 young in each nest. No data to permit determination of fledging success was provided. Since a clutch size of 2.83 was found in Maryland (Region III), Stewart evidently counted the number of young in the nest almost immediately after they hatched. He accounted for 2.81 eggs in each of the 47 successful nests (including 5 sterile eggs) he observed, which is similar to my estimate of clutch size for the region (Table 8). Stewart's figures must reflect a hatching rate instead of a fledging rate since he reported a 94 percent nest success.

Table 9. A comparison of information on productivity of red-shouldered hawks from six geographical regions in the United States.

Location	Clutch size	Number banded 1900-1945	Number banded 1946-1968	Percent change in number banded[a]	Percent of eggs[b] yielding bandable young
Region I	2.36	(2.00)[c]	---	---	(84.7)
Region II	2.76	2.22	---	---	80.4
Region III	2.83	2.50	2.33	-6.8	88.3
Region IV	3.04	2.52	2.30	-8.7	82.9
Region V	3.30	(2.67)	2.25	(-15.7)	(80.9)
Region VI	3.45	2.74	2.44	-10.9	79.4

[a] Compares period prior to 1946 with 1946-1968 (successful nests only).

[b] Refers to period prior to 1946 and successful nests only.

[c] In parenthesis if sample size is 10 or less.

Craighead and Craighead (1956) studied the red-shouldered hawk at Superior Township in Michigan in 1942 and 1948. The population present during their 2-year study included 38 nesting pairs and 6 additional non-nesting birds. Seventy-one young were fledged during the two years (1.87 per breeding pair). The average number fledged per nesting pair was 1.86 in 1942 and 1.88 in 1948. The Craigheads did not provide information on the percentage of nests that were successful. An estimated 68 percent of the nesting attempts were successful (1.87/2.74) if we assume that 2.74 young (the average for Region VI which includes Michigan) were fledged per successful nest and 1.87 young were fledged per nesting attempt. This estimate is in close agreement with the 71 to 74 percent of successful nests of the red-tailed hawk, which is very similar and found in the same genus as the red-shouldered hawk (Henny and Wight 1970 in press).

Population Dynamics

Mortality Rates

Mortality rates of the red-shouldered hawk were estimated from data of band recoveries throughout the range of the species for the years 1924-1945 and 1946-1965 (Tables 10 and 11). The overall annual mortality rates for the population during the two time periods were not significantly different ($t = 0.21$).

Age of Sexual Maturity

First-year birds are distinguishable from older birds during the nesting season since they retain their juvenile plumage for 18 months (Bent 1937). One-year-olds are known to return to the vicinity of their birth; however, John J. Craighead (personal communication) indicated

Table 10. Estimates of mortality rates of red-shouldered hawks banded as nestlings during the period 1924-1945. The table includes data from the United States and Canada. The mean date of banding was May 29.

Years of life	No. of recoveries	Alive at beginning	Mortality rate
1	69	120	0.575[a]
2	13	51	0.313 ± 0.020[b]
3	12	38	
4	8	26	
5	5	18	
6	5	13	
7	3	8	
8	4	5	
9	0	1	
10	0	1	
11	0	1	
12	1	1	
			0.424 ± 0.019[c]

[a] 1st-year

[b] 2nd and later

[c] Overall

Table 11. Estimates of mortality rates for red-shouldered hawks banded as nestlings between 1946 and 1965. The table includes data from the United States and Canada. The mean date of banding was May 28.

Year	Number banded	Years survived 1	2	3	4	5	6	7	8	9	10	11	12	13	First year recovery rate
1946-1953	717[a]	38	6	8	4	2	0	2	1	1	0	0	0	1	---
1954	29	1	0	0	0	0	0	0	0	0	0	0	0		.034
1955	47	0	0	0	0	0	0	0	0	0	0	1			---
1956	16	1	1	0	1	0	0	0	0	0	0				.062
1957	49	2	0	1	0	0	0	0	0	0					.041
1958	25	5	0	0	0	0	0	0	0						.200
1959	60	3	0	1	1	0	0	0							.050
1960	50	2	3	0	0	0	0								.040
1961	43	2	0	0	0	0									.046
1962	57	3	1	0	0										.053
1963	92	2	0	2											.022
1964	77	0	0												---
1965	69	4													.058
Totals	1331	63	11	12	6	2	0	2	1	1	0	1	0	1	.053
No. available		1331	1262	1185	1093	1036	993	943	883	858	809	793	746	717	
Rec./1000		47.33	8.72	10.13	5.49	1.93	---	2.12	1.13	1.17	---	1.26	---	1.39	
Alive at beginning		80.67	33.34	24.62	14.49	9.00	7.07	7.07	4.95	3.82	2.65	2.65	1.39	1.39	
Mortality rate	1st year = 0.587	2nd and later = 0.297 ± 0.024			overall = 0.418 ± 0.022										

[a]Obtained by assuming the same recovery rate as the average for the years 1954-1965.

he never observed immature plumage on red-shouldered hawks that were nesting. Craighead and Craighead (1956) reported 6 birds from a population of 82 that did not take part in the reproductive cycle in 1942 and 1948. Four of these birds were identified as 1-year-olds. Based on the mortality rate schedule, approximately 30.8 percent of the population should consist of 1-year-olds in a stable population instead of the reported 4.9 percent. Of course it was not known if the population was stable at that time. The same phenomena of a very high percentage of 1-year-olds molting their juvenile plumage that has occurred in red-tailed hawks (Henny and Wight 1970 in press) may be present in the red-shouldered hawk populations.

Assuming that a portion of the 1-year-olds were misidentified due to molting into adult plumage, the percentage of 1-year-olds in the population that was breeding may be estimated by the same formula used for the great horned owl (see p. 30). An average of 76.5 percent of the 1-year-olds in the population was estimated as those taking part in the reproductive cycle.

Fate of the Population

Production requirements must be calculated for a stable population to determine the fate of the red-shouldered hawk population. We may calculate the production requirements by using the model developed for a species in which a proportion of the 1-year-olds and all the older birds breed. It was assumed that 76.5 percent of the 1-year-olds attempted to nest. When using the average survival rates (1924-1965) which were 0.421 (s_o) and 0.692 (s), an estimated 1.58 young must be fledged for each nesting pair to maintain a stable population. In this estimate it was assumed that 76.5 percent of the 1-year-olds or 93 percent of the population was nesting. The observed production per successful nest prior to 1946 as weighted by the amount of the recovery data from each location in the life tables was 2.58 (Table 12). No published information on the percentage of nesting attempts that were successful was available for adjusting the number of young fledged per successful nest in relation to the number fledged per nesting pair. However, Craighead and Craighead (1956) found 1.87 young fledged per nesting pair in 1942 and 1948. It may be inferred from this productivity rate that the population was remaining relatively stable at that time. However, the number of young banded per successful nest has decreased from 6.8 to 15.7 percent (Table 9) during the years 1946-1968. Even though no changes in post-fledging mortality rates were detected, it can be concluded only that the population has declined in recent years as a result of reproductive failure. The magnitude of the decline (annual rate of change) cannot be estimated since information is lacking on the percentage of nesting attempts that were successful.

The red-shouldered hawk populations have dropped precipitously in numbers in New England (Peterson 1969). A 24 percent decline in red-shouldered hawks counted in fall migration at White Marsh, Maryland, was reported during a span of 7 years in the 1950's (Hackman and Henny, in prep). This represents an annual decline of 4 percent.

Table 12. A weighted estimate of productivity for red-shouldered hawks for the years prior to 1946.

	x	y	x × y
Location[a]	Percentage of recoveries in life table	No. banded per successful nest	Mean production[b]
Region I	2.02	2.00	.040400
Region II	6.05	2.22	.134310
Region III	23.39	2.50	.584750
Region IV	24.19	2.52	.609588
Region V	4.84	2.67	.129228
Region VI	39.52	2.74	1.082848
		Mean	2.58

[a]Shown in Figure 3.

[b]The number of young banded per successful nest in each region is weighted according to the percentage of recovery data for the life table (mortality rates) obtained from each region.

SPARROW HAWK

The range of the sparrow hawk of North America extends from northern Alaska through southern Quebec and Nova Scotia, south through the Americas, including the West Indies to the Juan Fernandez Islands and Tierra del Fuego (AOU 1957). This bird is the smallest and most abundant falcon in North America; four subspecies are recognized by the A. O. U. (1957). The breeding range of the sparrow hawk studied was subdivided into seven geographical locations to facilitate analyzing the productivity data (Figure 4). The subdivisions, similar to those previously used for other species, were dependent upon the amount of nesting information available.

Migration and Breeding Cycle

A portion of the sparrow hawk population in the northeastern United States is non-migratory. Numbers approximating one-fourth or less of the summer population were found in the winter near Syracuse, New York (Willoughby and Cade 1964). Similar results were found in the recovery distribution of banded birds, although a higher percentage of the birds was non-migratory at lower latitudes (Table 13). An accurate percentage of birds that are non-migratory cannot be obtained from the distribution of recoveries during the winter, since the recovery rate from each geographical location is

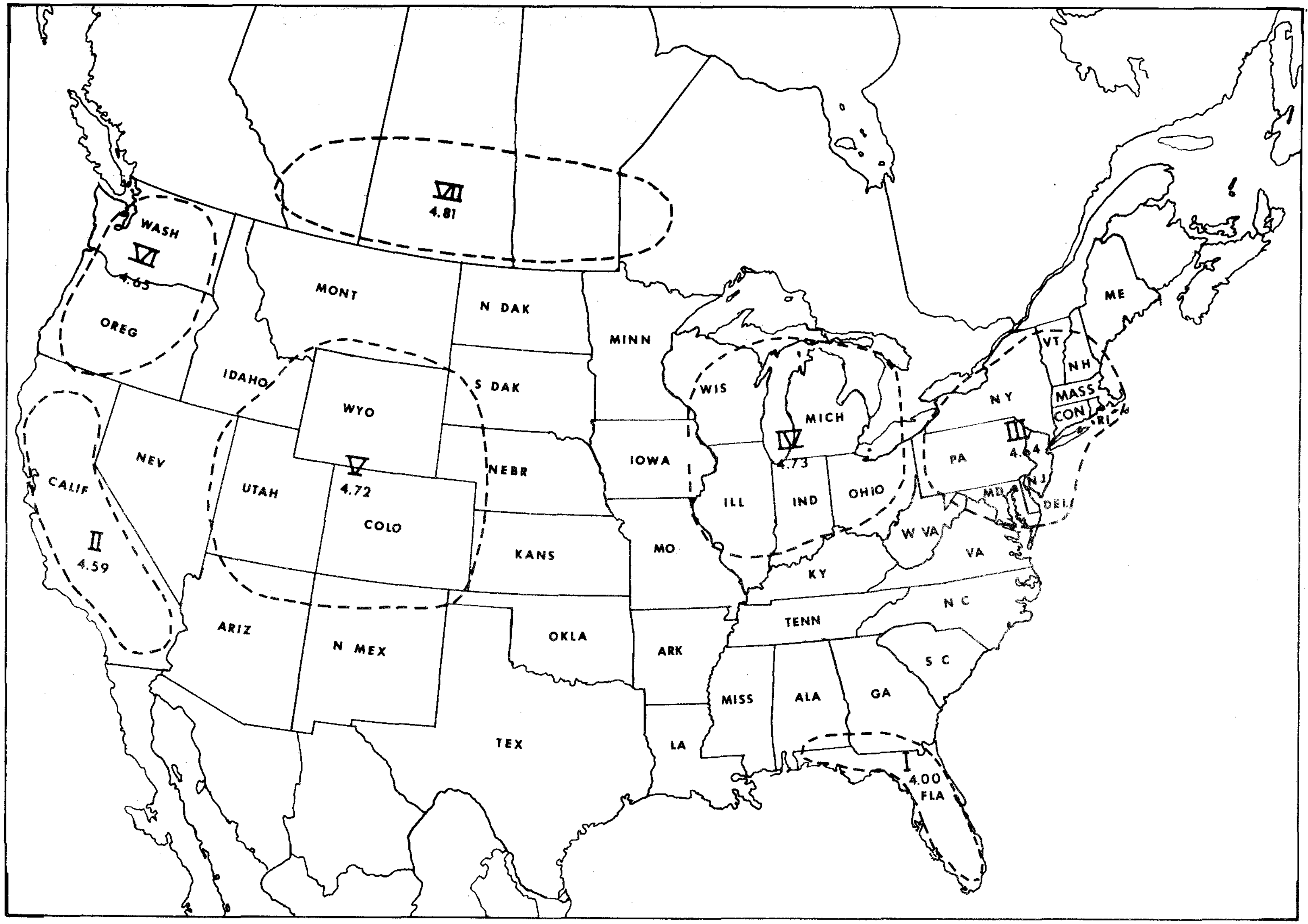

Figure 4. The seven subdivisions used for the productivity analysis of the sparrow hawk. The numbers refer to the clutch size.

dependent upon the number of people reporting bands and upon the numbers of birds in the areas.

Table 13. A comparison of the non-migratory characteristics of sparrow hawks at different degrees of latitude.

Latitude of banding	Total recoveries[a]	Percent recovered at latitude of banding (non-migratory)
⩾ 44	8	25
42-43	33	39
40-41	32	53
38-39	16	69
36-37	8	75
< 36	3	100

[a]Only recoveries from birds banded in May, June, and July and recovered from October through March (wintering grounds) were included. Also, only "exact dates" of recovery were used.

Band recoveries provided evidence that migratory sparrow hawks returned from their wintering range by April 1. Bent (1938) listed "egg dates" from New Jersey and Pennsylvania; one-third occurred between April 28 and May 14 and two-thirds between April 17 and June 3. The mean date for banding nestlings in the northeastern United States (Regions III and IV) was June 13.

Clutch Size

Bent (1938) reported that while the sparrow hawk ordinarily lays four or five eggs, it may occasionally lay only three and very rarely six or even seven. A mean clutch size of 4.38 (16 nests) was reported in Michigan and Wyoming during the years 1942, 1947, and 1948 (Craighead and Craighead 1956). Mean clutch sizes in Pennsylvania of 4.57 (7 nests in 1961) and 4.23 (13 nests between 1959 and 1966) were reported by Nagy (1963) and Heintzelman and Nagy (1968). Findings (Table 14) from my questionnaires indicated the clutch size in the northern United States ranges from 4.64 to 4.73; there was no general increase from east to west as previously reported for the buteos (red-tailed hawk and red-shouldered hawk). The clutch size of the northeastern population (4.64) is essentially identical to that of the northwestern population (4.65), with the highest rates occurring in the central United States (4.72 and 4.73). The general increase in clutch size with the increases in latitude occurred with the sparrow hawk as it did for the red-tailed hawk (Henny and Wight 1970 in press) and red-shouldered hawk. The geographical variation in clutch size of the sparrow hawk is somewhat different than other members of the North American falcon group. For example, the clutch size of the peregrine falcon (*Falco peregrinus*) decreased with increasing latitude (U. S. 3.72, So. Canada 3.50, and Arctic 3.00) (Hickey 1942).

Fledging Rate and Nest Success

The most complete study of sparrow hawk nesting to date was done by Craighead and Craighead (1956). They reported results of 16

Table 14. A summary of the clutch size for sparrow hawks in the United States and Canada.

Clutch size[a]	Region I[b]	Region II	Region III	Region IV	Region V	Region VI	Region VII
1	0	0	0	0	0	0	0
2	1	0	0	1	0	0	0
3	2	8	2	2	0	0	2
4	14	90	11	11	8	7	3
5	4	140	21	33	7	13	20
6	0	6	2	4	3	0	2
Mean	4.00±0.71[c]	4.59±0.60	4.64±0.67	4.73±0.75	4.72±0.75	4.65±0.49	4.81±0.68
Sample Size	21	244	36	51	18	20	27

[a]Nearly all of the clutch size information was collected prior to 1930.

[b]Regions refer to those listed in Figure 4.

[c]Standard deviation.

nesting attempts in Michigan and Wyoming (Table 15). An average of 3.88 young hatched per nesting attempt and 3.81 young fledged per nesting attempt (87 percent of the eggs laid). Sparrow hawks nest in cavities or holes, and the high fledging rate may reflect decreased mortality prior to fledging because of this adaptation. Only one nest was unsuccessful in the admittedly small sample of nests studied.

The number of young banded per nest was used as an index to the fledging rate (Table 16). Information was available for only three of the regions, and the New England and Great Lakes Regions (III and IV) were grouped since no significant difference in the clutch size was detected. The number of young banded per successful nest prior to 1946 was compared with the later information (1946-1959 and 1960-1968). A 7 percent decrease since 1959 in the number of young banded per successful nest in the northeastern United States was found; however, a chi-square test indicated that it was not statistically significant ($X^2 = 4.71$, d.f. = 5). Comparisons in other regions could not be made because of lack of information.

Population Dynamics

Mortality Rates

Mortality rates for sparrow hawks were estimated from band recovery data throughout the species' range for the years from

Table 15. A summary of the sparrow hawk nesting study of Craighead and Craighead (1956) in Michigan and Wyoming.

Year and location	No. of pairs	No. nesting pairs	Single birds	Eggs	Clutch size	Hatched	Fledged	No. fledged per nesting attempt
1942 (Mich.)	2	2	3	9	4.5	8	8	4.00
1947 (Wyo.)	11	11[a]	0	44	4.4	43	42	4.20
1948 (Mich.)	4	4	1	17	4.3	11	11	2.75
1949 (Mich.)	5	5	0	--	---	--	--	---
Totals[b]	17	17	4	70	4.38	62	61	3.81

[a]Studied only 10 of the nests.

[b]Not including 1949.

1925-1945 and from 1946-1965 (Tables 17, 18 and 19). No significant changes in adult mortality rates were detected during the last 45 years (t = 0.12). However, the first-year mortality rate has apparently decreased since 1945 (0.690 vs 0.607). Prior to 1946, 48 percent of the recoveries were obtained from birds reported shot. However, the percentage has decreased in recent years (34% in 1946-1957, and 16% in 1958-1965). Part of the change in the percentage of birds reported shot may be caused by people who report shot birds as being found dead; however the overall first-year recovery rate (shot and found dead) also has decreased from 6.4 percent to 1.9 percent (Table 20). It is my opinion that shooting pressure has decreased. I believe that first-year birds would be more vulnerable to shooting than the adults and that any change in shooting pressure would affect the first-year mortality rate; the observed change has been detected in this study. No change in overall annual mortality rates was detected (t = 1.37).

Age of Sexual Maturity

Mueller and Berger (1969) reported that most sparrow hawks breed at the end of the first year of life. Craighead and Craighead (1956) found 22 breeding pairs and 4 single birds on their study area in Michigan and Wyoming between 1942 and 1949. Non-breeding birds comprised 8.3 percent of the population. Band recovery information showed that all birds returned to the state where banded; this

Table 16. A summary of the number of young sparrow hawks banded per successful nest by time periods.

No. banded per successful nest	Regions III and IV[a]			Region VII
	1925-1945	1946-1959	1960-1968[b]	1925-1945
1	3	4	3	0
2	1	16	15	1
3	5	12	26	2
4	16	26	19	4
5	13	42	29	4
6	0	3	1	0
Mean	3.92 ± 1.15[c]	3.92 ± 1.27	3.63 ± 1.21	4.00 ± 1.00
Sample size	38	103	93	11

[a]Regions III and IV were grouped because there was no significant difference between the two regions.

[b]No significant change in productivity was detected between 1925-1959, and 1960-1968 ($X^2 = 4.71$, 5 d.f.).

[c]Standard deviation.

Table 17. Estimates of mortality rates for sparrow hawks banded as nestlings between 1925 and 1945. The table includes data from throughout the United States and Canada.

Years of life	No. of recoveries	Alive at beginning	Mortality rate
1	49	71	0.690[a]
2	13	22	0.468 ± 0.050[b]
3	4	9	
4	1	5	
5	2	4	
6	1	2	
7	0	1	
8	0	1	
9	0	1	
10	0	1	
11	1	1	
			0.602 ± 0.035[c]

[a]1st-year.

[b]2nd and later.

[c]Overall.

Table 18. Estimates of mortality rates for sparrow hawks banded as nestlings between 1946 and 1965. The table includes data from throughout the United States and Canada.

Year	No. banded	Years survived							First-year recovery rate
		1	2	3	4	5	6	7	
1946-1957	(650)[a]	26	12	4	3	0	0	2	---
1958	155	4	1	0	0	0	0	0	.0258
1959	191	3	1	1	0	0	0	0	.0157
1960	147	4	1	1	0	1	0		.0272
1961	204	5	1	0	0	0			.0245
1962	255	7	1	0	0				.0275
1963	272	5	1	0					.0184
1964	234	1	0						.0043
1965	267	5							.0187
Totals	2375	60	18	6	3	1	0	2	
No. available		2375	2108	1874	1602	1347	1143	996	
Rec/1000		25.26	8.54	3.20	1.87	0.74	--	2.01	
Alive at beginning		41.62	16.36	7.82	4.62	2.75	2.01	2.01	
Mortality rate	1st year = 0.607		2nd and later = 0.460±0.046			overall = 0.539±0.030			

[a]Assuming a 0.04 recovery rate for the period as recorded in Table 20.

Table 19. Estimates of mortality rates for adult sparrow hawks, 1946-1965. The initial date is January 1. The table includes recoveries from throughout the United States and Canada.

Year	No. banded	Years survived								First-year recovery rate
		1	2	3	4	5	6	7	8	
1946-1957	(1,788)[a]	49	17	12	8	2	1	1	1	---
1958	327	4	3	0	1	0	1	0	0	.0123
1959	580	10	1	2	0	0	0	2		.0172
1960	672	7	12	2	3	2	0			.0104
1961	649	10	5	0	2	0				.0154
1962	626	6	1	2	3					.0096
1963	420	5	1	0						.0119
1964	617	14	3							.0227
1965	865	9								.0104
Totals	6544	114	43	18	17	4	2	3	1	
No. available		6544	5679	5062	4642	4016	3367	2695	2115	
Rec/1000		17.42	7.57	3.56	3.66	1.00	0.59	1.11	0.47	
Alive at beginning		34.38	16.96	9.39	5.83	3.17	2.17	1.58	0.47	
Mortality rate	Adult = 0.465±0.017									

[a]Assuming 0.0274 recovery rate, this is same ratio as assumed in Table 18.

eliminated the possibility that a breeding segment of the population was located elsewhere.

Table 20. A summary by years of banding of first-year recovery rates for sparrow hawks banded as nestlings.

		First-year recoveries[a]		
Years banded	No. banded[b]	Shot	Other	Total
1928-1940	267	7 (.026)	10 (.037)	17 (.064)
1941-1945	116	2 (.017)	2 (.017)	4 (.034)
1946-1955	247	1 (.004)	9 (.036)	10 (.040)
1956-1960	263	1 (.004)	4 (.015)	5 (.019)

[a]Recovery rates in parentheses.

[b]Refers to a sample of banders.

Schedules of mortality rates show that between 46.0 and 46.8 percent of the population in the spring consists of 1-year-olds. The percentage of the 1-year-olds in the population that are nesting can readily be obtained by the same formula used for the great horned owl (see p. 30). Assuming that all non-breeders were 1-year-olds, it was estimated that 82 percent of the 1-year-olds and all of the older birds nested.

Productivity Requirements

No complete nesting studies have been conducted except the small study done on nesting of sparrow hawks in the monumental work on hawks and owls by the Craigheads (1956). However, it is important to report on a production standard for sparrow hawks so that future nesting studies will have a basis for comparison. The model in which only a proportion of the 1-year-olds breed was used to estimate the production standard. It was assumed that 82 percent of the 1-year-olds attempted to nest. The combined data were believed to provide the best estimates of the mortality rates (1925-1965), since no significant difference was detected in the overall annual survival rates between time periods. The first-year survival rate used in the model was 35.2 percent, and the adult survival rate was 53.6 percent.

Each breeding female in the population was required to produce 2.88 young to balance the demonstrated mortality rates. Seventy-seven percent of the band recovery data used for the mortality estimates was obtained from the northeastern United States (Regions III and IV). Sparrow hawk populations could have remained stable prior to 1959 with the observed 3.92 young fledged per successful nest if 73 percent of the nesting attempts were successful (Table 16). The lack of complete nesting studies (studies which include unsuccessful nests)precludes computation of the annual rate of change using the modeling approach. The number of young produced per successful nest appears to have declined approximately 7 percent since 1959 (Table 16); however, no significant difference could be detected. This may be due to small sample sizes. Hackman and Henny (in prep) have recorded a decline of 20 percent in numbers of sparrow hawks counted in fall migration at White Marsh, Maryland between 1951-1954 and 1958-1961 (a period of 7 years). This represents an annual decline of 3 percent.

OSPREY

Information on the osprey is summarized from two papers (Henny and Wight 1969, Henny and Ogden 1970) which resulted from this study. The published results followed the same format as the other species included in this study. The band recovery data were from New York and New Jersey. Production requirements for a stable population were then compared with the productivity rates available in the literature.

Migration and Breeding Cycle

Migration patterns of the ospreys from New York and New Jersey indicated that ospreys do not return to the place of birth until they are 3-year-olds. A Swedish worker also concluded that ospreys begin breeding when they are three years old. Most of the ospreys from New York and New Jersey winter in South America.

Nesting Parameters

Information available from seven states indicated that recent production rates per active nest ranged from 0.27 (Connecticut) to 1.22 (Florida) young fledged.

Mortality Rates

No significant change in mortality rates was detected between 1926-1947 and 1948-1961.

Production Standard

An estimated 1.22 to 1.30 young must be fledged per nesting pair to maintain a stable population if all ospreys 3-years-old and older attempt to nest and the mortality rate estimates were correct.

Fate of the Populations

It was estimated from the mathematical model that the population at Florida Bay, Florida was remaining stable, while populations in Minnesota, Maryland, Wisconsin, Michigan, Maine, and Connecticut were declining at annual rates of 2-3 percent, 2-3 percent, 12-13 percent, 12-13 percent, 12-13 percent, and 13-14 percent, respectively. Observed rates of decline, when available, were in close agreement with these estimates, thus providing further support for the assumptions used in the model. It appears that the declines were solely the result of reproductive failure since there was no change in post-fledging mortality rates.

BARN OWL

Information on the barn owl is summarized from a paper (Henny 1969) which resulted from this study. The population parameters of barn owl population in the northeastern United States were compared with a population in the southern United States (primarily southern California) and a population in Switzerland.

Nesting Paremeters

The number of young barn owls banded per successful nest was correlated directly with the degrees of latitude. In Switzerland 4.43 young were produced; in the northeastern United States 4.16 were produced; and in the southern United States 3.92 were produced. No significant change in the number of young produced per successful nest occurred between 1926-1947 and 1948-1967 although the rates fluctuated annually. The annual fluctuations apparently were due to changes in food supply.

Mortality Rates

Overall annual mortality rates were correlated directly with the degrees of latitude. The mortality rates for the three locations were approximately 56 percent, 50 percent, and 35 percent. No significant changes in mortality rates occurred between time periods.

Fate of the Populations

Although the production requirements for a stable population were estimated, the status of the barn owl populations could not be determined due to lack of complete information from nesting studies. Information needed from field studies before the status of these populations may be evaluated includes (1) the percentage of the breeding age birds that annually attempt to nest, and (2) the percentage of nesting attempts that are successful. The population parameters fluctuate tremendously from year to year; therefore, basic information for a series of years is needed.

COOPER'S HAWK

The information on the Cooper's hawk is summarized from a paper (Henny and Wight 1970, in press) which resulted from this study. Observers of Cooper's hawk at Hawk Mountain and Cape May have reported catastrophic declines in numbers counted annually in fall migration. Information on the Cooper's hawk was obtained from the northeastern United States.

Nesting Parameters

The number of young Cooper's hawks banded per successful nest has decreased from 3.53 prior to 1946 to 2.67 between 1949 and 1967. This represents a change of -24.4 percent. The percentage of the nesting attempts that were successful prior to 1950 was 81 percent while the percentage had declined to only 40 percent in 1967.

Mortality Rates

Mortality rates were higher prior to 1940 than they are today. Evidently this was the result of high shooting pressure on the "chicken hawk" in the earlier years.

Production Standards

In recent years it was estimated between 3.74 and 4.22 young must be fledged per nesting pair to maintain a stable population.

Fate of the Population

A 25 percent annual decline in the population was estimated for the northeastern United States. Hackman and Henny (in prep.) reported a 61 percent decrease in numbers observed at White Marsh, Maryland, during a 7 year period in the 1950's. The Cooper's hawk has been declining in numbers for many years. The decline early in the century can be attributed to heavy hunting pressure. This problem has been compounded in recent years by reproductive failure. There is little doubt that the Cooper's hawk is in serious jeopardy in the northeast.

RED-TAILED HAWK

The information on the red-tailed hawk is summarized from a paper (Henny and Wight 1970, in press) which resulted from this study. Mortality rates were estimated for portions of the red-tailed hawk range above 42° N. Latitude and below 42° N. Latitude.

Nesting Parameters

No change in the number of young banded per successful nest was detected between the years 1920 and 1945, 1946 and 1959, and 1960 and 1968. Although the clutch size was smaller in the southern United States, the number of young produced per nesting attempt was higher.

Mortality Rates

Mortality rates in each region were unchanged throughout the time span; however, the rates were higher below 42° N. Latitude as would be expected with the higher productivity rates.

Production Standards

It was determined the red-tailed hawks begin breeding as 2-year-olds. It was estimated that between 1.33 and 1.38 young must be fledged per breeding age female above 42° N. Latitude and between 1.79 and 1.89 below 42° N. Latitude.

Fate of the Population

The observed production above 42° N. Latitude was 1.31 to 1.36 and below 42° N. Latitude was 1.77 to 1.85. It was concluded that the red-tailed hawk populations were remaining stable throughout their range. Hackman and Henny (in prep.) found no change in numbers of red-tailed hawks counted at White Marsh, Maryland during 7 years in the 1950's.

GREAT BLUE HERON

The great blue heron is the largest, most widely distributed, and best known of the American herons. The species is found in much of Canada and throughout the United States with six subspecies recognized (AOU 1957). The gray heron (Ardea cinera) of the Old World is very similar to the great blue heron (Palmer 1962).

Migration and Breeding Biology

The great blue heron is migratory throughout the northern portion of its range but returns to its breeding range early in the season (Bent 1926). Reports of sightings in New Jersey are recorded for every month of the year, which indicates that at least a small portion of the population may not migrate (Stone 1937). However, Stone reported seeing over 100 birds flying in "V" formations and apparently migrating south on October 13, 1928.

The temporal and geographical distribution of recoveries from nestlings banded in the northeastern United States and southeastern Canada were examined (Figure 5) to determine the location of the various age classes through time (Tables 21 and 22). They moved in all directions for the first three months, but later recoveries indicated a southern movement in the autumn. Similar findings for the gray heron in Britain were reported by Owen (1960). Great blue herons

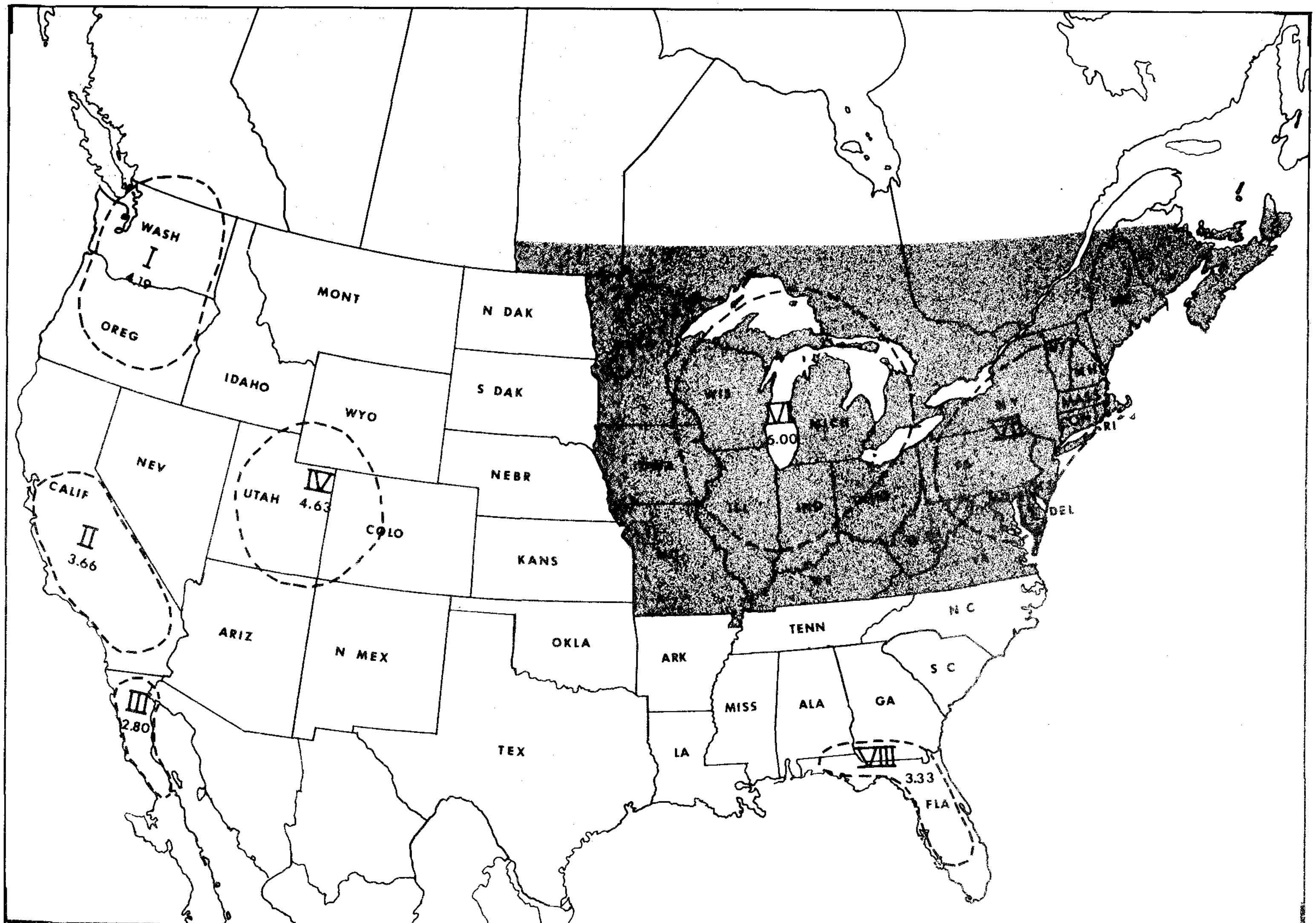

Figure 5. Location of the region of banding for the analysis of migration characteristics is crossed hatched. The encircled regions refer to the great blue heron productivity study (numbers refer to clutch size).

Table 21. Geographic and temporal distribution of recoveries of great blue herons in the first two years of life.

Location	First year of life											Second year of life										
	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Within region[a]	1	17	27	24	20	16	8	5	4	1		1	2	2		2	5			1	1	
Oklahoma				1																		
Arkansas					1	1	2															
Tennessee							1													1		
N. Carolina							3								1							
S. Carolina				1		1								1	1							
Texas						1																
Louisiana						1	1				1					2						
Mississippi							2	2	1													
Alabama					1	1		1														
Georgia						2	3	1	1									1	1			
Florida						2		2		1				1							1	1
Mexico							2	1														
Cuba					1		3	3	2	2												
Jamaica						2		1											1			
Haiti							1															
Br. Honduras						2																
Nicaragua								1								1						

[a]The region is shown in Figure 5.

Table 22. Geographic and temporal distribution of recoveries of great blue herons in the third year of life and the fourth and later years of life.

	Third year of life					Fourth and later years of life											
Location	May	Aug	Oct	Dec	Feb	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Within region[a]		1	1	1		6	3	2	2		4	2	1	1		1	4
Tennessee	1																
N. Carolina										1							
Texas													1				
Louisiana												1					
Alabama												1					1
Georgia			1														
Florida													1				
Cuba															1		
Br. Honduras					1												
Bahama Is.										1							
Colombia			1														

[a]The region is shown in Figure 5.

were recovered during the first year of life as far south as British Honduras and Nicaragua. Migratory characteristics of the great blue heron apparently are related to latitude where hatched. Few birds, if any, fledged above 48° N. Latitude winter in the area, but many of the birds fledged below 39° N. Latitude are relatively non-migratory (Table 23). No increase in number of recoveries within the region of banding (Figure 5) occurred during the first spring after banding; this indicates that few 1-year-olds return to their natal area for the reproductive cycle. In fact, the only recovery between April and June was a bird banded in Michigan and recovered in Ohio. Similarly, during the second year of life, the absence of recoveries from banded birds suggest that few birds, if any, were present within the region of banding in April, May, and June. Two recoveries reported during the interval were from Tennessee and Florida. At least a portion of the 2-year-olds may not be taking part in the reproductive process. It appears that birds 3-years-old and older are returning to their location of fledging and taking part in reproductive activity (Table 22).

Bent (1926:108) reports that young great blue herons are "ready to breed" after their second winter (2-year-olds), although they do not attain full adult plumage until the following post-nuptial molt. Signs of immaturity "may not wholly disappear for another year or two." Cottrille and Cottrille (1958) found most of the herons in a colony in Michigan were in full breeding plumage, although some immature birds were present. A. J. Meyerriecks (personal communication) indicated that some 1-year-old birds come to the breeding colonies and may "fool" with nest twigs, etc., but do not breed. The birds observed in immature plumage are probably the portion of 1-year-old birds in the population that did not migrate south (Table 21).

Table 23. A comparison of the non-migratory characteristics of great blue herons at different degrees of latitude.

Latitude of banding	Total recoveries[a]	Percent recovered at latitude of banding (non-migratory)
≥ 48	22	0
44-47	67	6
40-43	46	24
34-39	17	59
< 34	4	100

[a]Only recoveries from birds banded in May, June, and July and recovered from November through February (wintering grounds) were included. Also, only records containing the "exact date" of recovery were used.

Great blue herons gather at their breeding places early in the spring. Miller (1944) reported that March was the month of gradual infiltration of birds from the South. Stone (1937) reported 50 at a large rookery near Cape May, New Jersey, by March 30, 1925. The timing of the nesting season is similar in other portions of the range (summarized by Palmer 1962).

Nesting Parameters

Clutch Size

Clutch size varies from 3-7 (typically 4), but quantitative data are scarce (Palmer 1962). Miller (1944) summarized data on 347 clutches in the Philadelphia region, as follows: 63 (of 3 eggs), 117 (4), 141 (5), and 26 (6). The mean clutch size was 4.37. Miller believed this was an underestimate since a portion of the clutches containing 3 eggs was incomplete. Information about clutch size presented in Table 24 indicated a general increase from south to north. Clutch sizes were higher in the central portions of the country (Figure 5).

Fledging Rate and Nest Success

Miller (1944) stated that the great blue heron is definitely single brooded; when the eggs are lost, the birds may renest as many as two times. He further reported, "Infant mortality exceeds 40 percent," and "I have never found a nest with more than 3 young over 1/3-grown, and often there are only 2." More detailed information for this species is not available. Owen (1960) reported that 451 young gray herons were fledged from 185 successful nests. This represents 2.44 young fledged per successful nest. The percentage of successful nesting attempts was not reported.

Table 24. A summary of the clutch size information for great blue herons.

Clutch size	Region I[a]	Region II	Region III	Region IV	Region V	Region VI	Region VII	Region VIII
1	0	0	0	0	0	0	0	0
2	0	1	1	0	0	0	0	0
3	0	16	4	1	3	0	1	6
4	26	20	0	2	7	2	13	3
5	6	4	0	4	1	3	20	0
6	0	0	0	1	2	2	5	0
Mean	4.19±0.40[b]	3.66±0.69	2.80±0.45	4.63±0.92	4.15±0.99	5.00±0.82	4.74±0.72	3.33±0.50
Sample Size	32	41	5	8	13	7	39	9

[a]Regions shown in Figure 5.

[b]Standard deviation.

Present results would show a productive rate of 2.44 young per successful nest if we assume approximately a 40 percent loss to the clutch (4.37) as reported by Miller (1944). Regretfully, no complete nesting study has been published on the largest and most widely distributed heron in North America.

Population Dynamics

Mortality Rates

Mortality rates for the great blue heron of North America previously were estimated by Owen (1959). His estimate was for 1916-1945, but he used an initial date of July 1 instead of the date of banding as I used. In addition, only recoveries through 1958 were available and included at the time he published his work. Birds banded during the 1940's may have been alive in 1958 (13 to 18 years old) since banded birds have been reported to 21 years of age. Thus, there is the possibility that the estimates of mortality rates of Owen (1959) were too high since no adjustment was made for live birds in the banded cohort. Owen estimated the first-year mortality rate was 71 percent and the average annual mortality after the first year was 29 percent. For the same time period my estimates were slightly lower. I have estimated that the first-year mortality rate was 69.0 percent, the second year 36.3 percent, and an annual average after the second year of 21.9 ± 1.1 percent (Table 25). Estimates of mortality rates have decreased significantly since 1945 (Table 26). The estimates of the overall annual mortality rates has decreased significantly from 45.2 ± 1.2 percent to 41.5 ± 1.4 percent since 1945 ($t = 2.01$). The lowered mortality rates probably resulted from a decrease in shooting pressure.

Fate of the Population

The chronological age at which the majority of the young reach sexual maturity must be known before a production standard may be estimated. Two treatments of the data were used since the definite age of sexual maturity is unknown at this time. In the first case, it was assumed that all 2-year-old and older birds attempt to nest; in the second case, all 3-year-olds and older attempt to nest. The correct estimate undoubtedly lies somewhere in between.

For the period from 1946 to 1965, a production standard of between 1.91 (all breed as 2-year-olds) and 2.45 was necessary to maintain a stable population. The lack of information about current productivity precludes further analyses into the status of the species.

Table 25. Estimates of mortality rates for great blue herons banded as nestlings in the United States and Canada between 1916 and 1945. The mean date of banding was June 21.

Years of life	No. of recoveries	Alive at beginning	Mortality rate
1	227	329	0.690[a]
2	37	102	0.363[b]
3	13	65	0.219 ± 0.011[c]
4	12	52	
5	13	40	
6	5	27	
7	6	22	
8	5	16	
9	0	11	
10	1	11	
11	2	10	
12	0	8	
13	0	8	
14	2	8	
15	2	6	
16	1	4	
17	0	3	
18	2	3	
19	0	1	
20	0	1	
21	1	1	
			0.452 ± 0.012[d]

[a] 1st year

[b] 2nd year

[c] 3rd and later

[d] Overall

Table 26. Estimates of mortality rates for great blue herons banded as nestlings in the United States and Canada between 1946 and 1965. The mean date of banding was June 16.

Year	No. banded	Years survived 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	First year recovery rate
1946	161	9	1	0	1	1	0	0	1	0	0	0	0	0	0	0	.056
1947	98	8	0	0	0	0	0	0	1	1	0	0	0	0	0	0	.082
1948	202	11	4	0	1	0	0	0	0	1	0	0	0	0	0	0	.054
1949	162	10	0	1	0	0	0	1	0	0	0	0	0	0	0	0	.062
1950	200	12	3	0	1	0	1	0	0	0	0	0	0	0	0	0	.060
1951	152	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	.013
1952	355	14	3	1	0	1	0	2	0	2	0	0	0	0	0		.039
1953	270	5	0	0	0	0	0	2	1	0	0	0	0	0			.019
1954	379	13	5	2	1	0	0	0	1	0	0	0	0				.034
1955	256	15	2	0	2	0	0	0	0	1	0	0					.059
1956	316	10	2	0	1	0	0	0	0	0	0						.032
1957	286	14	3	2	0	0	0	1	0	0							.049
1958	122	2	0	0	0	1	0	0	0								.016
1959	338	11	3	1	1	0	0	0									.033
1960	110	3	1	0	0	0	1										.027
1961	150	6	0	1	0	1											.040
1962	304	9	1	1	0												.030
1963	608	18	3	3													.030
1964	343	7	3														.020
1965	518	9															.017
Totals	5330	188	34	12	8	4	2	6	4	6	0	0	0	0	0	1	.035
No. available		5330	4812	4469	3861	3557	3407	3297	2959	2837	2551	2235	1979	1600	1330	975	
Rec/1000		35.27	7.07	2.69	2.07	1.12	0.59	1.82	1.35	2.11	---	---	---	---	---	1.03	
Alive/bgnng.		55.12	19.85	12.78	10.09	8.02	6.90	6.31	4.49	3.14	1.03	1.03	1.03	1.03	1.03	1.03	

Mortality rates 1st year = 0.640 2nd = 0.356 3rd and later = 0.221 ± 0.016 overall = 0.415 ± 0.014

BLACK-CROWNED NIGHT HERON

The black-crowned night heron is one of the best known and most widely distributed of all herons in the world. Closely related forms to the North American subspecies are found throughout much of South America, Europe, Asia, and Africa (Bent 1926).

Migration and Breeding Cycle

Young black-crowned night herons, like the young of several other herons, are inclined to wander northward after the close of the breeding season (Gross 1923, May 1926, 1929, Bent 1926, Townsend 1931, and others). However, a definite migration southward begins in late September or October (Table 27). One first-year bird was recovered as far south as Cuba on September 15, 1952. The wintering range of the black-crowned night heron has been discussed previously (May 1929, Palmer 1962, Nickell 1966, Houston 1967, and others). The distribution of recoveries indicates that a portion of the population spend the winter in the northern states, but many herons winter in the gulf states or farther south (Tables 27 and 28). Fewer birds winter near the area where they hatched in the northern portions of the range than in the southern portions (Table 29).

Many of the 1-year-olds return to the vicinity of their natal area, although the percentage returning cannot be estimated from

Table 27. Geographical and temporal distribution of recoveries during the first two years of life of black-crowned night herons banded in the northeastern United States and southeastern Canada as nestlings.

	First year												Second year									
Location	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Jan	Mar	Apr
Within region[a]	7	11	35	78	49	30	30	10	11	3	5	4	9	7	4	5	2	2	1	1	1	
Tennessee							1															
No. Carolina						4				1												
Texas							1															
Louisiana																				1		
Mississippi								1						1								
Alabama					1	1	1															
Georgia						3	1	1														
So. Carolina								1														
Florida						1	7	4	2	2	1						1	1		3	1	
Cuba					1		1	2	4	3										1		1
Haiti								1										1				
Trinidad															1							
Nicaragua							1						1									
Costa Rica									1													
British Honduras									1													

[a]Region shown in Figure 5.

Table 28. Geographical and temporal distribution of recoveries during the third and later years of life of black-crowned night herons banded in the northeastern United States and southeastern Canada as nestlings.

	Third year								Fourth year and later											
Location	May	June	July	Aug	Nov	Jan	Feb	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Within region[a]	3	3	1	1		1		2	7	10	8	5	5	4	6	1	2	1		7
Tennessee																				1
No. Carolina					1															
Oklahoma													1							
Louisiana											1									
Alabama																				1
Georgia													1							1
So. Carolina																				1
Florida																	1		1	
Cuba					1		1									1	1	2		
Mexico					1															
British Honduras																				1
Jamaica														1		1		1		
Haiti															1					

[a]Region shown in Figure 5.

banding data. Evidence from three birds recovered in Mississippi, Trinidad, and Nicaragua during the nesting season indicated that a portion of the 1-year-olds were considerably south of their region of fledging. A large flock of black-crowned herons were observed on Rulers Bar Hassock (Long Island) at the start of the nesting season; this flock consisted of adult-plumaged birds, "dusky adults" (2-year-olds) and immatures (1-year-olds) (Palmer 1962).

Table 29. A comparison of the non-migratory characteristics of the black-crowned night heron at different degrees of latitude.

Latitude of banding	Total recoveries[a]	Percent recovered at latitude of banding (non-migratory)
⩾ 46	8	0
44-45	15	13
42-43	63	29
40-41	67	43
38-39	16	50
36-37	5	80
< 36	4	100

[a]Only recoveries from birds banded in May, June, and July and recovered from November through February (wintering grounds) were included. Also, only "exact dates" of recovery were used.

Night herons first appeared at Long Island, New York in late March (Allen and Mangels 1940), while birds in St. Clair County, Michigan, arrived during the four-week period of April 1 to May 1 (Nickell 1966). Spring arrival dates ranging from March 22

(Hamilton, Ontario) to May 5 (St. Clair Flats, Michigan) were listed by Bent (1926).

Nesting Parameters

Clutch Size

Clutches usually contained 3-5 eggs; however, sometimes only one or two eggs and occasionally six, seven, or eight eggs were found (Bent 1926). Bent believed that larger sets may be the product of two birds. Twenty nests containing 82 eggs (mean 4.10) were observed on Rulers Bar Hassock, Long Island in 1955 (Palmer 1962). Eight nests containing three eggs each were reported by Teal (1965) in Georgia. Information obtained from museums and private egg collections indicated 20 nests were reported in New England prior to 1945. The records included: 14 clutches (4 eggs), 3 clutches (5 eggs), 2 clutches (6 eggs), and 1 clutch (7 eggs), with a mean of 4.50. Information on clutch size obtained during a similar period of time below 38° N. Latitude in California included: 9 clutches (3 eggs), 22 clutches (4 eggs), and 4 clutches (5 eggs) for a mean of 3.86. Very little information was available for other locations.

Fledging Rate and Nest Success

Information available on nesting success indicated that between 2.2 and 2.4 young were produced per successful nesting attempt

(Table 30). Gross (1923) made a somewhat higher estimate when he reported 6,000+ young produced from 2,300 occupied nests (2.61 young per nest) at Sandy Neck, Massachusetts in 1920. At the time of his estimate, about 70 percent of the young could perch on the branches. Undoubtedly, additional pre-fledging loss occurred.

Table 30. Productivity estimates for black-crowned night herons.

Year	Location	Production rate: Per succ. nest	Production rate: Per nesting attempt[a]	Source
1932	Pennsylvania	2.24	---	Wood and Wood (1933)
1952	Quebec, Canada	(2.33)[b]	---	M. F. Hamel (banding records)
1954	Michigan	2.41[c]	---	Nickell (1966)
1955	Georgia	(2.43)	(2.13)	Teal (1965)

[a] Includes unsuccessful nesting attempts.

[b] Sample size less than 20, enclosed in parentheses.

[c] An overestimate since some eggs were included in the estimate.

Teal (1965) noted that of the heron, the black-crowned night heron was the most pugnacious and the most successful at nesting. He found that seven of eight nests observed (87.5 percent) were successful. No other estimates of nest success were available, although Palmer (1962) reported 100 percent hatching success from 20 nests on Rulers Bar Hassock in 1955.

Renesting attempts have been mentioned by Gross (1923) and Nickell (1966). Nickell reported about 150 renestings between May 24 and June 10 after high winds destroyed an estimated 200 nests between May 19 and 24. The 1,700 eggs recorded at Sandy Neck, Massachusetts, on June 22-23, 1920, (Gross 1923) also were probably the results of renesting attempts. Gross (1923) had concluded there was no evidence that black-crowned herons raise two broods. The assumption that a relatively high percentage of the breeding pairs (perhaps 75-85 percent) successfully fledged young seems reasonable because of the high hatching success and high percentage of renests.

Population Dynamics

Mortality Rates

Hickey (1952) estimated that black-crowned night herons banded as nestlings had a 61 percent first-year mortality rate and a 31 percent adult mortality rate after the first year. He used nestlings banded between 1926 and 1934 and their subsequent recoveries through 1946 for these estimates. Mortality estimates in the present study for the years 1926-1945 indicate a first-year mortality rate of 69.0 percent and an adult mortality rate of 0.233 ± 0.008 (Table 31). The estimate of adult mortaility by Hickey (1952) was too high since many birds subsequently were recovered after age 12-13; these birds were not accounted for in his truncated life table. No significant difference ($t = 1.01$) in the overall annual mortality rates (0.430 ± 0.009 and 0.414 ± 0.013) was observed between 1926-1945 and 1946-1965 (Tables

Table 31. Estimates of mortality rates for black-crowned night herons banded as nestlings in the United States and Canada between 1926 and 1945. The mean date of banding was June 19.

Years of life	No. of recoveries	Alive at beginning	Mortality rates
1	432	626	0.690[a]
2	43	194	0.233 ± 0.008[b]
3	35	151	
4	27	116	
5	27	89	
6	11	62	
7	11	51	
8	3	40	
9	10	37	
10	7	27	
11	4	20	
12	5	16	
13	4	11	
14	2	7	
15	3	5	
16	0	2	
17	1	2	
18	1	1	
			0.430 ± 0.009[c]

[a] 1st year

[b] 2nd and later

[c] Overall

31 and 32). The oldest wild bird recovered lived 18 years; however, a black-crowned night heron (*N. n. nycticorax*) in the London Zoo lived 20 years (Comfort 1962). The recovery data used in the life tables come from 41 states and provinces; however, 32 percent of the recoveries were from birds banded in Massachusetts. A high percentage of the recoveries occurred in Michigan, Illinois, Colorado, New York, Saskatchewan, and South Dakota.

Age of Sexual Maturity

Most black-crowned night herons do not breed until 2 or 3 years of age (Palmer 1962) however, breeding at the end of the first year of life has been reported (Gross 1923, Nobel *et al*. 1938). In general, there are 2 types of plumages for the adult black-crowned night heron: (1) fully adult, and (2) "dusky adult" (Allen and Mangels 1940). The "dusky adults" were believed 2-year-olds, and Allen and Mangels (1940) stated that Lorenz also found this true for the European subspecies. The percentage of dusky adults appeared to vary in different years; but when the entire population of the heronry had assembled, there was no time when these younger adults (2-year-olds) could have exceeded 10 percent of the total flock (Allen and Mangels 1940). The age composition of the population based on mortality rates indicates that between 23.7 and 24.9 percent of the population should be "dusky adults" or 2-year-olds. Therefore, it seems apparent that a *maximum*

Table 32. Estimates of mortality rates for black-crowned night herons banded as nestlings in the United States and Canada between 1946 and 1965. The mean date of banding was June 17.

Year	No. banded	Years survived													First year recovery rate
		1	2	3	4	5	6	7	8	9	10	11	12	13	
1946	202	5	1	1	0	0	0	0	0	0	0	0	0	0	.025
1947	94	2	0	1	0	1	0	1	1	0	0	0	0	1	.021
1948	187	4	0	0	0	0	0	1	0	1	0	0	0	0	.021
1949	241	7	3	0	1	0	0	0	0	0	0	0	0	0	.029
1950	354	4	1	1	1	0	0	0	0	1	1	0	0	0	.011
1951	493	11	1	0	0	0	0	0	0	1	0	0	0	0	.022
1952	412	3	1	0	0	2	3	0	0	0	0	0	0	0	.007
1953	850	7	3	0	1	3	0	4	2	0	0	0	0	0	.008
1954	798	9	1	2	0	0	1	0	0	0	0	0	0		.011
1955	2213	24	5	0	3	1	3	0	1	0	1	0			.011
1956	1445	24	2	3	2	1	2	0	0	0	1				.021
1957	529	11	3	1	1	0	0	0	0	0					.021
1958	335	7	1	2	0	0	0	0	0						.024
1959	370	9	0	1	0	0	0	0							.026
1960	536	14	2	0	0	0	0								.026
1961	341	9	0	0	0	0									.012
1962	345	4	0	0	0										.018
1963	729	13	2	1											.013
1964	1263	16	3												.012
1965	1734	20													.014
Totals	14,053	203	29	13	9	8	9	6	4	3	3	0	0	1	
No. available		14,053	12,319	11,056	10,327	9982	9641	9105	8735	8400	7871	6426	4213	3415	
Rec/1000		14.45	2.35	1.18	0.87	0.80	0.93	0.66	0.46	0.36	0.38	---	---	0.29	
Alive at beginning		22.73	8.28	5.93	4.75	3.88	3.08	2.15	1.49	1.03	0.67	0.29	0.29	0.29	

Mortality rate 1st year = 0.636 2nd and later = 0.258 ± 0.012 overall = 0.414 ± 0.013

of approximately 40 percent of the 2-year-olds are taking part in the reproductive process. One-year-olds in the population were not nesting (Allen and Mangels 1940). Meyerriecks (personal communication) stated "many 1-year-olds come to the nesting colonies, a few try to build nests, but I have not seen breeding by this age group."

Fate of the Population

An estimated 2.27 young must be fledged per nesting pair to maintain a stable population if it is assumed that 40 percent of the 2-year-olds and all of the older birds in the population attempt to nest. This estimate seems quite reasonable if high nesting success and observed productivity are considered (Table 30).

It must be emphasized that the above estimates are only preliminary. More information is required on the age composition of the breeding colony before the status of the populations can be estimated. The age composition of the breeding population then may be compared with the theoretical age distribution of population (obtained from life table) to determine what percent of the 1-year-olds and 2-year-olds (dusky adults) are taking part in the reproductive process.

Peterson (1969) has reported a 90 percent decline in black-crowned night herons on the eastern half of Long Island. Perhaps nesting studies should be conducted on this species in the near future to determine if the decline is a result of reproductive failure.

BROWN PELICAN

The 1967 Committee on Conservation (AOU, 1968:119) reported that "brown pelicans seem to have all but disappeared as breeding birds on the Gulf and Atlantic coasts of the United States except in peninsular Florida." A brief summary of the decline of the brown pelican in the Gulf States was provided by Williams and Martin (1968). Two colonies nesting on offshore islands near California suffered almost complete reproductive failure; the thin-shelled eggs were crushed by the incubating parents (AOU 1969). Condition of the brown pelican population in California was elucidated further by Schreiber and DeLong (1969) when they reported no successful nesting in that state in 1968 except on Anacapa and Santa Barbara Island. The California brown pelican (P. o. californicus) is listed as "status undetermined" in the Endangered Species List (U. S. Fish and Wildlife Service, 1968); the eastern brown pelican (P. o. carolinensis) on the Gulf States is not mentioned. This study includes information from North Carolina, South Carolina, and Florida.

Nesting Parameters

Clutch Size and Fledging Success

Bent (1922) reported that brown pelicans normally lay three eggs, but two eggs often constitute a full set. Anderson and Hickey (1970) reported the mean clutch size in 236 sets of North American brown pelican eggs was 2.95; this size did not vary geographically between populations in North America. Little information, if any, regarding the number of brown pelicans fledged per pair appears in the literature, although an excellent study has been completed in Africa on the great white pelican (P. onocrotalus roseus) (Brown and Urban 1969). Since nesting information on the brown pelican is scarce, I feel it is important to add the findings of J. W. Stiles. On July 8, 1934, Stiles banded 70 nestlings at a colony at Bird Island in Galveston Bay, Texas. The colony consisted of 100 pairs of adults and 200 young varying from one week of age to the stage where some primary feathers were sprouting on the wings. The report, written on his original banding schedule, is now filed at the Bird Banding Laboratory, Laurel, Maryland.

Brown pelicans fledge sometime between 9 weeks (Mason, in Palmer, 1962) and about 12 weeks of age (H. J. O'Connor and T. A. Beckett, III, personal communication). Palmer (1962) reported high mortality among birds prior to fledging. He also found that hatching evidently occurs over a span of days with the smallest chick presumably having the least opportunity to get adequately fed. Nesting losses of the great white pelican in Ethiopia have been about 20 percent of the total eggs laid in the first ten days of the fledging period and about 40 percent by the end of the first month (Brown and Urban 1969). Brown and

Urban concluded that 50 percent of the eggs laid by the great white pelican yielded fledged young. Comparable statistics for the brown pelican were not available although they probably approximate that of the great white pelican.

Population Dynamics

Mortality Rates

The date of fledging (not the date of banding) was used as the initial date in estimating the mortality rates. It was believed that pre-fledging mortality after banding could be estimated best by direct observation at the colony. These estimates for the population at Deveaux Bank, South Carolina, were provided by T. A. Beckett III. Beckett (personal communication) reported that brown pelicans, banded with size "9" bands, are larger at the time of banding, and they fledge about 4 weeks after banding. Birds banded with size "8" bands usually fledge at approximately 7 weeks after banding. Data on band recoveries between the date of banding and the date of fledging were omitted when using the fledging date, the production standard estimated from the modeling approach, refers to the number of young that must fledge per breeding pair.

Estimates show the brown pelican population in Florida had a first-year mortality rate of 69.5 percent for 1927-1934. Estimates of mortality rates increased significantly ($t = 3.36$) during the next 7 years in Florida with the overall annual mortality rate changing from 0.421 ± 0.023 to 0.517 ± 0.017 (Table 33). The method used for obtaining recoveries was checked in an attempt to determine the cause for the increase in mortality rates during the latter time period (Table 34). The 7 percent increase in percentage of birds reported shot during 1935-1941 probably influenced the 7 percent increase in the first-year mortality rates. Shooting seemed to be an addative factor in mortality since losses due to hunting were not compensated for by a reduction in natural mortality.

Estimates of overall mortality rates for the populations in North Carolina and South Carolina were significantly lower ($t = 6.68$) than the earlier rates from Florida (Table 35). However, no significant change ($t = 0.90$) in adult mortality rates was detected between the three time periods. The lowered mortality rates are probably the result of less shooting pressure (Table 34). The overall annual mortality rate for the Carolina population was estimated as 0.374 ± 0.013.

Table 33. Estimates of mortality rates for brown pelicans banded as nestlings in Florida during the years 1927-1934 and 1935-1941.

	1927-1934			1935-1941		
Years of life	No. of recoveries[a]	Alive at beginning	Mortality rate	No. of recoveries	Alive at beginning	Mortality rate
1	57	82	0.695[b]	173	226	0.765[b]
2	9	25	0.360[c]	21	53	0.396[c]
3	5	16	0.182 ± 0.018[d]	8	32	0.203 ± 0.015[d]
4	2	11		5	24	
5	3	9		5	19	
6	1	6		1	14	
7	1	5		3	13	
8	0	4		3	10	
9	0	4		1	7	
10	0	4		0	6	
11	0	4		1	6	
12	0	4		2	5	
13	1	4		1	3	
14	0	3		0	2	
15	1	3		1	2	
16	0	2		0	1	
17	0	2		0	1	
18	0	2		0	1	
19	1	2		0	1	
20	0	1		1	1	
21	0	1		0	0	
22	1	1		0	0	
			0.421 ± 0.023[e]			0.517 ± 0.017[e]

[a] Only band recoveries from birds believed to have been dead were used (see p. 12).

[b] 1st year.

[c] 2nd year.

[d] 3rd and later.

[e] Overall.

Table 34. Manner in which first-year recoveries of brown pelicans were obtained from birds banded as nestlings in Florida, North Carolina, and South Carolina between 1927 and 1966.

		Number of first-year recoveries		
Location	Years	Shot	Found dead	Totals
Florida	1927-1934	9 (.16)	48 (.84)	57
Florida	1935-1941	39 (.23)	134 (.77)	173
Florida	1952-1965	1 (.03)	33 (.97)	34
North and South Carolina	1946-1966	15 (.05)	294 (.95)	309

Age of Sexual Maturity

Brown pelicans are capable of breeding while in their second nuptial plumage which is produced when the birds are about two years old (Bent 1922, Palmer 1962). Beckett (1966) reported that brown pelicans sometimes breed when only two years old, but at least one of the pair was in adult plumage in all cases observed. Beckett determined by trapping breeding birds on the nest, that 3-year-old birds are in adult plumage. It is critical to obtain information on the percentage of 2-year-olds nesting before estimates of population parameters can be made. Therefore, further study should be conducted on the age of sexual maturity.

Two separate treatments of the data regarding the breeding age of the species were incorporated into the analysis: (1) it was assumed breeding began at two years of age, and (2) breeding began at three years of age. When information on the percentage of 2-year-olds that breed is available, the information easily can be incorporated into the

Table 35. Estimates of mortality rates for brown pelicans banded as nestlings in North and South Carolina between 1946 and 1966.

Year	No. banded	Years survived 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	First-year recovery rate
1946	200	12[a]	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	.060
1947	50	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.120
1950	683	40	2	1	2	1	1	5	4	1	0	1	0	0	0	0	1	.059
1956	100	7	3	0	0	0	0	0	0	0	0	0						.070
1957	6	2	0	0	0	0	0	0	0	0	0							.333
1958	100	3	0	0	0	1	0	0	0	0								.030
1959	189	7	2	2	0	0	0	0	0									.037
1960	95	6	2	0	0	1	0	1										.063
1961	250	16	0	0	1	0	0											.064
1963	1269	59	11	1	0													.046
1964	1578	36	6	4														.023
1965	1852	84	9															.045
1966	1232	31																.025
Totals	7604	309	36	9	3	4	1	6	4	1	0	1	0	0	0	0	1	.041
No. available		7604	6372	4520	2942	1673	1673	1423	1328	1139	1039	1033	933	933	933	933	933	
Rec/1000		40.64	5.65	1.99	1.02	2.39	0.60	4.22	3.01	0.88	---	0.97	---	---	---	---	1.07	
Alive at beginning		62.44	21.80	16.15	14.16	13.14	10.75	10.15	5.93	2.92	2.04	2.04	1.07	1.07	1.07	1.07	1.07	
Mortality rates		1st year = 0.651		2nd year = 0.259			3rd and later = 0.195 ± 0.016				overall = 0.374 ± 0.013							

[a]Only band recoveries from birds believed to have been dead were used (see p. 12).

model to provide a more accurate estimate of population parameters.

Productivity Requirements

The population in North Carolina and South Carolina (1946-1966) must fledge between 1.51 and 1.87 young per breeding female to balance the observed mortality rates (Table 36). This production standard seems high in view of the mean clutch size of 2.95 and the "stable" population of pelicans in Africa with young being fledged from approximately 50 percent of the eggs laid. It appears the population in the Carolinas could not remain stable even with maximum productivity.

Table 36. Production standards necessary to maintain a stable population of brown pelicans.

Location		Production standards[a]	
		Nest at 2 years	Nest at 3 years
Florida	1927-1934	1.86	2.28
Florida	1935-1941	2.86	3.59
North and South Carolina	1946-1966	1.51	1.87

[a]Number fledged per nesting pair.

Information about field observations on the number of young fledged per nesting attempt may prove difficult to obtain as the young (when nesting on the ground) congregate into large flocks or "pods." However, I feel this difficulty may be overcome by (1) making an initial count of the number of nesting attempts in the colony, and (2) making another count of the number of young just before fledging. It would seem data on the average number fledged per nest attempt could be obtained in this manner with a minimum number of visits to the colony.

Fate of the South Carolina Population

Beckett (1966) reported that in former years, the Deveaux Bank colony numbered over 5,000 pairs of brown pelicans, but by 1965 the colony had been reduced to an estimated 600 pairs. The brown pelican population of South Carolina was approximately 7,500 breeding pairs about a decade ago and now (1969) numbers slightly more than 1,000 pairs (Beckett, personal communication). An annual decline of 18 percent would account for the observed change if we assume this decline took place during a 10-year period.

Beckett (personal communication) estimated that 0.32 young were fledged per pair at Deveaux Bank, South Carolina in 1969. If the productivity rate of Beckett and the mortality rates in the Carolinas are considered (Table 35), the expected annual rate of change may be estimated from the model (solve for u). Again, two treatments of the data were used: (1) all brown pelicans two years old and older attempt to nest, and (2) all brown pelicans three years old and older attempt to nest.

Estimates using the modeling approach indicate that the brown pelican population was declining from 14.6 to 15.0 percent annually. The estimated annual rate of decline is in close agreement with the observed rate (18 percent). It should be emphasized that the weakest link in this approach is the knowledge regarding the mortality rate from the time of banding until fledging. Future researchers should concentrate on obtaining accurate estimates of preflight mortality in addition to the percentage of 2-year-old birds nesting in the population so that the population estimates may be refined.

In summary, post-fleding mortality rates of brown pelicans were higher prior to World War II than they are today. Reduction in shooting pressure was probably responsible for decreased mortality. Although mortality rates have declined somewhat, they continue to remain excessive. Optimum production could not produce a stable population with the existing mortality rates. The excessive mortality has been compounded recently by a reduction in the ability of the population to reproduce. Excessive post-fledging mortality and poor productivity indicate that the future of the brown pelican in the United States is very bleak.

BARN SWALLOW

The barn swallow is found as a breeding bird in North America from northcentral Alaska to western Greenland south to central Mexico and the Gulf Coast of the United States (AOU 1957). The species winters from western Panama to southern South America. Subspecies of the barn swallow are also found in Europe, Asia, and Africa.

Nesting Parameters

Clutch Size

In the United States the clutch size of barn swallows usually consists of four or five eggs; six eggs are fairly common and seven eggs rarely are observed. In Britain clutch sizes declined from 4.7 eggs at the end of April to 3.8 eggs in August, the mean clutch size observed in 1445 nests was 4.4 eggs (Adams 1957). In Japan size of the initial clutches averaged 5.21 while second clutches averaged 4.59 (Mizuta 1963). Published quantitative information on clutch size from the United States was not available.

Hatching and Fledging Success

The barn swallow hatches a high percentage of the eggs laid and raises a large proportion of the young hatched. For example, Adams (1957) reported from Britain that 90.5 percent of the eggs hatched in successful nests and 78.2 percent of the eggs hatched when unsuccessful nests are included in the computation. He further reported that 71.9 percent of the eggs laid yielded fledged young.

The barn swallow is multibrooded. Nearly 50 percent of a dozen pairs of barn swallows observed by Dean Amadon in New York raised a second brood (Bent 1942). At least 67 percent of the total number of pairs present had second broods in Groton, Massachusetts in 1938 (Mason 1953). Mason thought this high ratio seldom was exceeded and usually about 50 percent of the breeding females produced two broods. He also believed birds having two broods annually were older and had had previous nesting experience. Mizuta (1963) reported 40.5 percent of the pairs succeeded in raising two broods in Japan.

The annual reproductive rate per breeding pair at Groton, Massachusetts was 5.97 nestlings (Mason 1953). A similar fledging rate of birds in Japan was reported by Mizuta (1963). He found 143 pairs fledged 869 young (mean 6.08). To my knowledge annual reproductive rates for other locations are not available.

Age of Sexual Maturity

It is assumed that sexual maturity is attained at the end of the first year of life (breed as 1-year-olds) although the literature contains no information about age of sexual maturity. An unbalanced sex ratio in favor of males (117:100) has been reported in the adult segment of the population (Mason 1953).

Population Dynamics

Mortality Rates

An annual turnover of 73.34 percent in a barn swallow population in Groton, Massachusetts was estimated by Mason (1953). The estimate was made by assuming there was a stable adult population (217) and an annual production of 597 young. Thus, the total population (814) would decline during the year to 217 to yield an annual mortality rate of 73.34 percent.

Mortality estimates using the composite dynamic method were made for only one time period (1920-1957) since there was a small number of band recoveries. Fifty-six percent of the recoveries were from birds banded in Massachusetts and New York, and most of the others were from the northeastern United States. The first-year mortality rate was estimated at 68.6 percent, and the annual adult mortality rate (years 2-8) was 42.7 ± 3.7 percent (Table 37) when the date of banding (mean date July 3) was used as the initial date.

Table 37. Estimates of mortality rates for barn swallows banded as nestlings in North America between 1920 and 1957.

Years of life	No. of recoveries	No. alive at beginning	Mortality rate
1	70	102	0.686[a]
2	16	32	0.427 ± 0.037[b]
3	6	16	
4	4	10	
5	0	6	
6	2	6	
7	3	4	
8	1	1	

[a] 1st-year.
[b] 2nd and later.

It seems apparent that the first-year mortality rate was underestimated when the observed fledging rate per pair (5.97 and 6.08) is considered. High mortality immediately after fledging which is not represented by band recoveries may be the cause. The adult mortality rate is probably the least biased. A first-year survival rate which yields a stable population may be estimated by the formula originally used for determining production requirements for a stable population; if we assume that barn swallows breed as 1-year-olds, that the adult mortality rate is correct and that 5.97 young are

are fledged per breeding pair.

Using the above assumptions, the first-year survival rate was 14.3, and the mortality rate was 85.7 percent. A mortality rate of this magnitude may explain why Mason (1953) found only 2 percent of the nestlings and 34 percent of the adults he banded returned to the banding site.

Further analysis regarding the status of the population cannot be made at this time. Future productivity estimates should be compared with those of Mason (1953) and calculated in terms of the total number of young produced per breeding female on an annual basis. Tentatively it is concluded that the barn swallow has a first-year mortality rate of 85.7 percent from the time of leaving the nest and an adult mortality rate of 42.7 percent. With this mortality schedule, the population can remain stable if 5.97 young are fledged annually per breeding female.

CHIMNEY SWIFT

The chimney swift breeds in the eastern United States and southeastern Canada. The species is reported to winter in the upper Amazon drainage of South America; band recoveries have been recorded from northeastern Peru (AOU 1957). The breeding biology and life history of the species have been summarized in great detail by Fischer (1958). Therefore, the breeding season, migration routes, and the timing of migration will not be discussed.

Nesting Parameters

Clutch Size

Bent (1940) reported clutch size ranged from three to six eggs. Fischer (1958) recorded the clutch size for 25 nests in New York as 10 sets (5 eggs), 10 sets (4), 4 sets (3), and 1 set (2) for a mean of 4.16. He also cited R. W. Dexter who reported a mean clutch size of 4.00 from 27 nests in Ohio.

Hatching and Fledging Success

Seventy-seven eggs were hatched among 86 eggs observed in 20 nests at Beaver Hill, New York (Fischer 1958). Hatching success was 90.7 percent over a 13-year period. Eighty six eggs from 24 nests (evidently different than the above) hatched; 74 of the young survived to fly which indicated a fledging success of 86 percent (Fischer 1958). Therefore, it appears that approximately 78 percent of the eggs yield fledged young (90.7 × 86.0). Fischer's information would indicate that approximately 3.24 young are fledged per pair if a clutch size of 4.16 is assumed. Dexter (1956, 1961) summarized that reproductive performances of two 10-year-old chimney swifts from Ohio. During 18 breeding seasons he observed 48 young fledged for a mean of 2.67 per pair per year.

Renesting will occur if something happens to the eggs early in the breeding cycle (Widmann, in Bendire 1895, Moore 1902, Dexter 1951, Dexter 1969). However, present day ornithologists agree that the chimney swift is single-brooded (Fischer 1958). It appears that between 2.67 and 3.24 young are fledged annually per nesting pair.

<u>Age of Sexual Maturity</u>

Ten of 952 chimney swifts (10.8 percent) banded as nestlings were recaptured subsequently in the study area (Fischer 1958). Five of the 10 young returned to nest in their original hatching area the first summer after banding. Two others returned the first year, but it is not known if they nested. The other three nested in the second summer but not the first. In contrast, Dexter (1969) reported information that indicated they do not breed until two years of age.

He also indicated that between 1945 and 1968, 84 percent (836 of 995 birds) of the population in residence was breeding birds. No conclusions were made regarding sexual maturity because of these conflicting reports.

Population Dynamics

Mortality Rates

Mortality rates of chimney swifts have been discussed by several authors. Green (1940:51-52) felt that "perhaps more than one fourth of the swifts die each year of old age . . . and it seems likely that a large proportion die between two and three years of age." Bowman's (1952) comparable data from Kingston, Ontario did not support data of Green. Upon analyzing Bowman's data on 2,480 returns and recoveries, Fischer (1958) estimated approximately a 50 percent average mortality in each age class; however, Fischer grouped returns and recoveries together. Reliability of samples which combine records from birds recovered dead and birds recovered alive by trapping (returns) has been questioned by Plattner and Sutter (1947). Hickey (1952) summarized many of the biases that occur in data on returns and concluded that only the individual bander could interpret the data.

Over 20,000 returns of chimney swifts now are filed at the Bird

Banding Laboratory. Mortality estimates were calculated from the recovery data, and these mortality estimates were compared with estimates obtained from return data.

Band Recoveries -- Estimates of mortality rates from recoveries of chimney swifts banded in the United States and Canada during 1920-1935, 1936-1945, and 1946-1956 are presented in Table 38. No recoveries were included prior to the first January 1 after banding as it was difficult to age the birds accurately in fall migration when most of the birds are banded. The mortality rates after January 1 may be classified as representing those of adult birds. Estimates of adult mortality have remained unchanged ($t = 0.19$) at approximately 37 per-cent during the period 1920-1956. Banding of chimney swifts has decreased during the last ten years, and sufficient data were not available for a more recent estimate of the mortality. It is significant that Fischer (1958) obtained the same mortality rate from return data. He banded 40 adult swifts at their nests, and 25 returned (survival rate of 62.5% or mortality rate of 37.5%).

Band Returns -- Band returns of chimney swifts were handled in two ways to determine a method of using the information for estimating mortality rates: (1) all returns were incorporated into a table like that used in the composite dynamic life table for recoveries, and (2) the records of an individual bander (B. B. Coffey) who banded a large number of birds during a long period of time were analyzed

Table 38. Estimates of adult mortality rates for chimney swifts banded in North America during the years 1920-1935, 1936-1945, and 1946-1956.

	1920-1935			1936-1945			1946-1956		
Years of life	No. of recoveries	No. available	Mortality rate	No. of recoveries	No. available	Mortality rate	No. of recoveries	No. available	Mortality rate
1	207	544	0.370 ± 0.013	411	1156	0.373 ± 0.009	287	762	0.370 ± 0.011
2	138	337		295	745		170	475	
3	57	199		168	450		108	305	
4	40	142		102	282		64	197	
5	42	102		62	180		57	133	
6	24	60		44	118		25	76	
7	17	36		28	74		26	51	
8	5	19		23	46		9	25	
9	6	14		10	23		5	16	
10	4	8		8	13		7	11	
11	1	4		1	5		3	4	
12	1	3		3	4		0	1	
13	2	2		0	1		0	1	
14	0	0		0	1		1	1	
15	0	0		1	1		0	0	

separately.

<u>All Returns Combined</u> -- Since the maximum length of life reported for a wild chimney swift was 13 years (Dexter 1969), the life span of all birds banded prior to 1947 was believed completely by 1959 (the last year returns were processed by the Bird Banding Laboratory). A composite dynamic life table from the returns of all birds banded between 1924 and 1946 is presented in Table 39. The mortality rate of 57.3 percent was considerably higher than the estimate obtained from recoveries (Table 38). In both tables it was assumed that the year the bird was recovered, or the last year it was retrapped, was proof of its death. The assumption is definitely true for recoveries since the bird must be dead to be classified as a recovery. However, the last year a bird is retrapped does not necessarily mean that the bird died that year. Hickey (1952) has pointed out that the number of retrapped birds is dependent upon the intensity and efficiency of the individual banders. A serious bias also occurs when a bander discontinues his operation or moves to another location. Many of the living birds in the banded cohort would have no opportunity to be recaptured in later years, and this causes the mortality rates to be overestimated. I have reached the same conclusion regarding returns as Hickey (1952). Return data from more than one bander cannot be effectively grouped together to estimate mortality rates from the life table approach.

Table 39. Estimates of mortality rates for chimney swifts banded between 1924 and 1946. Only the last time a bird returned to a trapping station was considered.[a]

Years of life	No. of returns	No. alive at beginning	Mortality rate
1	7,069	11,632	0.572[b]
2	2,548	4,563	
3	1,015	2,015	
4	428	1,000	
5	289	572	
6	123	283	
7	85	160	
8	54	75	
9	16	21	
10	5	5	

[a]If the individual bird was recaptured 1 year, 5 years, and 8 years after banding only the record from the 8th year was used.

[b]Annual mortality rate for adults.

One Individual's Returns -- Hickey (1952) suggested that a set of return data from one bander be analyzed separately. Ben B. Coffey has banded chimney swifts in Tennessee since 1932; he banded between 2,000 and 10,000 birds annually from 1946-1959.

Equal trapping effort each year is desirable but this goal of banders seldom is achieved. A summary of the chimney swift banding records of Coffey is presented in Table 40. The returns were adjusted by two methods to counteract the biases resulting from unequal trapping effort: (1) the number of birds captured that year

Table 40. A summary of the <u>return</u> data of B. B. Coffey for the years 1946-1959.

Year	New bandings	Total captures[a]	Years survived								
			1	2	3	4	5	6	7	8	9
1946	9898	9898	213 (256)[b]	166 (194)	64 (71)	33 (37)	26 (29)	4 (4)	3 (4)	3 (3)	1 (1)
1947	4817	5073	225 (262)	77 (92)	44 (55)	41 (44)	4 (7)	3 (3)	4 (4)	2 (2)	1 (1)
1948	8248	8704	149 (168)	63 (81)	64 (66)	20 (21)	6 (7)	14 (16)	3 (3)	1 (1)	0 (0)
1949	6772	7103	87 (102)	87 (104)	13 (16)	9 (11)	25 (25)	6 (6)	0 (0)	0 (0)	2 (2)
1950	4767	5042	218 (237)	24 (27)	13 (14)	35 (39)	9 (9)	1 (1)	2 (2)	2 (2)	0 (0)
1951	9691	10171	107 (126)	71 (90)	111 (127)	42 (45)	15 (19)	7 (7)	17 (17)	2 (2)	
1952	4150	4351	38 (54)	77 (83)	17 (18)	11 (11)	2 (3)	7 (7)	2 (2)		
1953	3710	3893	74 (93)	27 (32)	14 (15)	5 (6)	10 (11)	4 (4)			
1954	5664	6054	136 (146)	45 (50)	19 (21)	42 (42)	11 (11)				
1955	4501	4763	25 (26)	14 (19)	34 (36)	10 (10)					
1956	2219	2343	37 (46)	52 (53)	2 (2)						
1957	2397	2501	75 (76)	18 (18)							
1958	6213[c]	6459	50 (50)								
1959	1919	2018									

[a] Including previously banded birds that were captured.

[b] The numbers in parentheses refer to the total number of birds captured during each period, while the numbers outside the parentheses refer to the last time the bird was recaptured.

[c] Note the high number of returns durings years of above average banding effort.

(including birds previously banded), and (2) the number of birds banded that year (excluding birds previously banded). These two values were used as an index to banding effort. Since returns are birds recaptured alive at the location of banding, they may be captured during several years. Thus, it must be decided if only the last return should be counted or if all the returns should be counted from an individual bird. Estimates of mortality rates from Coffey's return data were calculated in three ways: (1) last return only, adjusted by the number of birds banded (Table 41), (2) last return only, adjusted by the number of birds captured, and (3) all returns, adjusted by the number of birds captured. Estimates of mortality rates were 0.417, 0.419, and 0.426, respectively although the last two sets of data were not included in tables. Very similar estimates were obtained by all three methods. These estimates were considerably lower than the unadjusted return estimates (Table 39) but still higher than the estimates from the recovery data (Table 38).

One assumption made when using return data to calculate mortality rates is that the banded sample returns each year to the banding locale (homing ability) in proportion to its occurrence in the population and that the birds are available to be recaptured. To test this assumption, a comparison was made between trapping effort as expressed by the number of birds captured each year and the percentage of the trapped sample that were first-year returns the

Table 41. Estimates of mortality rates from the return data in Table 40.

	Years survived								
Year	1	2	3	4	5	6	7	8	9
1946	.0442[a]	.0201	.0095	.0069	.0027	.0010	.0008	.0005	.0002
1947	.0273	.0114	.0092	.0042	.0010	.0008	.0007	.0004	.0005
1948	.0220	.0132	.0066	.0048	.0016	.0025	.0007	.0005	.0000
1949	.0183	.0090	.0031	.0024	.0044	.0013	.0000	.0000	.0003
1950	.0225	.0058	.0035	.0062	.0020	.0005	.0008	.0003	.0000
1951	.0258	.0191	.0196	.0093	.0068	.0029	.0027	.0010	
1952	.0102	.0136	.0038	.0050	.0008	.0011	.0010		
1953	.0131	.0060	.0063	.0021	.0016	.0021			
1954	.0302	.0203	.0079	.0068	.0057				
1955	.0113	.0058	.0055	.0052					
1956	.0154	.0084	.0010						
1957	.0121	.0094							
1958	.0261								
Totals	.2785	.1421	.0760	.0529	.0266	.0122	.0067	.0027	.0010
Divided by[b]	13	12	11	10	9	8	7	6	5
Alive at beginning	.0214	.0118	.0069	.0053	.0030	.0015	.0010	.0005	.0002
No. available	.0516	.0302	.0184	.0115	.0062	.0032	.0017	.0007	.0002
Mortality rate	adult = 0.417								

[a] Only the oldest return for each individual bird is included and the returns each year are adjusted by the number of new birds banded. For example, .0442 in the first row is obtained by 213/4817 and .0201 by 166/8248.

[b] Divided by the number of data points since the information is in percentages.

following year (Figure 6). A positive linear relationship between the number of chimney swifts captured and the percentage of first-year returns occurring at the trap would indicate that a constant fraction of the banded sample returns each year to the locale of the trap site in proportion to its occurrence in the population. The spread of the points would indicate the degree of homing ability. This procedure, with a slight modification (used number of returns instead of percentage of returns because of approximately equal annual trapping effort) was used successfully by Wight et al. (1967) for returns of band-tailed pigeons (Columba fasciata).

A positive linear relationship was found between the percentage of first-year returns and the number banded the previous year (Figure 6). However, there was a considerable amount of spread in the points although the coefficient of determination was high ($r^2 = 0.93$). The high coefficient was the result of the line being forced through the origin and is not directly comparable to standard use of the term. This spread suggests that the same cohort was not banded annually. Thus, it was expected that the mortality rate would be slightly overestimated (indeed, it was approximately 5 percent higher than the estimate from the recovery data). Wight et al. (1967) estimated a 28.7 percent adult mortality rate for band-tailed pigeons from recovery data and an essentially identical mortality rate of 29.1 percent from returns. Wight et al. (1967) were trapping a breeding

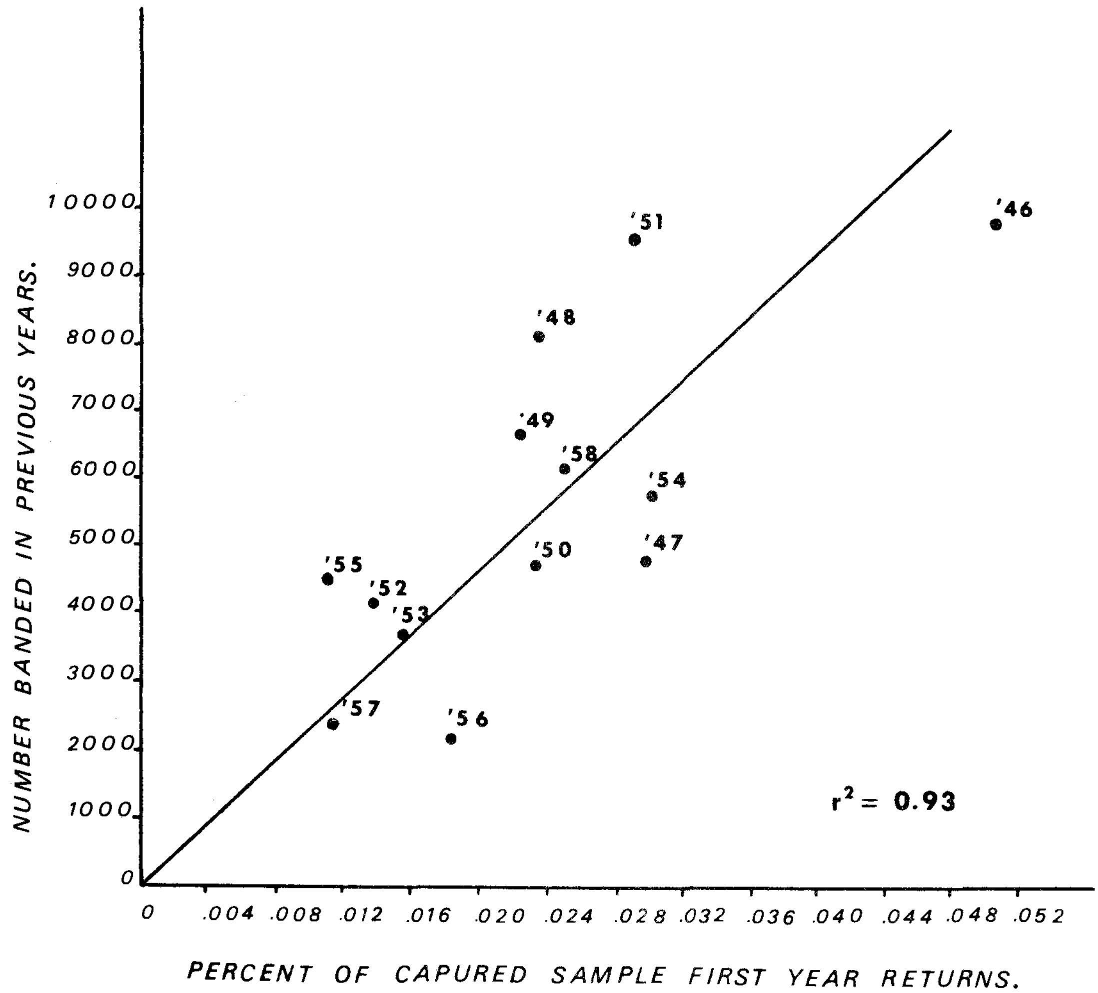

Figure 6. The relationship between the percent of the captured sample that were first year returns and the number of birds banded the previous year.

population of band-tailed pigeons, while the chimney swift data represent birds in fall migration. A breeding population undoubtedly has higher fidelity to their place of nesting than a population in fall migration. Any deviation from a 100 percent fidelity would cause an overestimation of the mortality rate. This appears to be the situation with the return data of chimney swifts.

It is concluded that some approximation of the homing ability of the species studied may be obtained by plotting the relationship between the percent of the captured sample that were first-year returns and the number of birds banded the previous year. However, it appears that data of returns can be used most effectively for species banded in their breeding area over a long period of time. An excellent example of this type of study is that of Wight et al. (1967).

Fate of the Population

The present status of the chimney swift could not be determined although the adult morality rates have not changed (Table 38). Information is needed on first-year mortality rate, on annual productivity rate, and on the chronological age of sexual maturity.

BLUE JAY

The blue jay is found in North America from central Alberta east to Newfoundland south to Texas, the Gulf Coast and southern Florida (AOU 1957). W. M. Tyler (in Bent 1946:33) defined the species as, "Originally a wild bird of the woods, the jay was canny enough to adapt itself to civilization, and nowadays it often builds its nest close to man, even in our gardens." The blue jay has changed since the beginning of the century from a shy bird to a regular customer at feeding stations (Nunneley 1964).

Migration and Breeding Cycle

The southward migration of blue jays from the third week in September until mid-October at Hawk Mountain, Pennsylvania was described by Broun (1941). Banding data was compiled for the eastern United States by Gill (1941) and he reported that birds banded in New Jersey and Pennsylvania were recovered in North and South Carolina. The northward movement during the last week in April and the first two weeks of May has been reported by Schorger (1961) from Wisconsin and Lewis (1942) from Pelee Island, Ontario. Laskey (1958) concluded that the majority of blue jays migrate in spring and fall from Nashville, Tennessee although others are permanent residents.

A portion of the range of the blue jay was divided into two regions (Figure 7) to determine the timing and distribution of the movement and the recoveries of the banded birds from outside each region were tabulated (Table 42). Less than 200 recoveries were reported south of the regional boundaries of the more than 2000 birds recovered from banding in each region. Reference to age at time of recovery could not be made since age designations at the time of banding were extremely unreliable. Also, the true magnitude of the movement south of Regions 6 and 8 could not be estimated since band reports are dependent upon human population at various locations and numbers of banded birds that are present. I believe that a relatively small portion of the breeding population from Regions 6 and 8 venture south of the regional boundaries, although many of the birds may move within the regional limits.

Evidence provided by band recoveries shows the southward movement in the fall begins in September (Table 42). This same conclusion was reached by Broun (1941). Apparently the northward movement begins in April, and very few northern birds are found south of their natal region by the end of the month.

Nesting activity has been reported in Regions 6 and 8 in late April. Bent (1946) lists "egg dates" from Illinois, Massachusetts, and Minnesota that range from April 18 to July 12; over one-half of the records between May 5 and May 26.

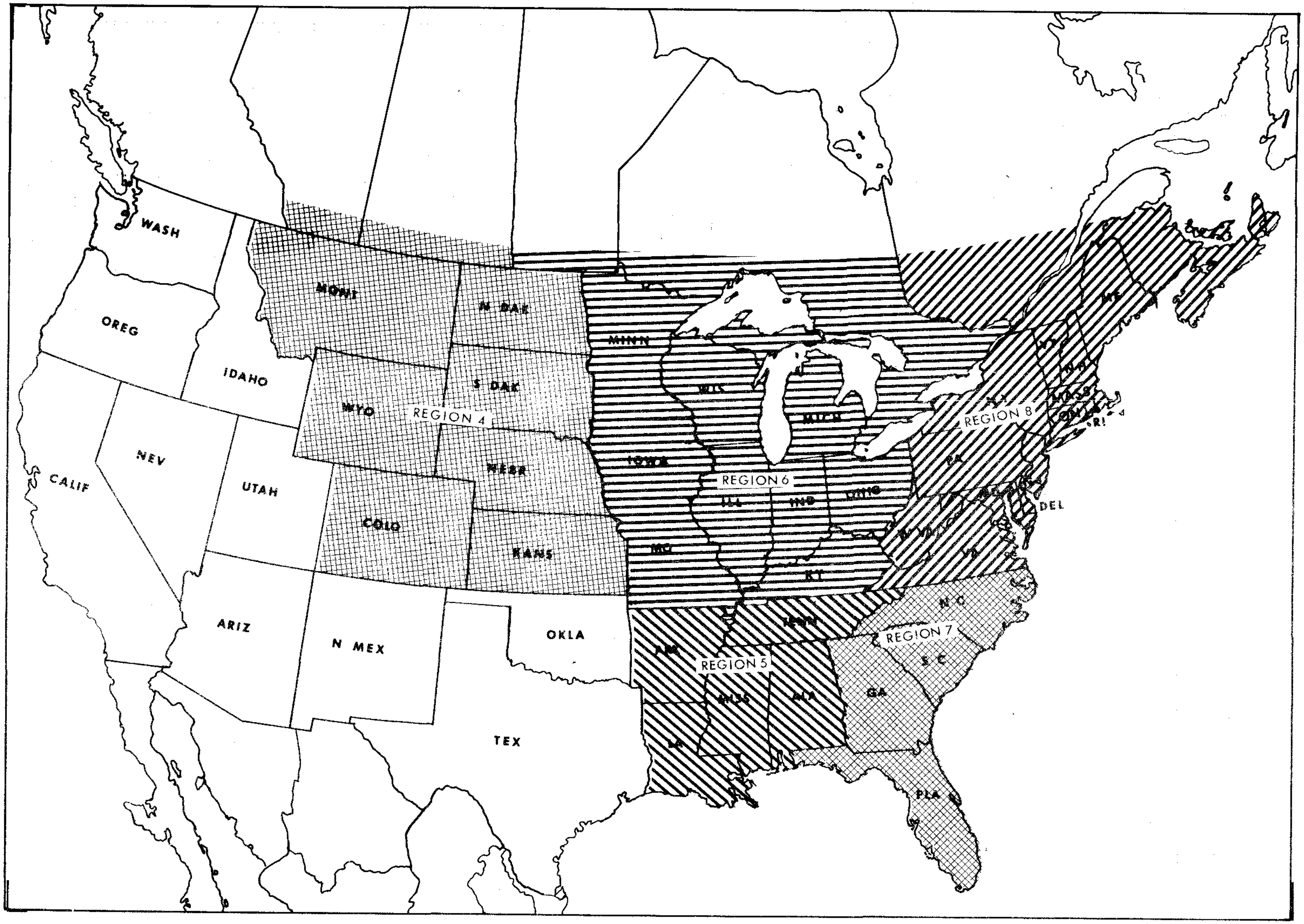

Figure 7. The geographical location of Regions 4, 5, 6, 7, and 8.

Table 42. Geographical and temporal location of band recoveries of blue jays south of Regions 6 and 8.

Banded in Region 6

Location of recovery	Month of recovery											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Arkansas	9	2	4	4	-	-	-	-	-	5	-	9
Tennessee	1	-	-	1	-	-	-	-	-	1	1	2
Oklahoma	-	2	-	-	-	-	-	-	1	1	-	3
Texas	3	1	1	-	-	-	-	-	1	3	-	1
Louisiana	1	1	1	-	-	-	-	-	-	2	-	3
Mississippi	1	1	1	-	-	-	-	-	1	2	1	-
Alabama	-	-	-	-	-	-	-	-	-	2	-	1
Georgia	-	-	-	-	-	-	-	-	-	-	1	-

Banded in Region 8

Location of recovery	Month of recovery											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Carolina	5	7	2	3	1	1	-	-	-	10	11	7
So. Carolina	9	3	-	1	-	-	-	1	-	10	9	9
Georgia	1	-	2	-	-	-	-	-	-	5	5	1
Tennessee	-	-	-	-	-	-	-	-	-	1	-	2
Alabama	2	-	-	-	-	-	-	-	-	1	6	-
Florida	-	-	-	-	-	-	-	-	-	-	1	-

Nesting Parameters

Clutch Size

Paucity of information on nesting parameters of the blue jay was noted by Hickey (1952) and has not changed appreciably. W. M. Tyler (in Bent 1946:37) reported that the northern blue jay (*C. c. bromia*) "ordinarily lays four or five eggs, sometimes as few as three, frequently six, and very rarely as many as seven." According to D. J. Nicholson (in Howell 1932), first sets of eggs of the southern race *C. c. cristata* nearly always consist of four eggs, second sets of three or four, and third sets of nearly always three. The latter statistics presumably applied to renestings following loss of eggs (Hickey 1952). Information on clutch size from Nashville, Tennessee included seven nests with five eggs and three nests with four eggs (two were first clutches and one a replacement set) for a mean of 4.70 eggs per clutch (Laskey 1958).

Fledging Rate and Nest Success

The only study known to the author on the fledging rate of blue jays was by Laskey (1958) who found an average of 2.60 young fledged per nesting attempt from ten nests. The annual production rate per breeding age female may be somewhat higher because of renesting attempts. Renesting undoubtedly occurs in the northeastern states as "egg dates" ranged from April 18 to July 12. Bendire (1895) believed that one brood is usually raised in a season, but two broods occasionally may be raised in the south. The species is normally single-brooded in southern Michigan (Hickey 1952). More quantitative information is needed to determine annual rates of production of blue jays.

Age of Sexual Maturity

Evidence was provided that one female in Nashville, Tennessee, nested as a 1-year-old (Laskey 1958). Hickey (1952) cited M. B. Hickey who observed 1-year-old birds as pairs and copulating. The percentage of 1-year-olds that take part in the reproductive cycle is unknown.

Population Dynamics

Mortality Rates

Very few blue jays are banded as nestlings; therefore estimates of rates of first-year mortality could not be obtained. An initial date of January 1 was used first for the analyses of mortality rates. However, the estimates of mortality rates from the first January 1 to the second were highly variable. This was probably the result of fluctuations in the percentage of birds of the year in the banded sample. Evidently the schedule of adult mortality rates may not be applied to birds of the year until sometime after January 1. Therefore, life tables that began with the second January 1 after banding were constructed so all birds were at least one year of age.

Adult mortality rates for Regions 6 and 8 are presented in Tables 43, 44, 45, 46 for the periods 1920-1945, 1946-1953, and 1954-1964. No significant changes in mortality rates were detected during the three time periods within each region ($t = 1.60$, 0.20, 0.58, 1.50) although mortality rates were significantly higher in Region 6 than in Region 8 ($t = 4.46$). Adult mortality rates estimated by Hickey (1952) were similar for blue jays banded during the years 1926-1936 although subdivisions for regions were not made.

Loss of bands could have resulted in an overestimated mortality rate (Hickey 1952). In fact, Hickey observed a blue jay with a thin, worn band that was partly open and about to come off the bird's leg. Bergstrom (1964) recorded that three jays definitely lost bands. The losses occurred between 3 years 6 months and 10 years of age. A test was made to determine if band-loss was biasing the recovery records (Figure 1). No loss could be detected.

Fate of the Population

The lack of quantitative data on first-year mortality rates of blue jays and productivity rates currently prevents a satisfactory analyses of the population dynamics for this species. The same

Table 43. Adult mortality rate estimates for blue jays banded in Region 6 during the years 1920-1945 and 1946-1953.

Years of life	1920-1945 No. of recoveries	1920-1945 Alive at beginning	1920-1945 Mortality rate	1946-1953 No. of recoveries	1946-1953 Alive at beginning	1946-1953 Mortality rate
1	248	545	0.422 ± 0.009	62	167	0.394 ± 0.015
2	108	297		46	105	
3	81	189		23	59	
4	41	108		16	36	
5	26	67		7	20	
6	16	41		2	13	
7	13	25		5	11	
8	8	12		2	6	
9	1	4		2	4	
10	2	3		1	2	
11	0	1		1	1	
12	1	1		0	0	

Table 44. Adult mortality rate estimates for blue jays banded in Region 6 during the years 1954-1964.

Year	No. banded	Years survived							Second-year recovery rate
		1	2	3	4	5	6	7	
1954	1,273	12	11	5	6	2	1	0	.009
1955	1,192	14	15	5	2	4	0	0	.012
1956	1,227	23	12	3	5	1	2	1	.019
1957	759	22	14	4	4	2	2	1	.029
1958	1,522	16	8	8	4	2	1	0	.011
1959	2,182	13	9	6	3	1	0		.006
1960	1,791	9	6	5	4	0			.005
1961	1,738	12	5	3	3				.007
1962	1,695	15	5	7					.009
1963	2,956	18	3						.006
1964	2,883	7							.002
Totals	19,218	161	88	46	31	12	6	2	.008
No. available		19,218	16,335	13,379	11,684	9,946	8,155	5,973	
Rec./10,000		83.78	53.81	34.38	26.53	12.07	7.36	3.35	
Alive at beginning		221.28	137.50	83.69	49.31	22.78	10.71	3.35	
Mortality rate		adult = 0.419 ± 0.012							

Table 45. Adult mortality rate estimates for blue jays banded in Region 8 during the years 1920-1945 and 1946-1953.

Years of life	1920-1945 No. of recoveries	1920-1945 Alive at beginning	1920-1945 Mortality rate	1946-1953 No. of recoveries	1946-1953 Alive at beginning	1946-1953 Mortality rate
1	114	327	0.362 ± 0.010	56	182	0.353 ± 0.012
2	76	213		44	126	
3	48	137		38	82	
4	38	89		13	44	
5	19	51		12	31	
6	13	32		5	19	
7	4	19		6	14	
8	6	15		4	8	
9	4	9		1	4	
10	1	5		2	3	
11	1	4		0	1	
12	3	3		1	1	

Table 46. Adult mortality rate estimates for blue jays banded in Region 8 during the years 1954-1964.

Year	No. banded	Years survived									Second-year recovery rate
		1	2	3	4	5	6	7	8	9	
1954	2, 320	14	11	14	6	5	4	1	0	1	.006
1955	2, 953	19	16	8	3	5	3	2	4	1	.006
1956	2, 333	22	13	6	6	4	3	4	2	0	.009
1957	3, 034	21	19	19	10	1	5	4	0		.007
1958	4, 066	34	19	17	5	6	1	1			.008
1959	4, 777	30	13	16	4	6	3				.006
1960	5, 787	24	26	14	12	7					.004
1961	7, 210	34	25	20	11						.005
1962	7, 060	29	30	9							.004
1963	7, 273	46	13								.006
1964	6, 847	18									.003
Totals	53, 660	291	185	123	57	34	19	12	6	2	.005
No. available		53, 660	46, 813	39, 540	32, 480	25, 270	19, 483	14, 706	10, 640	7, 606	
Rec. /10, 000		54. 23	39. 52	31. 11	17. 55	13. 45	9. 75	8. 16	5. 64	2. 63	
Alive at beginning		182. 04	127. 81	88. 29	57. 18	39. 63	26. 18	16. 43	8. 27	2. 63	
Mortality rate		adult = 0. 332 ± 0. 007									

conclusion was reached by Hickey (1952) almost 20 years ago, although more data are presently available for estimating adult mortality rates.

BLACK-CAPPED CHICKADEE

The black-capped chickadee is found in North America from central Alaska east to Newfoundland and south to northwestern California and western North Carolina (AOU 1957). The titmice, the family of birds to which the black-capped chickadee belongs, are widely distributed in the two hemispheres; they are represented in North America by numerous genera, species, and races.

Migration and Breeding Cycle

The black-capped chickadee is migratory, but it is difficult to determine the time and extent of its northward and southward movements (Tyler, in Bent 1946). The movements at various locations have been discussed by numerous authors (Wallace 1941, Odum 1941, 1942, Bryens 1948, Hussell and Stamp 1965, among others). Distance of winter movements has not been reported to my knowledge. A review of the data of band recoveries indicated that chickadees banded principally in the winter in Pennsylvania have been recovered in Quebec, Maine, New Hampshire, New York, New Jersey, West Virginia, and Virginia; this indicates that some birds banded in winter were produced north of Pennsylvania (Table 47). All recoveries outside the state of Maine from chickadees banded in Maine were found south of the state (Table 48). It must be emphasized that recoveries from

Table 47. Geographical and temporal distribution of black-capped chickadees banded in Pennsylvania and recovered outside the state.

Location of recovery	Month of recovery											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Quebec	-	1	-	-	-	-	-	-	-	-	-	-
Maine	2	3	-	-	-	-	-	-	-	-	1	2
New Hampshire	1	-	-	-	-	-	-	-	-	-	1	-
New York	-	1	1	-	1	1	-	-	-	-	-	-
New Jersey	-	-	-	1	-	-	-	-	-	-	-	-
West Virginia	-	1	-	-	-	-	-	-	-	-	-	1
Virginia	-	-	-	-	-	-	-	-	-	-	-	1

Table 48. Geographical and temporal distribution of black-capped chickadees banded in Maine and recovered outside the state.

Location of recovery	Month of recovery											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
New Hampshire	-	-	1	-	-	-	-	-	-	-	-	-
Vermont	-	-	-	-	-	-	-	-	-	-	1	-
Pennsylvania	-	-	-	-	-	-	-	-	-	-	1	-
Maryland	-	-	-	-	-	-	-	-	-	-	1	-
Delaware	1	-	-	-	-	-	-	-	-	-	-	-

outside the state of banding represent only a small portion of the total recoveries.

The nesting season in southeastern Michigan usually begins about the third week in April (Nickell 1956). The first evidence of courtship and definite breeding pairs in New York occurred during April 10-25 (Odum 1941). Bent (1946) listed "egg dates" from April 20 to June 11 in Illinois and from May 7 to July 12 in Massachusetts; the peak of the nesting occurred between May 2 and May 29.

Nesting Parameters

Clutch Size

Bent (1946) reported that 5 to 10 eggs may be found in the chickadee's nest; but 6 to 8 are the most common numbers, and as many as 13 eggs have been recorded. Brewer (1963) noted a trend of increasing clutch size with increasing latitude and found a mean clutch size of 6.82 from 79 nests above 38° N. Latitude. His information was obtained from literature, correspondence, and personal observations. As very little information on clutch size has been published since 1963, Brewer's estimate is the best available.

Fledging Rate and Nest Success

The chickadee, like many other hole-nesting birds, has been credited by many observers to have a much greater nesting success than most birds which nest in the open. Nice (1957), reviewing published data, concluded that about 46 percent of the eggs laid by nidicolous birds in open nests and about 66 percent of the eggs laid in nests in holes develop into young that leave the nest successfully.

Various writers disagree on the number of broods raised each season (Nickell 1956). Barrows (1912:696) in Michigan stated: "The chickadee is often said to rear two broods, but we have no data which warrants such an assertion." Forbush (1912:373) in Massachusetts reported: "It nests in April or May and sometimes rears two broods in a season." Todd (1940) in Pennsylvania stated that there is no proof that more than one brood is raised in a season. Only one of 11 pairs in New York raised two broods successfully in 1940 after a late spring, and one pair nested successfully on the second attempt (Odum 1941). At least two of the seven pairs studied by Odum in 1941 had two broods after an earlier spring. Nickell (1956) observed no second broods although 5 of 35 breeding records (14 percent) could have been renestings due to time of occurrence during the nesting season.

The number of young fledged per nesting attempt and per pair (including renesting and multibroods), as summarized from the literature, is presented in Table 49. Brewer's (1963) report of 4.52 fledged per nesting attempt is probably the best estimate since it is a compilation of several studies (66.3 percent of eggs yielded fledged young). However, his estimate is not adjusted for renesting attempts or multibroods. The estimates of Odum (1941) and Kluyver (1961) for the number fledged per pair (adjusted for renests and multibroods) were 10 percent and 11 percent higher than the number fledged per nesting attempt. At this date, the best available annual production rate per breeding female is 4.99 (4.52 × 110.5%), which is in close agreement with the 4.95 determined from a recent study by Smith (1967).

Table 49. Nesting success of black-capped chickadees.

Location	No. nests	Years	No. fledged	No. fledged per nesting attempt	No. fledged per pair[a]	Source
New York	11	1939-1941	53	4.82	5.30	Odum 1941
Michigan	9	1941-1954	59	6.56	---	Nickell 1956
Massachusetts	25	1959	85	3.40[b]	3.78[b]	Kluyver 1961
British Columbia	20	1964-1965	99	---	4.95	Smith 1967
Not given[c]	49	---	222	4.52	---	Brewer 1963

[a]Includes renesting and multibroods.

[b]Low because five broods completely destroyed by house wrens (Troglodytes aedon).

[c]A review of the literature, number of nests based on his average clutch size reported (6.82).

Age of Sexual Maturity

Black-capped chickadees reach maturity and breed the first year after hatching (Smith 1967). She also found no unmated males during the breeding season, and only one unmated female was found each year in the study area. Odum (1941:533) also reported "few, if any," unmated birds after May 1.

Population Dynamics

Mortality Rates

A mortality rate of about 30 percent from winter, 1937, to winter, 1938, and over 40 percent (possibly 50%) from 1938 to 1939 was reported at Lenox, Massachusetts by Wallace (1941). He also believed the mortality from 1939 to 1940 may have been greater than during the previous two winters. Odum (1942) calculated an annual mortality rate of about 44 percent. Brewer (1963) grouped living (returns) and dead birds and estimated a mortality rate of 60.6 percent after the first January 1. As pointed out earlier in the section on chimney swifts, records from living and dead birds should not be grouped together for estimating mortality rates. Speirs (1963) assumed various rates of adult mortality and rates of production and calculated possible combinations that would yield a stable population. His paper is theoretically sound, but he had little actual data for deciding which combination was correct for the black-capped chickadee.

When chickadees are banded in the fall or early winter, as most of them are, the banded sample contains both adults and birds of the year. The first January 1 after banding was first used as the initial date to estimate the rate of adult mortality; however the rate appeared high. Evidently birds of the year continue to have a higher mortality rate after the first of the year than the older birds in the black-capped chickadee. The second January 1 after banding was used as the initial date to estimate the adult mortality rate (Tables 50 and 51). No significant change in estimates of adult mortality (t = 0.75) was detected between 1923-1945 and 1946-1964 (0.477 ± 0.024 and 0.503 ± 0.025). The best estimate of mortality available is the average of the two rates (0.490). This rate is similar to the rate found in European tits (Kluyver 1961).

Table 50. Estimates of the adult mortality rate for black-capped chickadees banded in Regions 4, 6, and 8 during the years 1923-1945.

Years of life	No. of recoveries[a]	Alive at beginning	Mortality rate
1	49	98	0.503 ± 0.025
2	24	49	
3	12	25	
4	8	13	
5	0	5	
6	5	5	

[a]See Figure 7 for location of Regions.

Fate of the Population

The lack of quantitative information on rates of first-year mortality precludes an analysis into the fate of the population. However, by using the average population parameters available at this time, the first-year survival rate necessary for maintaining a stable population may be determined. Assuming that the average productivity

Table 51. Estimates of the adult mortality rate for black-capped chickadees banded in Regions 4, 6, and 8 during the years 1946-1964.

Year	No. banded	Years survived							Second-year recovery rate
		1	2	3	4	5	6	7	
1946-1956	27,083[a]	24	7	5	1	2	2	0	---
1957	6,008	8	0	1	2	0	0	0	.0013
1958	5,607	3	0	1	4	1	0	1	.0005
1959	7,965	5	1	0	0	0	0		.0006
1960	8,404	3	2	3	1	0			.0004
1961	12,376	8	4	0	0				.0006
1962	10,412	11	3	1					.0011
1963	13,382	7	4						.0005
1964	9,546	3							.0003
Totals	100,783	72	21	11	8	3	2	1	.00065
No available		100,783	91,237	77,855	67,443	55,067	46,663	38,698	
Rec./10,000		7.13	2.30	1.41	1.19	0.54	0.43	0.26	
Alive at beginning		13.27	6.13	3.83	2.42	1.23	0.69	0.26	
Mortality rate		adult = 0.477 ± 0.024							

[a]Assuming the average recovery rate for the period 1957-1964 (.00065). Also, see Figure 7 for location of regions.

rate per pair (4.99) and the average adult mortality rate (0.490) are correct and that all birds attempt to nest as 1-year-olds, the first-year survival rate which yields a stable population may be estimated by the formula originally used for determining production requirements for a stable population.

Using the above information the population can remain stable with a first-year mortality rate from the time of fledging of 80.4 percent. At this time it should be emphasized that future nesting studies should be compared with the average estimates of Brewer (1963) when he reported that 4.52 young fledged per nesting attempt or 4.99 fledged per pair including renesting and multibroods. The annual rate of change in the population cannot be determined since the rates of first-year mortality are not known definitely.

CARDINAL

The cardinal formerly was considered a southern bird and a member of the Carolinan fauna of the Austral Zone (Bent 1968). During recent years, the cardinal has been extending its range northward. It is steadily increasing in abundance and has established itself as a breeding bird in regions where it was formerly only a casual visitor. Bent (1968:1), in summarizing the range of cardinals as reported in the AOU Check-lists, noted, "Our 1886 Check-list gave its range as only casual north of the valley of the Ohio River, which forms the northern boundary of Kentucky; the 1895 edition extended the range to the Great Lakes; and the 1910 edition included southern Ontario and the southern Hudson River valley."

Migration and Breeding Cycle

The cardinal cannot be classified as a regularly migratory species. Evidence on movement in the species was summarized by Bent (1968), and he concluded that many individuals are decidedly sedentary and seldom wander more than a few miles from their area of hatching. Bent also cited a few records of banded birds that moved from 100 to 200 miles, and he indicated a trend of movement northeastward and northward in the late summer and fall. This movement may have been encouraged by feeding stations and may have been the reason for the northward expansion of the species (Bent 1968).

Nesting usually begins in Lansing, Michigan in mid-April and reaches a peak in May or early June although some nesting continues all summer; young have been found in the nest during September (Burns 1963). The laying season at London, Ontario lasted approximately 16 weeks in both 1955 and 1956 (Lemon 1957). Bent (1968) has provided "egg dates" which range from March 2 to August 27 with peak numbers recorded in May for Illinois, Maryland, Michigan, New Jersey, New York, and Ontario. Cardinals in Tennessee usually begin laying in late April, and the nesting season may extend into August and September (Laskey 1944).

Nesting Parameters

Clutch Size

The cardinal lays from two to five eggs, but three or four eggs most often form the set (Bent 1968). Gainer (1941) stated that around Nashville three eggs was the normal complement but about one in 30 nests had four eggs; however, the full complement was two eggs during the attempts at late nesting. Laskey (1944) also reported that the typical clutch size near Nashville was three eggs; 32 of 35 nests had three eggs and only 3 nests had four eggs (mean 3.09). Lemon (1957) reported a similar mean clutch size from 31 nests at London, Ontario (mean 3.13). In the Smithsonian Institute collection, of 25 sets of eggs, 2 sets contained two eggs, 18 sets contained three eggs, and 5 sets contained four eggs which yields a mean clutch size of 3.12. The eggs in the Smithsonian collection were obtained from Alabama, District of Columbia, Florida, Georgia, Indiana, Louisiana, Mississippi, Missouri, Ohio, Virginia, and West Virginia.

Number of Clutches or Broods per Year

A pair of cardinals may build five nests in a season, although usually not more than four broods are reared successfully (Shaver and Roberts 1930). A pair of birds building a nest in Nashville on April 1, 1934 had four nests that season; three of the four were successful and yielded six young (Laskey 1944). In 1935 a female again had three out of four nests termed successful, and five young were raised. Two broods are usually raised per season in Iowa if nothing has hampered the start of the nesting cycle (Hodges 1949). In London, Ontario Lemon (1957) reported that 13 pairs made 60 nests (mean 4.6 nests) and fledged approximately three young per pair per year. In summary, it appears that from two to three broods are raised successfully per year; this yields approximately three to six fledged young per nesting pair. More information on this population parameter is needed.

Age of Sexual Maturity

First-year cardinal males acquire a scarlet plumage which is practically undistinguishable from the adult in August or earlier in early broods (Bent 1968). Plumage wear causes this plumage to intensify to bright red in the spring. Pointed retricies were used as a criteria for age determination at London, Ontario (Scott 1967). Based on observed mortality rates, Scott expected 17 birds in his breeding sample would have pointed retricies (1-year-olds). This value agreed closely with the observed value of 19 and supported his assumption that all 1-year-olds in the population nest. Since non-breeding segments of populations have not been reported, and 1-year-olds have breeding plumage, it is believed that cardinals breed as 1-year-olds.

Population Dynamics

Mortality Rates

Approximately 35 percent of the breeding birds did not return to the study area in London, Ontario, for the following breeding season (e.g., approximately a 35% adult mortality rate) (Scott 1967). Farner (1952) estimated a 48 percent adult mortality rate for cardinals in the eastern United States when an initial date of the first January 1 after banding was used. Farner (1952) tested the hypotheses that the adult mortality rate of the cardinal did not vary extensively with age.

This hypotheses was acceptable only at the 20 percent probability level. I believe that the mortality rate was higher from the first January 1 after banding until the second January 1 because the birds of the year in the essentially non-migratory cardinal (like the blue jay and black-capped chickadee) do not attain an adult mortality schedule by January 1. The inflated mortality rate (from first January 1) probably resulted from the percentage of birds of the year exhibiting higher mortality rates.

Since very few birds were banded as nestlings, the second January 1 after banding was used as the initial date in my analyses so that all birds were known to be at least one year old (estimates of adult mortality rates only).

The range of the cardinal was subdivided into three geographical areas (Regions 5 and 7, Region 6, and Region 8), (Fig. 7), and into two time periods (1923-1945 and 1946-1964) (Tables 52, 53, 54, and 55) for the adult mortality analyses. No significant change in mortality rates was detected within the Regions during the two time periods ($t = 0.64$, 1.58, and 1.28) (Table 56). However, the more recent mortality rate estimates from Region 8 were significantly lower than the rates from Regions 5 and 7 ($t = 2.77$) and Region 6 ($t = 2.70$). The more recent rates from Region 6 and Regions 5 and 7 were not significantly different from each other ($t = 0.19$).

Table 52. Estimates of adult mortality rates for cardinals banded in Regions 5 and 7, Region 6, and Region 8 during the years 1923-1945.

	Regions 5 and 7			Region 6			Region 8		
Years of life	No. of recoveries	Alive at beginning	Mortality rate	No. of recoveries	Alive at beginning	Mortality rate	No. of recoveries	Alive at beginning	Mortality rate
1	28	55	0.420 ± 0.028	44	108	0.396 ± 0.019	6	22	0.324 ± 0.032
2	6	27		26	64		6	16	
3	8	21		18	38		3	10	
4	5	13		2	20		2	7	
5	5	8		4	18		3	5	
6	1	3		8	14		0	2	
7	1	2		2	6		0	2	
8	0	1		3	4		1	2	
9	1	1		1	1		0	1	
10	0	0		0	0		1	1	

Table 53. Estimate of the adult mortality rate for cardinals banded in Regions 5 and 7 during the years 1946-1964.

Years	No. banded	Years survived									Second-year recovery rate
		1	2	3	4	5	6	7	8	9	
1946-1953	13502[a]	32	17	12	2	3	1	1	0	2	.0024
1953	952	1	0	0	0	0	0	0	0	0	.0011
1955	760	3	2	0	0	0	0	0	0	0	.0039
1956	872	2	2	0	1	1	0	1	0	0	.0023
1957	1208	4	1	0	0	0	0	0	0		.0033
1958	1228	5	2	1	0	1	0	0			.0041
1959	941	6	1	1	3	0	0				.0064
1960	2160	4	2	4	0	0					.0019
1961	2068	5	2	1	1						.0024
1962	1319	4	0	1							.0030
1963	1920	2	0								.0010
1964	2177	1									.0005
Totals	29107	69	29	20	7	5	1	2	0	2	.0024
No. available		29107	26930	25010	23691	21623	19463	18522	17294	16086	
Rec/10,000		23.71	10.77	8.00	2.95	2.31	0.51	1.08	---	1.24	
Alive at beginning		50.57	26.86	16.09	8.09	5.14	2.83	2.32	1.24	1.24	
Mortality rate		adult = 0.442 ± 0.020									

[a]Obtained by assuming the same recovery rate as the average for the years 1954-1964.

Table 54. Estimate of the adult mortality rate for cardinals banded in Region 6 during the years 1946-1964.

Years	No. banded	Years survived							Second-year recovery rate
		1	2	3	4	5	6	7	
1946-1953	9189[a]	34	18	7	3	4	2	1	.0037
1954	482	6	0	0	2	0	0	0	.0124
1955	392	5	2	2	2	0	0	0	.0128
1956	735	1	5	3	1	2	0	0	.0014
1957	699	3	3	1	1	0	1	0	.0043
1958	845	4	3	3	2	1	1	0	.0048
1959	723	4	4	0	1	1	0		.0055
1960	1171	2	2	0	1	1			.0017
1961	1252	1	2	0	1				.0008
1962	1103	6	4	0					.0054
1963	1480	2	1						.0014
1964	1190	3							.0025
Totals	19261	71	44	16	14	9	4	1	.0037
No. available		19261	18071	16591	15488	14236	13065	12342	
Rec. /10,000		36.86	24.35	9.64	9.04	6.32	3.06	0.81	
Alive at beginning		90.08	53.22	28.87	19.23	10.19	3.87	0.81	
Mortality rate		adult = 0.437 ± 0.018							

[a]Obtained by assuming the same recovery rate as the average for the years 1954-1964.

Table 55. Estimate of the adult mortality rate for cardinals banded in Region 8 during the years 1946-1964.

Years	No. banded	Years survived 1	2	3	4	5	6	7	8	Second-year recovery rate
1946-1953	4839[a]	15	12	2	1	0	1	1	1	.0031
1954	679	1	1	2	1	1	0	0	0	.0015
1955	676	1	2	0	1	1	1	0	1	.0015
1956	743	4	1	0	0	1	0	1	0	.0054
1957	1235	4	2	0	0	1	2	0	0	.0032
1958	1081	5	2	0	0	0	1	1		.0046
1959	882	9	2	1	0	1	1			.0102
1960	2127	3	1	2	1	0				.0014
1961	2351	4	4	4	1					.0017
1962	2749	13	2	1						.0047
1963	3062	4	1							.0013
1964	3402	7								.0021
Totals	22826	70	30	12	5	5	6	3	2	.0031
No. available		22826	20424	17362	14613	12262	10135	9253	8172	
Rec/10,000		30.67	14.69	6.91	3.42	4.08	5.92	3.24	2.45	
Alive at beginning		71.38	40.71	26.02	19.11	15.69	11.61	5.69	2.45	
Mortality rate		adult = 0.370 ± 0.017								

[a]Obtained by assuming the same recovery rate as the average for the years 1954-1964.

Table 56. A summary of rates of adult mortality for cardinals by Region and time period.[a]

Location[b]	Time Periods	
	1923-1945	1946-1964
Regions 5 and 7	0.420 ± 0.028	0.442 ± 0.020
Region 6	0.396 ± 0.019	0.437 ± 0.018
Region 8	0.324 ± 0.032	0.370 ± 0.017

[a]Taken from Tables 52, 53, 54, 55.

[b]Regions shown in Figure 7.

A large percentage of the papers concerning cardinals refer to their behavior toward newly applied leg bands (Young 1941, Laskey 1944, Chapman 1946, and Lovell 1948). Several authors have mentioned the necessity to replace bands where butt ends were overlapped due to pressure from the birds' beak. Lovell (1948) has reported definite proof of four cardinals removing their bands within 54 days of their date of banding. This type of band loss may be classified as initial loss (see earlier discussion in Methods section) and has very little effect, if any, on mortality estimates from banding data. Gradual loss of bands from wear is of little or no consequence (Figure 1).

Fate of the Population

Most papers written about cardinals have been concerned with two topics: (1) the behavior toward bands (mentioned above) and (2) the range expansion of the species (see summary by Beddall 1963). The cardinal population in southern New England (Region 8) has increased spectacularly in the past 15 years (Beddall 1963), while relative stability has been reached in Michigan (Region 6) following an increase that began about 1900 (Burns 1958). This information makes it easier to explain the mortality schedules for the various Regions (Table 56). Mortality rates appeared to be lower in both Region 6 and Region 8 prior to 1946 as compared with 1946-1964. This may have been due to lower population densities. It is apparent that the recent mortality rates of birds in Region 8 are significantly lower than for birds in Regions 5 and 7, and Region 6. I have not been able to detect a mortality rate pattern of this type in any other North American avian species. It is tempting to speculate on the causes for the pattern. It appears that the low mortality rate may have been the result of a low population density in Region 8. Population densities of cardinals in Region 8 in 1967 were still somewhat lower than the more southern location (Regions 5 and 7) according to Robbins and Van Velzen (1969). The population of Region 6 (Michigan) has been reported as relatively stable and presently has a mortality rate similar to that found in the southern United States.

Further analyses into the population dynamics of the species cannot be made at this time because of lack of information on fledging rates per breeding pair and lack of a first-year mortality rate. It is apparent from the information on range expansion that the species is not declining in numbers.

ROBIN

The robin is found in North America from the limit of trees in northern Alaska, northern Canada, and Newfoundland south to southern Mexico and the shores of the Gulf of Mexico (AOU 1957). The wide distribution, abundance, and accessibility of the robin have made it a popular subject for study, especially banding studies.

Migration and Breeding Cycle

Robins are sedentary in the southern portion of their habitat but most robins that nest in the northern United States and Canada go south to winter in the Gulf states (Dorst 1962). Dorst also reported the chief wintering area was the southeastern United States, especially Florida, where flocks numbering up to 50,000 birds assemble in roosts. Similar results were reported by Speirs (1956) who found most of the robins from east of the Rocky Mountains concentrated in the Gulf States and the Carolinas during the months of December, January, and February. Robins breeding in the east tend to winter farther east than robins breeding in the west, but some over-lapping in areas occurs (Speirs 1953). As robins move northward, they follow very closely the advance of the average daily temperature of 37° F.; they appear in eastern Massachusetts soon after March 10 (Bent 1949).

The chronology of the nesting season with respect to latitude has been summarized by Howell (1942). The earliest nests were started during the first week of April in each year of a 3-year study at Madison, Wisconsin (Young 1955). Similar nesting dates were found at Ithaca, New York, during a 2-year study by Howell (1942).

Nesting Parameters

Clutch Size

Bent (1949:22) reported, "Four eggs comprise the usual set for the robin, but often only three are laid; five eggs in a set are rare, and I have taken one set of six, and sets of seven have been reported." The average clutch size ranged from 3.3 to 3.6 during two years (1937 and 1938) of investigation at Ithaca, New York, and three years (1947-1949) at Madison, Wisconsin; the average clutch size was 3.4 in 273 sets (Howell 1942, Young 1955). The average clutch size was 3.2 in 29 complete clutches at Carbondale, Illinois, in 1955 and 3.4 from 81 complete clutches in Iowa from 1946-1958 (Klimstra and Stieglitz 1957). Howard (1967) reported a mean clutch size of 3.5 ± 0.02 for Massachusetts-New York and an overall mean clutch size of 3.2 ± 0.04 for the Maritime provinces. Clutches laid after May 15 usually are smaller and consist of three eggs (Howell 1942).

Fledging Rate and Nest Success

The robin sometimes raises three broods in a season (Howell 1942, Nice 1941, Brackbill 1952). One robin in seven pairs represents the maximum proportion of pairs that raised three broods, and the robin seems to raise at least two broods in all parts of its range (Howell 1942). Eleven pairs of robins were observed in Baltimore between 1942 and 1951; one pair (9%) was 3-brooded, eight pairs were 2-brooded, and two pairs were 1-brooded for a mean of 1.91 broods per pair (Brackbill 1952). The breeding activity of a single bird was followed for a 3-year period (Young 1955); the bird made ten known attempts to nest, and six of these were successful. Of the 30 eggs laid, 21 hatched and 16 were fledged (2 broods per year and 5.33 young per year). In summary, information obtained from the literature indicates an average of approximately two successful broods are fledged per breeding pair per year.

It was necessary to determine the number of young fledged per successful nest in order to estimate a mean annual fledging rate per pair (Table 57). Between 2.40 and 2.88 young were fledged per successful nest; by assuming that 1.91 to 2.00 successful broods were fledged per pair annually, the mean annual fledging rate was estimated from 4.58 to 5.76 young per pair. Previous estimates of annual productivity by Farner (1945) and Young (1955) were within this range (5.0 and 5.6 young per pair respectively).

Table 57. Number of young robins fledged per successful nest.

Years	Location	No. nests successful	No. young fledged	No. fledged per successful nest	Source
1932-1942	Massachusetts	86	248[a]	2.88	Mason (1943)
1937	New York	42	101	2.40	Howell (1942)
1947-1949	Wisconsin	86	246	2.86	Young (1955)

[a] Refers to number banded per nest and may be an overestimate of the number fledged per nest.

Population Dynamics

Mortality Rates

Mortality rates of robins have been estimated previously from banding data by Farner (1945, 1949). He concluded in the more recent paper that the first January 1 after banding should be used as the initial date, and he calculated an annual adult mortality rate of 52 percent. Since there were very few robins banded as nestlings and the age of many of the birds banded in the fall could not be correctly identified, it was concluded that the first January 1 after banding would be the best initial date if all age classes had attained a schedule of adult mortality rates by that time (same as Farner 1949). All birds, including birds of the year, had attained an adult mortality rate schedule by January 1.

Initially, the range of the robin was subdivided into six regions for separate estimates of mortality rates. However, no significant differences between regions were detected, and all data from throughout the United States and Canada were combined. It must be emphasized, however, that a large percentage (approximately 85%) of the records were from Regions 6 and 8 (Figure 7).

Mortality rates were estimated for two time periods (1916-1945 and 1946-1965) (Tables 58 and 59). No significant change in adult mortality rates (0.504 ± 0.005 vs. 0.508 ± 0.005) was detected ($t = 0.57$).

Table 58. Estimate of the adult mortality rate for robins banded in North America during the years 1916-1945.

Years of life	Number of recoveries	Alive at beginning	Mortality rate
1	1114	2290	0.504 ± 0.005
2	613	1176	
3	310	563	
4	134	253	
5	59	119	
6	21	60	
7	17	39	
8	11	22	
9	5	11	
10	3	6	
11	2	3	
12	1	1	

Table 59. Estimate of the adult mortality rate for robins banded in North America during the years 1946-1965.

Years	No. banded	Years survived												First-year recovery rate
		1	2	3	4	5	6	7	8	9	10	11	12	
1946-1956	67027[a]	496	244	122	52	17	10	7	4	2	1	0	1	---
1957	9805	84	38	15	7	5	5	0	1	0				.0086
1958	8474	93	39	20	7	2	2	1	2					.0110
1959	10499	78	19	16	5	7	3	0						.0074
1960	9530	72	47	28	12	4	4							.0076
1961	12890	106	76	27	20	4								.0082
1962	16392	119	58	32	11									.0073
1963	16190	109	55	28										.0067
1964	15850	94	50											.0059
1965	14061	83												.0059
Totals	180718	1334	626	288	114	39	24	8	7	2	1	0	1	.0074
No. available		180718	166657	150807	134617	118225	105335	95805	85306	76832	67027	57027	47027	
Rec/10,000		73.82	37.56	19.10	8.47	3.30	2.28	0.84	0.82	0.26	0.15	---	0.21	
Alive at beginning		146.81	72.99	35.43	16.33	7.86	4.56	2.28	1.44	0.62	0.36	0.21	0.21	
Mortality rate		adult = 0.508 ± 0.005												

[a]Obtained by assuming the same recovery rate as the average for the years 1957-1965.

Fate of the Population

Records of robins' deaths attributed to DDT used for Dutch elm disease control are found throughout the ornithological literature (Barker 1958, Hickey and Hunt 1960, Bernard 1963, Wallace et al. 1964, Hunt 1969a). Hunt (1969a) emphasized that the peak mortality of robins, occuring during late April on the Madison campus of the University of Wisconsin, coincided with maximum availability of DDT-laden earthworms. Considerable die-off of robins followed the initial application of pesticides, although no dead specimens were being reported from adjacent unsprayed sites (Hickey and Hunt 1960). The robin deaths referred to by Hunt (1969) occurred between April 6 and June 20 with the peak occurring in late April. Therefore, these birds were all adults; and if the die-off was widespread, it should be detected by changes in the adult mortality rates (Tables 58 and 59). No changes were detected. It should be pointed out, however, that other forms of mortality may have decreased as a compensation for the additional mortality resulting from DDT.

Since very few dead birds, if any, have been detected at a distance from areas of direct pesticide application it would seem that the population parameter that should be monitored is the number of young fledged per pair. The basis for this suggestion is that no significant increase in post-fledging mortality rates at a regional or continental level has been detected in any of the species studied. Reproductive failure has been the cause for all declines reported. Nesting studies should be designed to determine the number of young fledged per breeding female. The observed fledging rates then may be compared with the previously discussed rate of 4.58 to 5.76.

The lack of quantitative information on the first-year survival rate precludes a complete analysis of the status of the population from the modeling approach. However the first-year survival rate necessary for maintaining a stable population may be determined by using the population parameters available at this time. If it is assumed, (1) that all birds attempt to nest as 1-year-olds, (2) that the annual productivity is between 4.58 and 5.76, and (3) that the annual adult mortality rate is 0.506, the first-year survival rate which will yield a stable population may be determined by applying the formula originally used for determining production requirements for a stable population. Based on the above information, it is assumed the population can remain stable with a first-year mortality rate of between 0.779 and 0.824 from the time of fledging.

DISCUSSION

The discussion will be divided into two sections: (1) the approach and its limitations, problems, and potentials, and (2) the interpretation of results obtained.

The Approach

Cole (1954) and Cody (1966) have argued forcefully that our understanding of the population consequences of life histories has been quite inadequate. It must be emphasized that an understanding of the life history of a species is necessary before a population dynamics approach, such as used in this study, can effectively estimate the status of a population. In this study it soon was discovered that Cole and Cody were correct in their general assessment of the state of knowledge regarding life history parameters. This is particularly true of the question of the age of sexual maturity for many birds. A considerable amount of information was available in the literature as separate and dispersed entities. The status of all species studied could not be estimated; however, the basic information from the literature was compiled and the types of information needed in the future were stressed. In many cases, the rates of observed production obtained from present-day studies can be compared with nesting studies conducted in the 1920's and 1930's, to determine if reproductive parameters have changed.

The synthesizing factor that brought many loose ends together and allowed effective use of the population dynamics approach was the development of the mathematical model (Henny *et al.* 1970, in press), which showed the relationships that yield stable populations with the various combinations of mortality and recruitment schedules. Many non-game species are not good subjects for the census method of population study because of the habitat in which they are found. Therefore, in some situations the modeling approach appears to be the only acceptable method for determining the status of the population.

Reliability of the approach has been demonstrated in studies of the osprey where the estimated annual rates of change were in agreement with observed rates of change (Henny and Ogden 1970). There has been discussion about the suitability of either the date of banding or the date of fledging as the initial date for analysis of mortality rates (Farner 1949, Hickey 1952). The consistency of the agreement between the status of the population, the observed rates of production, and requirements of production to maintain a stable population suggests that either the date of banding or date of fledging can be used effectively for analysis of populations of larger species banded as nestlings. Neither of the dates can be used effectively with smaller birds (barn swallow) since the first-year mortality rate is underestimated. The same conclusion about smaller birds was reached by

Hickey (1952). It is apparent that migratory passerines achieve a schedule of adult mortality by the first January 1 after hatching; however, the more sedentary species (cardinal, black-capped chickadee, blue jay) in the northern portion of the United States do not attain their schedule of adult mortality rates until later.

The bird banding program in North America has provided a source of data that enables an effective monitoring system for rates of avian mortality. In addition, the banding program provided the impetus for many amateur ornithologists to conduct nesting studies, to determine the age at which the species reach sexual maturity, and to study many other population parameters. Recovery records, representing the efforts of thousands of bird banders, were used in this study which involved only 16 species. The approach can be used effectively for many additional species.

The need for productivity information (number of young banded per nest) has been stressed throughout this study, and I believe bird banders can provide much data of this type with little additional effort. Sufficient data on reproductive rates were not available from 9 of the 16 species studied. I would suggest a standardized form be used for recording the information. The information could then be either punched onto the banding summary records or filed separately for later analysis. The banding program could then be an effective monitoring system of both the rates of mortality and the rates of productivity of the population.

Production standards have been estimated, although the status of all the species studied could not be determined. Evaluation, as presented here will provide a basis for interpretation of nesting studies and will provide a technique for estimating the annual rates of change in size of the population. I must caution against the comparison of productivity information collected over a short term in a localized area with the production standard obtained with the modeling approach. The production standard is an average value calculated from many years data; and annual rates of mortality and productivity can be expected to vary from year to year.

Interpretation of Results

Mortality Rates

The information that post-fledging mortality rates have not increased since 1945 in any of the 16 species studied is probably the most significant result obtained from this study. In fact, several of the species including the Cooper's hawk, sparrow hawk, great blue heron, and brown pelican have exhibited lower mortality rates during later time periods. This was believed to be a result of a decrease in shooting pressure. Since post-fledging mortality rates have not increased, it may be concluded that any decline during the last 20 years in the size of populations studied must be the result of lowered reproductive rates. The large "die-offs" of robins and other species in the immediate area where pesticides have been used must represent a very localized situation.

Reproductive Rates

A summary of the reproductive performances of the species studied is presented in Table 60. Several of the populations studied have declined at an alarming rate due to reproductive failure while other populations in the same location have remained stable. For example, no change was detected in the reproductive rates of the red-tailed hawk, barn owl, or great-horned owl in the northeastern United States, but the sparrow hawk, red-shouldered hawk, and the Cooper's hawk in the same locations have reproductive rates which decreased 7 percent, 7-16 percent, and 24 percent, respectively, since the end of World War II. Other species in which reproductive rates have decreased include the brown pelican and the osprey. The brown pelican in California has shown virtually no reproduction during the last 3 years, while the production rate of the population at Deveaux Bank, South Carolina, has decreased 79 to 83 percent. The reproductive performance of the osprey was highly variable throughout its range. Reproduction in the population at Florida Bay, Florida, was normal, while reproduction in the population in Connecticut had decreased between 78 and 79 percent. Very little information on reproductive rates was available for herons and passerines.

Reproductive Performance and Food Habits

Peterson, in 1965, discussed the effects of contamination of food chains and made some predictions on the fate of populations of raptors based on the food habits of the species (Peterson 1969:529). He noted that ". . . the most likely food chains to be contaminated and to affect the top predators would be chains involving birds and fishes. In other words, the bird-eating birds and the fish-eating birds would be most vulnerable. Mammal-eating birds would be less affected. . . ." Moore (1966) verified these predictions when he examined species of birds with differing food habits and compared levels of insecticide residues. In Alberta and Saskatchewan, similar results were obtained from a survey of eggs of 13 species of falcons, hawks, eagles, and owls (Keith 1969).

It is clear that the species which have lowered reproductive success were feeding principally on fish, reptiles and amphibians, and birds (Table 61). The red-tailed hawk, great horned owl, and barn owl, which feed principally on mammals, have no apparent change in reproductive rates.

Table 60. A summary of the reproductive performances of the species studied in addition to data on eggshell weights.

Species[a]	Change in fledging rate from normal (percent)		Percent change in eggshell weight[d]
	Per successful nest[b]	Per nesting pair[c]	
Brown pelican			
California	--	-100	-26.0
South Carolina	--	-79 to -83	-16.9
Osprey			
Connecticut	--	-78 to -79	-25.1
Maryland	--	-16 to -21	-2.0 to -2.8
Florida	--	no change	--
Great blue heron	--	--	--
Black-crowned night heron	--	--	--
Cooper's hawk	-24	--	--
Red-shouldered hawk	-7 to -16	--	--
Sparrow hawk	-7	--	--
Red-tailed hawk	no change	no change	-3.6 to +2.7
Great horned owl	no change	no change	+2.4
Barn owl	no change	--	--

[a] Sufficient information on productivity rates for the passerines was not available.
[b] The normal rate was considered the rate observed prior to 1947.
[c] The normal rate was determined by the modeling approach.
[d] The eggshell data was obtained from Hickey and Anderson (1968), Anderson and Hickey (1970), and Blus (in press). The change was computed from eggs collected prior to 1945.

Table 61. A summary of the food habits of the birds studied.

Species	Food consumed (percent)						Source
	Fish	Amphibians and Reptiles	Birds	Mammals	Invertebrates	Plants	
Brown pelican	100	--	--	--	--	--	Palmer 1962
Osprey	100	--	--	--	--	--	Palmer 1962
Great blue heron	72	4	--	5	17	--	Palmer 1962
Black-crowned night heron	52	6	--	3	38	--	Palmer 1962
Cooper's Hawk	--	T	75	24	1	--	Latham 1950
Red-shouldered hawk	--	20	13	48	18	--	Latham 1950
Sparrow hawk	--	11	11	15	63	--	Latham 1950
Red-tailed hawk	--	5	16	67	12	--	Latham 1950
Great horned owl	--	2	22	74	3	--	Latham 1950
Barn owl	--	T	2	98	T	--	Latham 1950
Chimney swift	--	--	--	--	100	--	Martin *et al.* 1951
Barn swallow	--	--	--	--	100	--	Beal 1918
Black-capped chickadee[a]	--	--	--	--	78	22	Martin *et al.* 1951
Robin[a]	--	--	--	--	43	57	Martin *et al.* 1951
Cardinal[a]	--	--	--	--	35	65	Martin *et al.* 1951
Blue jay[a]	--	--	--	--	27	73	Martin *et al.* 1951

[a] Calculated annual mean from the seasonal averages.

Reproductive Performance and Changes in Eggshell Thickness

The reproductive performances of the species studied were directly correlated with reported thicknesses of the eggshells (Table 60). Eggshell thickness had decreased 26 percent in the populations of brown pelicans in California which had nearly complete reproductive failure. A 16.9 percent decrease in eggshell thickness in South Carolina was accompanied by a 79 to 83 percent reduction in the reproductive rate. Similar information was available for two populations of ospreys that were reproducing at different rates. Eggshell thickness was unchanged in the great horned owl and red-tailed hawk--two species in which reproductive rates were unchanged. Information on eggshell thickness for the remaining species was not available.

Ratcliffe (1967), investigating the peregrine falcon (Falco peregrinus) and sparrow hawk (Accipiter nisus) in Britain, noted a correlation between the magnitudes of decreases in eggshell weights, decreases in breeding populations, and exposure of populations of these species to persistent organic insecticides. Laboratory experiments with American sparrow hawks fed a diet containing DDT and dieldrin produced the same pattern of reproductive failure (increased egg disappearance, increased egg destruction by parent birds, and reduced eggshell thickness) that has occurred in several of the populations of raptors in the United States and western Europe (Porter and

Wiemeyer 1969). Ames (1966) reported that the mean total level of DDT, DDD, and DDE residues in 21 osprey eggs from Connecticut (6.0 μg/ml) was twice that found in 25 eggs from Maryland (3.0 μg/ml). Furthermore, he found that the total DDT residues in fish eaten by ospreys in Connecticut were 5-10 times greater than those in fish eaten by ospreys in Maryland. Hickey and Anderson (1968) reported a 25.1 percent decrease in weights of eggshells of ospreys in New Jersey (approximately 200 miles from the Connecticut colony) since 1940 but only a 2.0-2.8 percent decrease in weights of eggshells of ospreys in Maryland. The magnitude of eggshell weight decreases in New Jersey and Maryland compares closely with the estimates of population declines of 13-14 percent annually in Connecticut and only 2-3 percent in the apparently less affected population in Maryland. Evidence is extensive that chlorinated hydrocarbon pesticides are responsible for declines of many species of birds that obtain their food from upper levels of the food chain.

CONCLUSION

The evidence that chlorinated hydrocarbon pesticides are responsible for the decline of many species of birds is reinforced by the results of this study. The mechanism is shown to be interference with the reproductive capacity. This result is consistent with other recent findings. Species affected are those predators near the top of the food chain; a result which was predicted on theoretical grounds. It is important to emphasize that no evidence was found of increased post-fledging mortality rates, which implies that the observed effects have resulted from sub-lethal dosages in breeding birds.

The implications of the latter result in interpretation of "dead bird" studies on campuses and LD 50 toxicology studies are obvious.

SUMMARY OF SPECIES

Great Horned Owl. -- It was estimated that this species must fledge 1.46 young per nesting attempt, and the current production was found to be 1.44. The populations appear to be stable, and there has been no change in eggshell thickness.

Red-Shouldered Hawk. -- It was estimated that 1.58 young must be fledged per breeding pair to maintain a stable population. This productivity rate was apparently being achieved prior to 1945. The number of young banded per successful nest has decreased 6.8 to 15.7 percent since 1945. Complete nesting studies were not available; thus the annual rate of change could not be estimated. However, Peterson has reported that the population of the species have dropped precipitously in numbers in New England.

Sparrow Hawk. -- It was estimated that 2.88 young must be fledged per breeding pair to maintain a stable population. The lack of complete nesting studies precludes an analysis into the status of the population.

Osprey. -- The status of the species in the United States varies from region to region. The population at Florida Bay, Florida, is stable while the population in Connecticut is declining at an estimated annual rate of 13-14 percent. Numerous other locations have somewhat lower annual rates of decline. The rate of decline is correlated with pesticide levels in fish eaten by the birds. It was estimated that between 1.22 and 1.30 young must be fledged per breeding pair to maintain a stable population.

Barn Owl. -- The barn owl productivity is highly variable from year to to year. However, there has been no apparent change in trends since 1945. Productivity requirements for a stable population could not be estimated due to the highly oscillatory reproductive behavior.

Cooper's Hawk. -- This species has been declining for many years, and much of the decline prior to 1945 can be attributed to shooting pressure. Since 1945, the number of young banded per successful nest in the northeastern United States has decreased 24.4 percent. The counts of Cooper's hawks at Cape May today are less than one-tenth as many as in the 1930's.

Red-Tailed Hawk. -- This species is remaining stable in North America. No changes in mortality or productivity rates have been detected, and the observed rates of productivity yielded a stable population. The productivity rate and mortality rate below 42° N. Latitude were higher than found in the more northern locations.

Great Blue Heron. -- It was estimated that between 1.91 and 2.45 young must be fledged per breeding pair to maintain a stable population. The lack of productivity studies precludes further analysis into the status of the species.

Black-Crowned Night Heron. -- A 90 percent decline has been reported for the species on the eastern half of Long Island. It was estimated that 2.27 young must be fledged per breeding pair to maintain a stable population. However, complete nesting studies have not been conducted on the species in recent years.

Brown Pelican. -- The species has all but disappeared as a breeding bird in the Gulf States. The production in South Carolina is down 79 to 83 percent from normal, while the production in California during the last three years has been negligible. It is estimated that the population in South Carolina is declining at approximately 15 percent annually and the California population at about 20 percent annually. It was estimated that between 1.51 and 1.87 young must be fledged per breeding pair to maintain a stable population.

Barn Swallow. -- It was observed that between 5.97 and 6.08 young were fledged per pair annually. The lack of a first-year mortality rate precluded an estimate of the status of the population. However, the population could remain stable with the observed productivity rate if it had a first-year mortality rate of approximately 86 percent and the computed adult mortality rate of 42.7 percent.

Chimney Swift. -- Very little information is known regarding the chimney swift except that it has approximately a 37 percent rate of adult mortality which has remained unchanged since 1920. Observed annual production rates range from 2.67 to 3.24 young fledged per pair.

Blue Jay. -- The adult mortality rates within regions have not changed. However, the mortality rates in Region 6 are significantly higher than in Region 8. The lack of information on productivity precludes an analysis into the status of the species.

Black-capped Chickadee. -- The observed number of young fledged annually per pair was 4.99. The lack of a first-year mortality rate again precluded an analyses into the status of the population. However, with the observed productivity rate, the population could remain stable with an 80.4 percent first-year mortality rate and a 49.0 percent adult mortality rate.

Cardinal. -- The cardinal has been expanding its range northward during the last century. The mortality rates of the cardinal appeared low in the northern portion of its range prior to 1945. This was evidently the result of low population densities. The mortality rates in Region 8, where the population continues to increase, are significantly lower than in any other portion of the range. Very little information is available on productivity.

Robin. -- It was observed that between 4.58 and 5.76 robins are fledged annually per pair. The lack of a first-year mortality rate precluded an estimate of the status of the population. However, the population could remain stable with the observed productivity rate if it had a first-year mortality rate of between 78 and 82 percent and an adult mortality rate of 50.6 percent.

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APPENDIX

Appendix Table. The names of the 103 individuals and 8 organizations that contributed nesting records to this study.

R. R. Adams	S. A. Grimes	J. E. Lester	S. D. Robbins
W. Anaka	D. C. Hagar, Jr.	S. H. Levy	O. M. Root
K. A. Arnold	J. A. Hagar	S. N. Luttich	W. R. Salt
G. R. Austing	F. Hamerstrom	V. H. Maddy	P. H. Schafer
A. L. Bailey	W. C. Hanna	C. D. Marti	F. C. Schmid
R. M. Bailey	C. L. Hauthaway	J. D. McCarty, Jr.	D. E. Seal
K. E. Bartel	N. D. Hay	H. E. McClure	C. Sindelar
A. M. Baumgartner	P. F. Hickie	H. K. Meng	H. H. Southam
D. D. Berger	H. M. Hill	G. S. Mersereau	R. M. Stabler
C. R. Berrey	J. B. Holt, Jr.	J. C. Miller	P. A. Stewart
C. T. Black	J. E. Horning	L. M. Moos	M. G. Street
D. L. Bordner	C. S. Houston	F. H. Moyer	F. V. Strnad
B. S. Bowdish	D. A. James	T. E. Musselman	C. A. Sturdevant
J. H. Buckalew	C. M. Johnson	P. Nighswonger	E. L. Summer, Jr.
B. P. Burtt	M. T. Jollie	J. Oar	J. Taft
L. R. Corn	L. B. Keith	G. H. Orians	E. S. Thomas
W. N. Davey	M. L. Killpack	C. O. Owens	R. F. Tobnson
R. W. Dexter	C. M. Kirkpatrick	G. Page	V. A. Travis, Jr.
R. E. Dixon	W. K. Kirsher	F. H. Pegg	L. F. Van Camp
H. Drinkwater	V. Koppelberger	D. L. Peterson	H. Webster
S. A. Eliot, Jr.	D. L. Kraus	S. B. Peyton	D. W. Whitfield
H. S. Fitch	F. R. Kuhlman	R. D. Porter	J. R. Williams
A. S. Fox	K. H. Kuhn	R. H. Pough	L. R. Wolfe
G. A. Fox	A. R. Laskey	W. S. Randle	E. J. Woolfolk
F. N. Gallup, Sr.	W. H. Lawrence	J. Reese	M. Zardus
C. J. Goetz	M. R. Lein	E. J. Reimann	

Alaska Nest Record Scheme, University of Alaska, College.
Braley Egg Collection, Oregon State University, Corvallis.
Museum of Vertebrate Zoology, University of California, Berkeley.
Pacific Nest Record Scheme, Vancouver, Canada.
Royal Ontario Museum, Toronto, Canada.
Santa Barbara Museum of Natural History, Santa Barbara.
Smithsonian Institution, Washington, D. C.
Thomas Burke Memorial Washington State Museum, Seattle.