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GEOGRAPHICAL VARIATION IN MORTALITY RATES AND PRODUCTION REQUIREMENTS OF THE BARN OWL (*TYTO ALBA* ssp.)[1]

BY CHARLES J. HENNY

INTRODUCTION

The purpose of this paper was to determine the dynamics of populations of two subspecies of Barn Owls (two populations of *Tyto alba pratincola* in the United States, and one population of *T. a. guttata* in Switzerland). Mortality rates were estimated from band recoveries, and were used in a model developed by Henny *et al.* (in press) to estimate the number of young per female of breeding age necessary to maintain a stable population. Estimates for two time periods (1928-1947 and 1948-1963) were made for the two populations in the United States. Observed production rates (from nesting studies) were compared with production necessary to maintain a stable population, and the status of populations at the three locations was evaluated.

METHODS

Information regarding the productivity of the population as well as the mortality of a population is basic to understanding the dynamics of that population. Material used in this paper was obtained from three sources: (1) a listing of band-recovery records from the Bird Banding Laboratory, Laurel, Maryland, (2) a questionnaire sent to individuals who had banded Barn Owls, and (3) the original banding schedules of some early banders of Barn Owls who could not be contacted. Information regarding the number of young banded per successful nest was obtained by the questionnaire.

Composite dynamic mortality rate estimates (Hickey 1952) were calculated for populations in two locations in the United States from 410 recoveries of Barn Owls banded as nestlings. One hundred sixty recoveries were from owls banded south of 38° latitude (princi-

[1]Technical Paper No. 2591. Oregon Agricultural Experiment Station, Corvallis, Oregon.

pally southern California) and 250 recoveries from 38° latitude north to 43° latitude (the northeastern states) which included Wisconsin, Michigan, Illinois, Indiana, Ohio, Pennsylvania, New York, Massachusetts, Rhode Island, New Jersey, Maryland, and Delaware. Mortality rate estimates were based on all recoveries (25 percent shot, 53 percent found dead, and 22 percent "unsure"). Initially, only shot and found dead recoveries were used. However, addition of the "unsure" (not sure if dead or alive when recovered) category did not significantly change the mortality estimates, hence the "unsure" recoveries were included. Because Barn Owls in the northeastern states nest throughout the year, the date of banding was chosen as the initial date for the mortality analysis. Thus, each bird had a different initial date.

Mortality rates also were estimated for Barn Owls in the United States for two time periods (1928-1947 and 1948-1963). This division was chosen because changes in eggshell thickness were noted in the Peregrine Falcon (*Falco peregrinus*) and Sparrowhawk (*Accipiter nisus*) in Britain between these periods (Ratcliffe 1967). Catastrophic declines of three raptorial species, Peregrine Falcons, Bald Eagles (*Haliaeetus leucocephalus*), and Ospreys (*Pandion haliaetus*), in the United States have involved similar decreases in eggshell thickness that began after World War II (Hickey and Anderson 1968). The period after World War II may be classified as the modern pesticide era.

A procedure developed by Henny *et al.* (in press) was used to estimate production necessary to maintain a stable population based on the mortality series derived from banding data. In addition, the current status of the population may also be estimated if present production rates are available. When a species begins to breed at the end of its first year of life, the following model is used to calculate mean productivity required to maintain a stable population:

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

$\bar{m}$ = number of *females* produced per breeding age female to maintain a stable population.

($2\bar{m}$ = number of *young* produced per female of breeding age, assuming equal sex ratio of young).

s = adult survival rate.

s_o = first-year survival rate.

The number of young banded per successful nest was used as an index to Barn Owl production since complete nesting studies were available for only one location. Because this estimate does not include unsuccessful nesting attempts, it cannot be compared directly with the production required for a stable population computed through use of the model.

MIGRATION AND BREEDING BIOLOGY

The dispersal and migration of Barn Owls in the United States was summarized by Stewart (1952a). He noted that 65.7 percent and 77.1 percent of birds banded as nestlings and adults, respectively, were recovered within 50 miles of the banding site. The longest distance travelled by a Barn Owl was 1,075 miles. Stewart concluded that Barn Owls native to the northern part of the United States were "partly migratory;" those native to California were relatively sedentary.

Bent (1938) reported that eggs were found in the northeastern United States (Pennsylvania, New Jersey, and Delaware) from February 22 to October 31 and young being found on January 12. Stewart (1952a) corroborated this statement when he reported nestlings banded in the northeastern states in every month except February.

The length of the breeding season in California was reported to be much shorter. In California eggs were found from January 17 to June 7 with half of the records between March 9 and April 16 (Bent 1938). These dates correspond closely with the dates that nestling Barn Owls in the southern states, primarily southern California, were banded. In view of the possibility that banders may have been more active during the period of April through June, several of the more active banders were questioned on this point by Stewart (1952a). In each case, they reportedly checked their nesting sites at different periods of the year, thus rendering the distribution of their banding dates as an unbiased estimator for nesting dates. Stewart (1952a) cited personal correspondence with Fred N. Gallup who pointed out that the shorter breeding season in southern California seemed to be correlated with the rainy season.

Barn Owls were reported to nest at the end of their first year of life (Schneider 1937, Stewart 1952a). However, in general, Barn Owls seem to breed irregularly. Wallace (1963: 209) stated, "The Barn Owl may breed almost continuously during peak years in the *Microtus* (Meadow Mouse) cycle, but slow down or skip a breeding season when its staple prey is scarce." Similar observations were recorded for the Tawny Owl (*Strix aluco*) in England (Lack 1966: 140). He reported that 59 percent of the population were breeding pairs, but the percentage that nested in specific years ranged from 0 to 90 percent.

Increases in clutch size also were reported in years when rodents were abundant. Lack (1968: 180) reported that the Short-eared Owl (*Asio flammeus*) may lay 9 eggs during a vole plague, though only about half that many during other years. The number of nestling Barn Owls banded per brood by Fred N. Gallup in southern California was highly variable and ranged from a high of 4.71 in

TABLE 1. COMPOSITE DYNAMIC LIFE TABLES OF BARN OWLS BANDED AS NESTLINGS IN THE UNITED STATES PRIOR TO 1948[1]

	Southern U. S. (Latitude 32-37)			Northeastern U. S. (Latitude 38-43)		
Years of Life	No. of Recoveries	Alive at Beginning	Mortality Rate	No. of Recoveries	Alive at Beginning	Mortality Rate
1	36	75	46.7%	89	133	66.9%
2	15	39	"	19	44	"
3	4	24	"	9	25	"
4	3	20	"	6	16	"
5	8	17	"	2	10	"
6	0	9	28.7%	3	8	36.1%
7	1	9	"	1	5	"
8	3	8	"	3	4	"
9	2	5	"	0	1	"
10	1	3	"	0	1	"
11	2	2	"	0	1	"
12				0	1	"
13				0	1	"
14				0	1	"
15				0	1	"
16				0	1	"
17				0	1	"
18				1	1	"
	Overall		35.6%	Overall		52.2%

[1]Seventeen recovery years have passed since the last nestling was banded and it is concluded that all recoveries from the banded cohort have occurred.

1951 to a low of 2.75 in 1961 (Figure 1). Gallup (pers. comm. 1968) noted that cannibalism occurred in some years, evidently when the food supply was extremely low.

Wallace (1948) reported that a banded female Barn Owl produced two broods in New York in 1939. The two broods were produced 4 months and 8 days apart. Bent (1938) indicated that approximately 3 months elapsed from the time of egg laying to the time of fledging. Therefore, since 94 percent of the nestlings were banded in southern California during the 3-month period of April, May, and June, it would seem that only a very small percentage of the owls could produce two broods in any year. However, two broods per year would be more likely in the northern portion of the range due to the prolonged breeding season. Only 79 percent of the nestlings in the northeastern United States were banded during the 3 months of April, May, and June.

TABLE 2. COMPOSITE DYNAMIC LIFE TABLE FOR BARN OWLS BANDED IN THE SOUTHERN UNITED STATES AS NESTLINGS BETWEEN LATITUDES 32 AND 37 DURING THE PERIOD 1948-1963.

Year	No. Banded	Number of Years Survived 1	2	3	4	5	6	7	8	9
1948	9	1	—	—	—	—	—	—	—	—
1949	6	—	—	—	—	—	—	—	—	—
1950	19	1	—	1	1	—	—	—	—	—
1951	89	2	—	1	1	—	—	—	1	—
1952	55	2	—	—	—	—	—	1	—	—
1953	57	4	—	—	1	—	—	—	—	1
1954	34	5	—	—	—	—	—	—	—	—
1955	108	3	1	—	—	—	—	—	—	—
1956	106	5	1	1	1	—	—	—	1	—
1957	130	4	2	2	1	1	—	2	1	
1958	280	9	2	2	2	—	2	—		
1959	103	5	2	—	—	—	—			
1960	98	4	—	—	—	—				
1961	66	3	—	—	—					
1962	92	3	—	—						
1963	32	1	1							
Totals	1284	52	9	7	7	1	2	3	3	1
No. Available		1284	1252	1160	1094	996	893	613	483	377
Recoveries/1000		40.50	7.19	6.03	6.40	1.00	2.24	4.89	6.21	2.65
Alive going into period		77.11	36.61	29.42	23.39	16.99	15.99	13.75	8.86	2.65
Mortality Rate		1st Year 52.5%			Adult 24.8%			Overall 34.3%		

MORTALITY OF POPULATION

Estimates of mortality for the periods 1928-1947 and 1948-1963 were made for the northeastern and southern United States using the composite dynamic methods (Tables 1, 2, and 3). The relationship between overall annual mortality rates and degrees of latitude for populations at two locations in the United States and for Switzerland are presented in Table 4. The overall annual mortality estimate ranged from 34.3 percent (southern United States) to 55.8 percent in Switzerland. Increases in population mortality were correlated directly with the increase in latitude.

There was evidence that high mortality in Barn Owl populations occurred in severe winters. A large winter die-off of Barn Owls was reported by Speirs (1940) in Illinois, and by Baumgartner and

TABLE 3. COMPOSITE DYNAMIC LIFE TABLE FOR BARN OWLS BANDED AS NESTLINGS IN THE NORTHEASTERN UNITED STATES BETWEEN LATITUDE 38 AND 43 DURING THE PERIOD 1948-1963.

Year	No. Banded	Number of Years Survived 1	2	3	4	5	6	7	8
1948	35	5	1	—	—	—	—	—	1
1949	30	3	3	1	1	1	—	—	—
1950	28	1	1	—	—	—	—	1	—
1951	17	3	1	1	—	1	—	—	—
1952	47	2	2	—	—	—	—	—	—
1953	48	6	2	—	1	1	—	1	1
1954	94	7	3	—	—	1	—	—	—
1955	91	9	5	1	—	2	—	—	—
1956	66	8	2	—	—	—	1	—	—
1957	69	2	1	—	—	—	—	—	
1958	46	4	1	—	1	—	—		
1959	44	8	—	—	—	—			
1960	79	3	—	2	1				
1961	60	7	1	—					
1962	38	2	—						
1963	45	4							
Totals	837	74	23	5	4	6	1	2	2
No. Available		837	792	754	694	615	571	525	456
Recoveries, 1000		88.41	29.04	6.63	5.76	9.74	1.75	3.81	4.39
Alive going into period		149.53	61.12	32.08	25.45	19.69	9.95	8.20	4.39
Mortality Rate		First Year 59.1%		Adult 38.0%		Overall 48.1%			

Baumgartner (1944) in Oklahoma. In the former instance the die-off was due to forced exposure to cold; in the latter, it was related to concurrent cold and failure of the staple food supply. Numerous winter mortality "bursts" in Europe were summarized by Honer (1963). In an attempt to measure changes in food availability, Errington (1931) used pellet contents as an index. He reported a winter decrease in pellet contents from three to six prey animals per pellet to only one per pellet. Stewart (1952b) suggested that the amount of snow covering was presumably the decisive factor (food factor) in survival of Barn Owls, and that low temperatures may be incidental in that they normally follow periods of heavy snowfall. Piechocki (1960) found that the Barn Owl had the lowest percentage of fat reserve of five species of owls studied. Honer (1963) concluded

TABLE 4. A SUMMARY OF BARN OWL MORTALITY RATE ESTIMATES BY GEOGRAPHICAL LOCATION FOR TWO TIME PERIODS

	Prior to 1948			1948-1963			
Location	First Year	Adult	Overall	First Year	Adult	Overall	Source
Switzerland[1]	63.6%	45.9%	55.8%	....	....	....	Schifferli 1957
Northeastern U. S.	66.9%	36.1%	52.2%	59.1%	38.0%	48.1%	Tables 1, 3
Southern U. S.	46.7%	28.7%	35.6%	52.2%	24.8%	34.3%	Tables 1, 2

[1]Recalculated to make data comparable.

that the low margin (normal weight vs. starvation weight) in the Barn Owl arose directly from its lower fat reserves. He also concluded that the fat reserve (safety factor) of 20 percent may preclude long survival under certain unfavorable conditions. The Barn Owls of the southern United States are not subjected to cold winters or heavy snowfall which may explain why their overall rate of mortality is about 15 percent less than that of the more northern birds (Table 4).

Mortality rates for Barn Owls for the two time periods were judged to be essentially the same (Table 4). However, mortality estimates for Ospreys also were judged to show no change for similar time periods, even though New York-New Jersey population was rapidly declining as a result of poor production (Henny and Wight 1969). Thus, unchanged mortality rates of the Barn Owl do not necessarily indicate that population levels have remained at levels similar to those in the past.

PRODUCTIVITY OF POPULATION

Numbers of young banded per successful nest were used as an index to Barn Owl productivity in Switzerland, the northeastern United States, and the southern United States (Table 5). Numbers banded per successful nest ranged from 4.43 to 3.92. Production rates, in agreement with the mortality rates, were higher in the more northern locations. Schifferli (1957) indicated that the 4.43 young fledged per successful brood in Switzerland seemed to keep the population stable. No significant differences in the numbers of young banded per successful nest occurred between the two time periods in the United States ($P < 0.05$).

A tendency for the mean clutch size of owls to increase directly with the latitude was noticed by Lack (1947: 306). Owls presumably have larger clutches at higher latitudes because of the increased availability of small mammals (Lack 1968: 180). A mean clutch size of 5.3 (38 clutches) was reported by Schifferli (1957)

TABLE 5. NUMBER OF YOUNG BARN OWLS BANDED PER SUCCESSFUL NEST FOR GEOGRAPHIC LOCATIONS IN THE WORLD, WITH NUMBER OF NESTS IN PARENTHESES

	Degrees	TIME PERIODS		
Location	Latitude	1926-1947	1948-1967	1926-1967
Switzerland[1]	46-47	....	....	4.43 (56)
Northeastern U. S.[2]	38-43	4.10 (69)	4.18 (164)	4.16 (233)
Southern U. S.[3]	32-37	4.04(110)	3.89 (351)	3.92 (461)

[1]Schifferli (1957). The exact time period is unknown.

[2]Fifty percent were banded by Laurel F. Van Camp near Genoa, Ohio.

[3]Eighty-nine percent were banded by Fred N. Gallup near Escondido, California.

from Switzerland. The most complete Barn Owl nesting study in the United States that I was able to find was generously contributed by Jan Reese (unpublished data) from Maryland. He found a mean clutch size of 4.9 (68 clutches), a mean number fledged per successful nest of 3.24, and a mean number fledged per nest (including unsuccessful nests) of 1.81 between 1963 and 1968.

The nesting study by Reese was conducted in conjunction with an Osprey nesting study. Ospreys nest on the roof of offshore duck blinds in Maryland while Barn Owls nest inside. The 3.24 young fledged per successful nest (Table 6) was considerably below the 4.16 banded per successful nest in the northeastern United States or the 3.92 banded per successful nest in the southern United States (Table 5). This suggested that (1) the number banded per successful nest was a 17 to 22 percent overestimate of the number fledged, or (2) the data collected by Reese may represent a series of years during which production was below average. I do not believe that a discrepancy of 17 to 22 percent can be attributed to mortality between the time of banding and the time of fledging. Many of the banders reported that they did not band the nestlings until they were almost fully grown and indicated that mortality would be minimal before leaving the nest. I concluded that the production in Maryland (1963-1968) was below the average found in other northeastern states. It was difficult to ascertain if this was a temporary low (due to fluctuations in food supply) or a long-term trend (due to a contaminated environment). A third possibility may be that the Ospreys (nesting in close proximity to the Barn Owls) were interfering with the feeding routine of the parents and nestlings. Keith (1964) reported a "mean brood size" (44 broods) of 4.4 in Massachusetts when all young banded or observed were assumed to have survived. Since nestlings only a few days old were probably included in this count, it was most likely an overestimate of the number of young fledged per successful nest.

TABLE 6. MEAN PRODUCTION REQUIREMENTS ($2\overline{m}$) PER BREEDING AGE FEMALE BARN OWL AND THE MINIMAL PERCENTAGE OF THE POPULATION THAT MUST BREED SUCCESSFULLY EACH YEAR TO MAINTAIN A STABLE POPULATION[1]

Location	Switzerland	Northeastern U. S.	Southern U. S.
Production requirements ($2\overline{m}$)	2.52	1.86–2.18	1.04–1.08
Percentage of population that must successfully breed (minimal)[2]	57%	44–53%	26–27%

[1]Values calculated for the two time periods (1926-1947 and 1948-1963) in the United States, and may be considered a range.

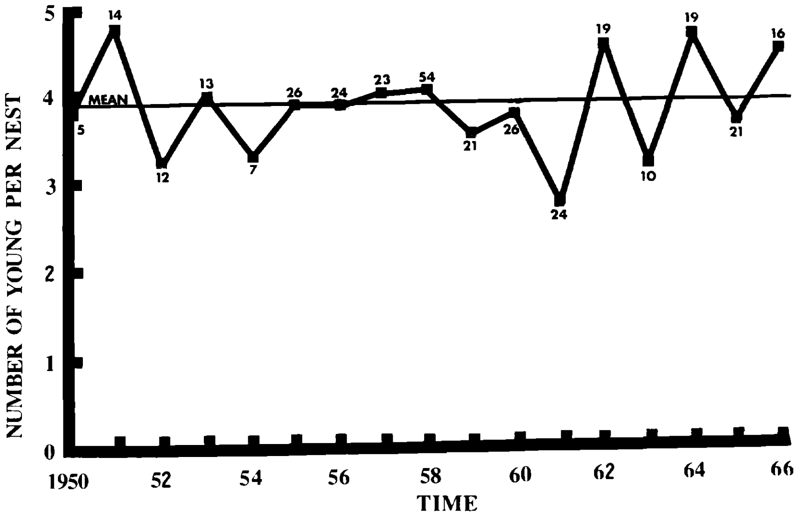
[2] $\dfrac{2\overline{m}}{\text{No. banded per successful nest (Table 5)}}$

MAINTENANCE OF THE POPULATION

Annual production rates per breeding age female necessary to maintain a stable population in the three geographical locations were estimated using the model developed by Henny *et al.* (in press). It was assumed that Barn Owls begin to breed at the end of their first year of life. Estimates of production rates for a stable population ranged from 1.04 to 2.52 young per breeding-age female (Table 6), which were considerably below production rates determined from nesting studies. This suggests one or more of the following: (1) a bias exists in the band recovery data, (2) the population is increasing, or (3) a relatively high percentage of the breeding age Barn Owls fail to attempt to nest or are unsuccessful.

To test the hypothesis that estimates of mortality were biased by band loss, the number of birds alive at the beginning of each year were plotted against age on semilogarithmic paper (Ludwig 1967; Henny and Wight 1969). Assuming that mortality rates after the first year (adult mortality rate) are constant, a straightline relationship would indicate that little or no band loss occurred. The straightline relationship indicated that the recovery records were unbiased (Figure 2). Mortality estimates also may be biased upwards by a decreasing band-reporting rate. Reduced rates of reporting bands from ducks were noted between 1960 and 1962 by Martinson (1966) and from geese by Martinson and McCann (1966) and Henny (1967). Bands are reported because the people who find them are curious. Waterfowl hunters may have lost some of this curiosity after reporting several bands and learning that they were all banded in the same location. However, it is my belief that people finding hawks and owls with bands have the same curiosity now as they did in earlier years (it is doubtful that a person would find more than one banded hawk or owl in his lifetime), thus I believe the recovery records were unbiased.

Figure 1. Mean number of Barn Owls banded per successful nest near Escondido, California for the period 1950-1966.

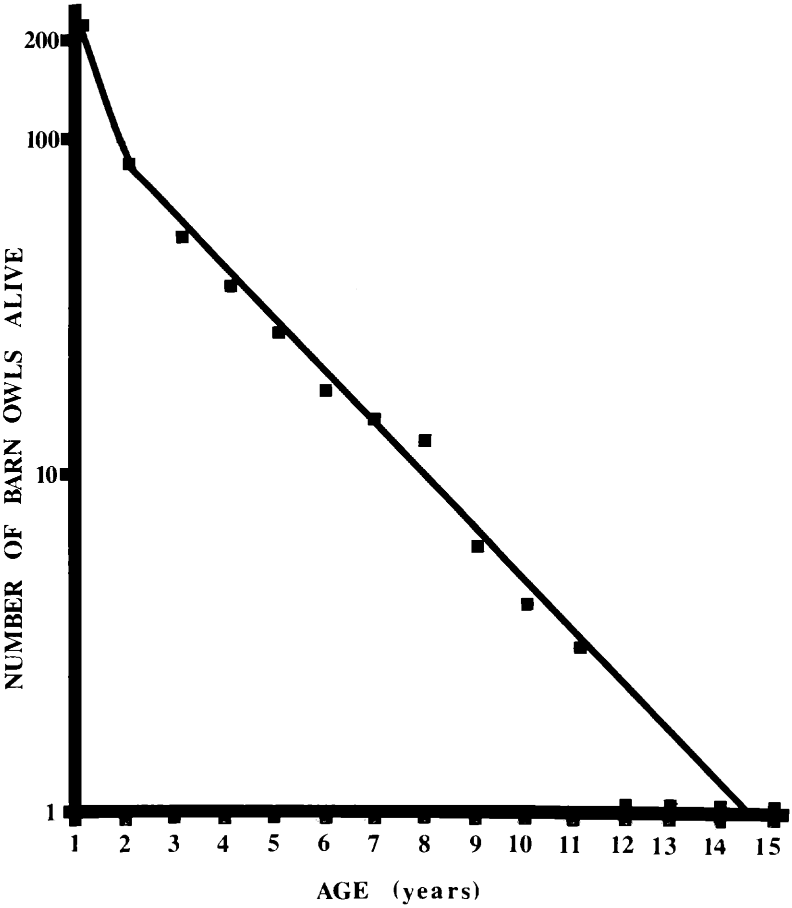


The population of Barn Owls in Switzerland seems to be stable (Schifferli 1957) while the Barn Owl population in New England has decreased slightly in the last 30 years (Keith pers. comm. 1968). It was concluded that Barn Owl populations were not increasing. Therefore, the discrepancy between observed production and production necessary to maintain stability probably cannot be accounted for by increases in populations of Barn Owls.

The third alternative (a portion of the population of Barn Owls of breeding age fail to attempt to nest or are unsuccessful) most likely accounts for the discrepancy between the number banded per successful nest and the production required per breeding age female. Information obtained by Reese confirmed this hypothesis. During the 6 years of his study, 56 percent of the nesting attempts were successful in Maryland and 1.81 young were fledged per nesting attempt. As mentioned earlier, the production rate of 1.81 young per nesting attempt (not per breeding age female) in Maryland was believed to be below the average production rate in the northeastern United States. It was also very unlikely that all breeding age females were attempting to nest in Maryland. A rate between 1.86 and 2.18 must be fledged per female of breeding age (assumes all birds 1 year old and older attempt to nest) nesting in the northeastern United States to maintain a stable population.

A logical question to ask at this time is, why do Barn Owls have a much higher reproductive potential (lays approximately 5 eggs) than is necessary to maintain a stable population? In answering this question, it must be remembered that the mortality estimates, as well as the production requirements, are averages for many years. The composite thus includes both "good" and "poor" years, es-

Figure 2. Number of Barn Owls alive at the beginning of each year. Data are a composite from Table 1.



pecially in a species such as the Barn Owl which has a highly oscillatory reproductive rate.

By assuming that the number of young banded per successful nest in each location was a reasonable estimate of the number of young fledged per successful nest (it was probably a slight overestimate), the average percent of the population of breeding age that must nest successfully may be estimated (Table 6). This percentage is minimal if, in fact, some mortality occurs in the nest between the time of banding and the time of fledging. However, the relationship between geographical locations was considered to be real, as nestling mortality after banding should be similar in each area. The percentage of the population that must nest successfully increased with the increase in latitude (Table 6). I do not believe that the differences between the percentage of the nests that must be successful at each location was related solely to changes in nest success (percent of nests successful), but was evidence of a smaller percentage (on the average) of the birds attempting to nest in the more southern locations. Production per successful nest in southern California was highly oscillatory (Figure 1), suggesting that food availability may be a major factor. If nesting success in southern California was similar to the 56 percent in Maryland, an average of approximately 50 percent of the breeding-age females failed to attempt to nest each year.

The high biotic potential (reproductive rate and mean generation time) of the Barn Owl, as opposed to average production necessary to maintain a stable population, seems to be a built-in compensating factor that affords some protection against "poor" years in the rodent cycle and hard winters, and provides a means to quickly restore the population to its previous size in "good" rodent years. In the more northern areas where the annual mortality rates are higher, the possibility of providing two broods per year (nests recorded in 11 of the 12 months) may also be an important factor in quickly restoring populations to previous levels.

SUMMARY

Barn Owls from the southern United States have lower mortality rates (about 15 percent overall) than the more northern birds. The observed difference was believed to be related to the more severe winters occurring in the more northern locations. Rates of production were also lower in the southern locations. To maintain stable populations in the three locations, an estimated (minimal) 26 to 57 percent of Barn Owls of breeding age (depending on latitude) must nest successfully. The high biotic potential as opposed to the production required to maintain a stable population allows an oscillatory species like the Barn Owl to quickly restore its population to previous levels after a "poor" production year.

In general, no changes in the number of young banded per successful nest or in the annual mortality estimates were detected between the periods 1926-1947 and 1948-1963, although the annual rates of production were oscillatory. The production rates in Maryland (1963-1968) seemed to be below average.

The status of the Barn Owl populations in Switzerland, the northeastern United States, and the southern United States could not be determined due to the lack of complete 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 the nesting attempts that are successful.

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The contribution of the numerous banders whose nesting data and band recovery data were prerequisite to this analysis is gratefully acknowledged. Special recognition is due Fred N. Gallup who provided over 400 nesting records, and Laurel F. Van Camp who provided over 100 records. Others who contributed between 10 and 50 nesting records include: R. H. Pough, H. M. Hill, R. W. Dexter, H. F. Drinkwater, and F. C. Schmid. Sixteen others contributed less than 10 records. I wish to thank Jan Reese for the use of his unpublished nesting data for Maryland and Allan R. Keith for his comments on the Barn Owl in Massachusetts. The advice and assistance provided by Chandler S. Robbins, W. T. Van Velgen, Earl B. Baysinger, and the clerical staff of the Bird Banding Laboratory is gratefully acknowledged. The editorial assistance of Howard M. Wight, B. J. Verts, and James R. Graybill was very much appreciated.

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Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

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THE YELLOW-SHAFTED FLICKER (COLAPTES AURATUS) ON NANTUCKET ISLAND, MASSACHUSETTS

By John V. Dennis

Flickers, more than any other of the North American woodpeckers, can adapt to relatively treeless situations. The Yellow-shafted Flicker shows this through its ability to establish itself in prairie regions of the Great Plains and relatively treeless islands and coasts in New England and the Maritime Provinces. Nantucket Island off the southeastern coast of Massachusetts offers an interesting example. This gently rolling seventeen-mile-long island was denuded of trees not many years after settlement began in 1659. Except for a few pockets of original timber in low places and a few plantings, the Island was essentially treeless for the two hundred years between 1700 and 1900.

Cutting of trees for firewood and lumber, and sheep grazing, seem to have been the chief factors in keeping the Island open for this long period of time. Salt spray, storms, and fires were contributing factors. A decline in farming and sheep grazing, beginning early in this century, and more and more interest after 1850 in establishing