

I will hazard a guess as to the association of redness of gape with molt. It is clear that in adult males at the postnuptial molt a considerable quantity of carotenoid pigment must be available just beneath the skin in chromatophores from some of which it will be transferred to the developing feathers. It is not unlikely that some of these chromatophores always develop some pigment. It also seems reasonable that an increase in pigmentation around the feather follicles may be accompanied by an increase over the rest of the pigmented surface of the body. The gape is the only such area which is not also rather heavily pigmented with melanin. Hence the gape is the only unfeathered area likely to show reddening in molt in adult males. We may carry our hypothesis a step further and suppose that more or less concentration of carotenoids occurs at molt in all Purple Finches but that in females and most male birds of the year the pigment simply fails to be transferred from the chromatophores to the feathers.

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**INTERRELATIONS BETWEEN CLUTCH-SIZE, BROOD-SIZE,
 PREFLEDGING SURVIVAL, AND WEIGHT IN
 KENT ISLAND TREE SWALLOWS (concluded)**

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DISCUSSION

Throughout this paper a number of curious phenomena have been exposed; some are easily explained in the light of other observations in this study or by reference to other studies, some seem reasonable although their underlying causes are obscure, and some seem to be baffling contradictions or outright errors. An attempt will now be made to reconcile these data and to present a clearer picture of the complexities of the breeding biology of the tree swallow.

It has been shown that the mean clutch-size of the first nestings of the season is significantly higher than that of later nestings, but because we do not know the frequencies of repeat laying and of late first nestings within the sample, it is impossible to ascribe a cause for the reductions in clutch-size later in the season. It has been suggested that the late nestings in this study may actually represent layings after the desertion of earlier nests. The close uniformity in the time of the late nestings seems to indicate that the birds abandoned their nests after a storm earlier in the spring and all came into breeding condition again at approximately the same date. However, we know that at least one bird did not have a first clutch since one more nest was built late in the season than was abandoned. There may have been others. It is well known that when normally single-brooded birds lay second

clutches, almost invariably fewer eggs are laid in the repeat clutch (e.g., Lack and Arn 1947). It is also known that late first layings often have fewer eggs than early first layings. This has been well discussed by Lack in many of his papers and need not be repeated here, but the important point is that we do not know whether repeat layings are smaller than first layings because they are later in the season or whether an entirely different cause, such as physiological fatigue, is operative. The tree swallow data cannot aid in clarifying this problem.

Annual variation in clutch-size in a given region has been demonstrated for the tree swallows at Kent Island and at Cape Cod and is evident, although it cannot be proved with the data given, at Princeton, Massachusetts, and East Westmoreland, New Hampshire. It has been found in other passerines (Lack 1950, Lack and Arn 1947, Kluijver 1951) and in the Anatidae (Lewis 1949, Paynter 1951), Falconidae, Phasianidae, etc. (see Lack 1947a for complete list). Variation in the abundance of food, the type of spring weather, the amount of winter mortality, the density of the population, etc. have been suggested as altering clutch-size and in some instances seem to be reasonably documented. However, from what is known of the Kent Island population, as well as the others, the food, weather, and population size do not appear to have varied noticeably from year to year. Therefore, it must be admitted that while annual variations seem definitely proved we are again unable to offer suggestions as to their causes.

Geographical variation in clutch-size has been recognized for over 100 years but it is only recently that considerable interest has been taken in the subject. It is not appropriate at this time to attempt to review completely the occurrence of geographical variations and to discuss thoroughly the many theories put forth in explanation of this phenomenon, but a brief outline will be presented for those not already familiar with the subject. For a more detailed account the reader is referred to the excellent papers of Moreau (1944) and of Lack (1947a, 1948a).

There are three, and possibly four, patterns within which geographical variations in clutch-size seem to fall. The first pattern, and the best known, is the increase in clutch-size with higher latitude. Many species which have an extended range show an increase in clutch-size from south to north in the northern hemisphere and from north to south in the southern hemisphere. This is not true for all species, by any means, but many passerines and near-passerines, as well as some hawks, owls, shore birds, etc., do exhibit such a trend.

The second pattern, which is much less well known, is the west-to-east trend found in Europe. The average clutch-size has been found to increase from west to east in some passerine and near-passerine species, hawks, owls, and gallinaceous species. It seems to be found only in species that also exhibit latitudinal variations, although not all of those that have a south-to-north trend also show the west-to-east pattern.

The third type of geographical variation is the irregularly distributed but consistent variations found for a number of species in Europe.

This is best documented for four species of titmice (*Parus*) in Holland (Lack 1950:286) where the mean clutch-sizes at five localities, located within a circle with a radius of 40 miles, may all differ significantly from one another.

A fourth pattern, which appears not to have been previously discussed, may be an altitudinal trend of increased clutch-size. In searching for records of clutches of tree swallows an interesting note was found in a paper by Ray (1913) on the birds of the Lake Tahoe region of California. The lake is at an altitude of 6225 feet. In this paper Ray records a swallow's nest with seven eggs and states (p. 113), "In this locality seven eggs is the usual complement although from all I have been able to learn five is the common number in the coast region. From this it might appear that a comparison of the number of eggs laid by the same species in high and low altitudes would be worthy of investigation. In those localities where seasonal conditions do not allow the raising of a second brood it may be found that this is partially compensated for by the increased size of the initial complement." So little is known about second broods in the tree swallow that it is impossible to suggest how valid this theory may be, but I know of no record for second broods in California and it would appear then that this may be a strictly altitudinal trend without the added complications of second broods. Undoubtedly, this warrants closer study in tree swallows, as well as in other species.

A number of hypotheses have been suggested to explain the causative mechanisms which determine clutch-size. Clutch-size is not controlled by any single factor common to all species. In fact, several controls may be exerted which mutually aid in keeping the clutch-size relatively constant for a given species. The fundamental principle underlying all of the hypotheses is that birds, ". . . raise not only all the offspring that they need, but also all that they *can*." (Lack 1949: 455-456.) Or, in other words, the most common clutch-size is the one that results in the maximum number of birds that survive to breed. However, it should be borne in mind that while we seem to be able to account for the mechanisms determining clutch-size in many species, there are many cases for which no satisfactory explanation has been put forth. This interesting phase of avian biology offers many possibilities for future research.

The most common mechanism limiting clutch-size appears to be the ability of the adults to feed the young. Naturally, there is a limit to the number of nestlings that the adults can feed. If this limit is exceeded, all of the young may suffer and either starve in the nest or having fledged in a weakened condition, are prone to greater post-fledging mortality than birds from smaller broods. This has been documented by Lack (1948b) for the starlings (*Sturnus vulgaris*). If some of the adults lay small clutches and rear fewer birds than they are potentially able to care for, in time the genotype for smaller clutches will be swamped and the birds inherently capable of laying larger clutches and fledging more young will predominate.

The cline of increased clutch-size with higher latitude may be explained in two ways; each explanation appears appropriate for some

species. The first is based on the fact that during the breeding season the periods of daylight are progressively longer from south-to-north (or north-to-south in the southern hemisphere). Therefore, in the higher latitudes the adults have more time available for food-gathering and consequently are able to feed and rear more young than birds living at lower latitudes.

The second explanation is based on the fact that in many species the breeding season begins progressively later from south to north. Thus, birds breeding in the north do so nearer the summer solstice than do those birds which breed farther south. This may explain why geographical variation in clutch-size is evident in populations only a few hundred miles north or south of one another. On a given date there is little difference in daylength between localities so near, but if the populations should breed several weeks apart there may be a difference in the periods of daylight great enough to be of significance when feeding the young. For example, the longest day (including civil twilight) at the latitude of Kent Island is about 16 hours and 41 minutes while that at the latitude of Cape Cod is approximately 16 hours and 25 minutes (List 1951), a difference of only 16 minutes. However, the first young hatched at Kent Island in 1948 on June 20, when the daylength was longest for the year, but on Cape Cod in 1931 the first young are estimated (from Austin and Low 1932) to have hatched about May 21, when the day was only 15 hours and 45 minutes long. Presumably the breeding seasons are equally dissimilar each year. The reason for the dissimilarity in the breeding seasons is beyond the scope of this paper.

Seasonal variations in the amount of daylight also appear to cause some of the many fluctuations in clutch-size. Lack (1945) has shown that in England the clutch-size of the robin (*Erithacus rubecula*) reaches a peak in early June and then declines. This is probably related to the increasing and decreasing periods of daylight. The correlation is not perfect, however, since the peak is reached about three weeks before the summer solstice. However, by the time the eggs hatch, the days are longest and the adults have the maximum periods of daylight in which to hunt for food. The proleptic or "anticipatory" behavior, which is not unusual in birds, raises evolutionary problems, and will be considered further below.

The availability of food may account for some of the consistent local differences in clutch-size. If food is scarce the adults must spend more time hunting and therefore they are unable to rear broods as large as those birds in regions where food is abundant. There is very little evidence in support of this theory, but it does not seem unreasonable to expect that if the food supply in a given region remains low from year to year the clutch-size would become adjusted, thereby permitting the survival of the species. In line with this, although not exactly comparable, is the study of Lack and Arn (1947) and Lack and Lack (1951) of the common swift (*Apus apus*) in which it was found that the clutch-size is larger in Switzerland than in England. This they attribute to the fact that, although the periods of daylight are longer in England than in Switzerland, inclement weather is more frequent in

England and the swifts have greater difficulty in feeding their broods.

Seasonal and annual variations in clutch-size may also be caused by changes in the food supply but again the data are few and not always conclusive. As has already been pointed out, the clutch-sizes of some hawks and owls (e.g., Elton 1942) rise sharply during periods of rodent plagues. This may be due to better nutrition since it is practically axiomatic with poultry raisers that better feeding will increase egg production. Whether smaller annual fluctuations can be attributed to food changes is unknown.

Lack (1950) has presented data for the genus *Parus* which show a correlation between clutch-size and the seasonal abundance of caterpillars (*Cheimatobia brumata*), the chief food of titmice in the area studied. The clutch-size is high in April but drops off in May shortly before there is a sharp decline in the number of caterpillars. It appears that the titmice anticipate the decline in food since their clutches decrease in size before the drop in the caterpillar population. By the time the eggs hatch food is in short supply but the birds have smaller broods to feed. While the implied prescience may seem impossible at first sight, it is very much like the apparent anticipation of the summer solstice by the robin, and it is easy to imagine how natural selection may have brought out the phenomenon. Birds that laid large clutches in May would find it difficult to feed their young and the genotype would be lost gradually and replaced by birds laying smaller clutches, since these would be the ones better able to rear their broods. Such a mechanism is purely hypothetical, of course, and involves the assumptions (1) that the caterpillar population shows the same regularity in abundance and decline each year, (2) that clutch-size and the period at which the birds lay are genetically determined, and (3) that caterpillars are by far the most important source of food. Some of these assumptions have an *ad hoc* character but none seems entirely unreasonable.

The abundance of food and the time available for gathering it have received much attention, and some workers appear to believe that these are the only factors which control clutch-size. Skutch (1949) strongly attacked Lack's view, at least in its application to tropical birds, on the grounds that in the tropics there is very abundant food, but still the birds lay smaller clutches than their more northern counterparts. While the presence of a vast abundance of food in the tropics is debatable, and obviously varies among species, Skutch's paper is a useful corrective to the undue emphasis that has been placed on the nourishment of the young as a determinant of clutch-size. Although Lack's work has dealt mainly with the food factor, even he does not claim it is the only mechanism at work.

It has been shown for the eider (*Somateria mollissima*) that the feeding of the young cannot be a controlling factor in this species because the adults merely protect the young and do not find the food for them (Paynter 1951). Not enough is known about the ecology of the eider to offer an explanation of why clutch-size varies but it serves to illustrate the principle that food is not always the controlling mechanism.

Kluijver (1951) has found an inverse correlation between population density and clutch-size which accounts for annual variations in fecundity in *Parus m. major*. This effect is produced by mutual disturbance rather than by competition for food. The importance of this documented discovery is very great since it appears to be the first time the phenomenon has been demonstrated in a natural population of vertebrates. It is doubtful that this factor caused the annual variation in clutch-size at Kent Island, because in 1948 the mean clutch-size and population density were both higher than in 1947.

There must be an upper limit to the number of eggs that can be covered, in both nidifugous and nidicolous species, but it is unknown how often this provides a check on clutch-size. It may be only of secondary importance. Lack (1947b) has shown for the partridge (*Perdix perdix*) that the usual clutch is about 15 eggs but the bird can incubate at least 20 eggs with no decline in their hatchability. Perhaps the number of eggs a bird can cover is a more important clutch-size control in species laying very large eggs, or a large total volume of eggs, in relation to the size of the bird. The observation that seven-egg clutches among tree swallows require longer periods of incubation than smaller clutches may indicate that seven eggs is very nearly the maximum number the bird can cover.

Skutch (1949) has made the valuable suggestion that the size of the brood may be important in nidicolous species which suffer from predation in the nestling stage. The more young there are in the nest the more noise they create and the more often the adults must make trips to the nest with food. The larger broods, therefore, are more easily found by predators. Although there is no supporting evidence for this, it seems to be a plausible suggestion and may even extend to many nidifugous species. It does not appear unlikely that a large brood of chicks foraging on the ground is more conspicuous than a small brood. However, the thesis is not without objectionable features. Most nidicolous species lay clutches of fairly definite sizes and it is difficult to believe that noise at the nest, or more frequent visits by the parents, would create a threshold so distinct that one or two extra birds would make the nest very much more conspicuous. The objection is less serious for a nidifugous species as, for example, a gallinaceous bird that lays between six and 12 eggs. Here the clutch-size limit is not so rigid and is more like what one would expect if predation were the controlling force. Nevertheless, as was previously mentioned, very often more than one mechanism may play a role in limiting clutch-size in a given species and with our present knowledge no clear-cut solutions to the problem are possible.

It is well known that increased daylength causes increased physical and gonadal activity (e.g., Bissonnette and Wadlund 1931, 1932) and that birds do not lay until the periods of daylight have reached a particular length for a given species. This leads one to wonder if there may not be some subtle relationship between increased daylength and clutch-size, after the threshold for laying has been reached. This might account for some of the seasonal variations in clutch-size which do not seem to be correlated with the availability of food. The intensity of

the radiation may also play a role, since Bissonnette and Wadlund have shown that in the starling the speed of reaction of the testes is increased with light of higher intensities. Thus, if clutch-size increases with altitude the effect may be caused by greater solar radiation.

Not enough is known about clutch-size of the tree swallow to offer concrete explanations of how it is determined and into what patterns geographical variations may fall. Data are available from only a small part of the total range of the species, but an analysis of the material that is at hand indicates the following. At Fortine, Montana, approximately four degrees of latitude north of Kent Island, the clutch-size for the first nestings is about four-fifths of an egg larger than at Kent Island. Although nothing is known of the yearly variation in clutch-size at this locality, it may be assumed that years of large clutches and years of small clutches are probably included in the sample and that an average clutch-size of 6.23 eggs for the first-brood nests is fairly close to the true mean. At Kent Island the mean for the two years is 5.44 ± 1.94 and the distribution of the clutch-sizes each year is nearly equivalent, with the mode at six-egg clutches. If it is assumed that the Montana average is nearly exact and that of Kent Island is approximately what a sample over a longer period of years would indicate, we find a decrease in clutch-size of about one-fifth of an egg for each degree of latitude from north to south. The mean of the averages for the three years at Cape Cod is $4.80 \pm .24$. The Cape Cod locality is slightly less than three degrees south of Kent Island, and assuming that clutch-size decreases at a constant rate from north to south, which it may or may not do, the mean is almost exactly what would be expected. The New Hampshire and Princeton, Massachusetts, localities are only about one degree, at the most, north of Cape Cod and with such crude computation could not be expected to fit into the picture very accurately. However, the Connecticut mean, which has been shown to be significantly larger than that at Cape Cod raises a serious problem. Why should the means differ in the two localities although both areas are at approximately the same latitude?

Of course, it is possible that the differences have been brought about through a sampling error, *i.e.*, years when the clutches were small at Cape Cod are being tested against years when the clutches were large at Kent, Connecticut. However, it appears more probable that we are dealing with a phenomenon like that found by Lack and Arn (1947) and Lack and Lack (1951) for *Apus apus*, in which the clutch-size was shown to be larger in Switzerland than in England and seems attributable to better feeding conditions in Switzerland. Although food is probably no less abundant at Cape Cod than at the Connecticut locality, there are undoubtedly differences in the general weather conditions. A coastal area, exposed to storms and without doubt having more fog and fewer days with light winds or calms, is naturally less suitable for species feeding on aerial plankton than an inland area with lakes and marshes in sheltered valleys.

But what is the evidence in support of the theory that food is taking an important role in determining the general clutch-size of this species and is also accounting for the observed geographic variations? Since

we have no observational data on the rate of feeding and no quantitative data on the abundance of food throughout the season in each locality the problem must be attacked deductively.

The markedly heavier nestling mortality at Cape Cod led Kuerzi (1941:39) to suggest that the location of his Connecticut colony better suited the requirements of tree swallows. Since predation and disease do not account for very much of the mortality at either locality, it does not appear incorrect to assume that the differences are brought about by variations in the availability of food or in the length of the periods for gathering it. Of course, the fact that fledging success has been found to increase with clutch- and brood-size, and the most productive clutch-size is not the most common one, seemingly indicates that food cannot be a controlling factor. However, it should be pointed out that we are dealing with a late stage in an evolutionary process in which selective pressure has already determined the optimum clutch-size and that these controls may be expected now to act only when a bird lays more than the optimum number of eggs. It will be a rare occasion when the optimum is exceeded and we can observe the deleterious effects accompanying it. Lack (1948c:49) has presented a very clear discussion of these problems as related to litter-size that can be projected to birds as well. He has said, ". . . , owing to the existence of adaptive modifications, the litter-size which is most productive will not necessarily be that which occurs most frequently. Indeed the difference between the most frequent and most productive litter-size will provide some indication of the extent of adaptive modification in the species concerned. . . . , as natural selection will be severe on characters affecting reproductive rate, hereditary differences resulting in litter-sizes above or below those at which maximum productivity occurs will be very rare. Hence, while one should be able to demonstrate the rise in proportionate mortality with increased litter-size, it is unlikely under natural conditions that one will have enough material to demonstrate the point at which further increase in litter-size causes a fall in productivity."

It is very important that the limits of clutch-size be not too rigid. For example, if six eggs were the optimum number for a given species and all of the birds laid that number, if food suddenly became particularly scarce in one year, the entire crop of nestlings might be wiped out. But if there were also some smaller clutches, in the time of pressure only the larger clutches would be eliminated and the young in the smaller clutches would survive to breed. If some of these young should lay one or two more eggs than their parents, and there were food in abundance, they could safely raise these young. Again the trend would be toward larger families limited only by the ability of the adults to feed them in times of ample food. This idea does not conflict with the suggestion that clutch-size is genetically determined. A bird of one genotype may breed with one of another genotype, or a mutation for smaller or larger clutches might arise, so that clutch-size is never stabilized. The trend toward larger clutches with higher latitudes which has been found in the eider by Paynter (1951) brought to the fore an interesting problem which at first sight seems to contradict any theory of the genetic determination of clutch-size. Breeding eiders were nearly

exterminated in the southern part of their range at the turn of the century but now breed there in large numbers. Since this repopulation has been much more rapid than would seem possible merely through the normal productivity of the few scattered birds that were present in the southern part of their range during the low ebb, it seems that the northern birds must have moved down and built up the population. However, the mean clutch-size in the south is smaller than that found in the north and because of the rapid change it would appear that clutch-size could not be genetically determined. This objection may be dispelled if it is recalled that while poultry breeders may perfect a strain of birds inherently capable of producing large numbers of eggs, if the birds are poorly fed, or are kept in subdued light, egg production will drop severely. The same plasticity no doubt characterizes wild birds. Food and light are only two of the environmental factors that may be supposed to operate in this way.

If it is granted that the availability of food is important in determining clutch-size in the tree swallow, the near approach of the mean in Connecticut to that at Kent Island probably can be explained. The location of the Connecticut colony and its low nestling mortality seem to indicate that it is existing under nearly ideal conditions and therefore egg production is at its optimum for that latitude. The Kent Island colony has markedly longer periods of daylight when the young are in the nest, which permit larger broods to be raised, but the detrimental climatic conditions of its coastal location may partly offset this advantage and reduce the mean clutch-size below that which would be found at the same latitude but under better ecologic conditions.

Evidence that the Kent Island colony may not be existing under ideal conditions may be found in the discoveries that the smallest broods have shorter nestling periods and also gain weight more rapidly than other broods in the same colony. This seems to indicate that the larger broods are not receiving all of the food that they can utilize. Since the Cape Cod material also indicates a positive correlation between brood-size and the duration of the nestling period, and a high rate of nestling mortality is found, whereas the relationship could not be found at the Connecticut colony, in spite of abundant data, it seems even more certain that the colonies at Cape Cod and on Kent Island are not able to produce all of the young that they might under better conditions at the same latitudes.

Because it is believed that the nestling period at Kent Island may have been shortened by human disturbance, these data cannot be used for comparative purposes, but the fact that the nestling period at Cape Cod was so much longer than at the colony in Connecticut may be highly significant. It may offer additional indications that the Cape Cod colony was not being fed so well as the Connecticut colony and consequently the young did not fledge so early. This lends support to the observation that fails to show any relationship between brood-size and the duration of the nestling period in Connecticut, which has been interpreted as meaning that all brood-sizes were fed all of the food that they needed.

Of course, with local variations in the availability of food taking such an important part, the difference between the means at Kent Island and in Montana is probably not so significant and the analysis presented above is not so clearcut. But, until more data are available from throughout the extensive range of the tree swallow, it may be said that geographical variation in clutch-size undoubtedly exists in the area studied and although clutch-size seems to increase with latitude, local variations in the availability of food may complicate the over-all picture.

SUMMARY

1. In 1948 the mean clutch-size of 30 nests was $5.63 \pm .98$ (Table I); 22 early nests had a mean clutch-size of $5.86 \pm .80$ and 8 late nests, some of which were second attempts, had a mean of 5.00 ± 1.12 ; the difference between the means of the early and the late nests is significant.
2. In 1947 the mean clutch-size of 22 nests was 5.18 ± 1.07 (Table I); the difference between the means of 1947 and 1948 is probably significant.
3. At Cape Cod the mean clutch-size in 1931 was $4.56 \pm .95$ and in 1932 it was $5.14 \pm .88$ (Table II); a significant difference between the means is indicated; the average in 1933 was 4.71.
4. Data from Montana, New Brunswick, New Hampshire, Connecticut, and two localities in Massachusetts (Table III) suggest that clutch-size increases with latitude, but yearly and local variations appear to obscure the phenomenon.
5. In 1948 the duration of incubation at Kent Island was 15.83 ± 1.46 days (Table V); at Cape Cod in 1931 and Kent, Connecticut in 1937-39 the means were $14.55 \pm .87$ and $14.38 \pm .94$ days respectively (Table VI); the Kent Island period is longer than the other two owing to a storm which interrupted incubation (Table VII).
6. The single three-egg clutch in the Kent Island sample required longer to hatch than the four-, five-, and six-egg clutches; it is suggested that the small clutch may have failed to stimulate the bird to incubate as closely as those birds with large clutches; the three seven-egg clutches seem to have been incubated significantly longer than the mean for the four-, five-, and six-egg clutches; difficulty in covering large clutches may lengthen incubation.
7. In 1947 hatching failures occurred in 5.26 percent of the incubated eggs but in 1948 rose to 15.04 percent (Table IX); in the latter year 18.28 percent of the eggs in the early nests failed to hatch and 7.50 percent in the late nests; the difference is presumably attributable to disrupted incubation because of a storm early in the season; egg mortality is probably independent of clutch-size and the order in which the eggs are laid.
8. The mean nestling period at Kent Island in 1948 was $19.21 \pm .81$ days (Table X); there appears to be a trend toward longer nestling periods in broods larger than four birds; three-bird broods definitely have shorter nestling periods than other brood-sizes (Table XI, Fig. I).

9. The nestling period at Kent, Connecticut in 1937-39 was slightly shorter than that at Kent Island in 1948, but may not differ significantly; Cape Cod in 1931 had the longest period of the three localities.

10. It is fairly certain that in 1947 and in 1948 there existed a positive correlation between clutch-size and fledging success, with the exception of the smallest clutch which was completely successful each year (Table XII); since fledging success seems to be independent of brood-size (Table XIII) and hatchability seems to be independent of clutch-size, it is obvious that there is a contradiction in the interpretation of the data; it is believed that the over-all picture is correct and that subdivision of the data has given misleading results at some point.

11. The nestlings exhibit a simple logistic growth curve until about five days before fledging, when they reach a peak in weight and then decline (Fig. II); three- and four-bird broods attain heavier weights than larger broods (Table XIV, Fig. IV).

12. All birds do not have variable clutch-sizes, but among those that do one or more of the following patterns may be distinguished:

- A. Seasonal variation.
 - B. Annual variation.
 - C. Geographical variation.
 - a. Positive correlations of clutch-size with latitude.
 - b. Increased clutch-size from west to east.
 - c. An irregular but consistent pattern.
 - d. Positive correlation of clutch-size with altitude.
- (Unproved.)

13. Not all agents which regulate clutch-size are known; the mechanisms are rarely observed exerting their effects since selection has already determined the optimum clutch-size; the following factors, which may act singly or jointly, are believed to be of principal importance in determining the size of a clutch:

- A. The number of young the adults can nourish, which in turn is dependent on:
 - a. The nature of the food.
 - b. The amount of daylight available in which to find food.
 - c. The availability of food.
- B. The density of the population (*vide*, Kluijver 1951).
- C. The number of eggs the bird can incubate.
- D. In nidifugous species, the number of young which can be protected from predators.
- E. In nidicolous species, possibly the number of nestlings, since beyond some ill-defined point the visits of the adults and the noise of the young probably render the nest too conspicuous to escape predation.

14. The nourishment of the young is probably the main determinant of clutch-size in the tree swallow; the Kent Island and Cape Cod colonies seem to exist under less than optimum conditions for food-gathering, owing to their coastal climates, and therefore produce smaller clutches than they might at more favorable localities at the same latitudes; the Kent, Connecticut colony, which is better situated, may produce the maximum clutch-sizes for that latitude.

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GENERAL NOTES

On White-throated Sparrow Plumages. — Nichols' note under this title (*Bird-Banding*, **25**: 60, 1954) leads me to offer my records of two color-banded White-throats (*Zonotrichia albicollis*). One of these in at least its second winter, and the other in at least its third winter, had not yet attained the plain gray breast and unmarked throat patch that I suppose to be typical of fully adult plumage at this season; they had the breast streaked, with a spot in the center, and the throat patch crossed by two dark lines, one running downward from each side of the bill. Both of these birds were spring singers; however, as Odum collected a female in the act of singing on her wintering ground (*Wils. Bulletin*, **61**: 12, 1949), the sex of my birds is still uncertain; a wing measurement of 73 mm. for one of them is also inconclusive.

First bird. WA-O 48-147883 was banded November 11, 1951; its breast was streaked, with central spot, its throat patch bore the two dark lines, all whites were dull or buffy. WA-O spent the winter of 1951-1952 in the neighborhood of my home. On March 18, 1952, it looked patchy, as if molting; on April 1 I recorded its plumage as "pretty bright." Four other White-throats that wintered in unstreaked plumage changed from the dull to the bright phase between March 15 and April 6. WA-O was present through April 22, and on April 6, 9 and 19 I saw it sing.

In the winter of 1952-1953 my only date for WA-O was April 23; I again recorded its plumage as "pretty bright."

In the winter of 1953-1954 WA-O was present from at least December 20 through March 22 in a plumage that included short dark streaks running down from the lower edge of the throat patch, and a distinct central breast spot; I failed to record the appearance of the throat patch itself. I believe I glimpsed this bird once more, on April 8, in "brilliant" (i.e., "high") plumage, but this identification was not beyond error. One unstreaked winterer was gaining "high" plumage on March 27 in this spring.

Second bird. B-AW 21-111612 was banded November 12, 1952; its plumage then was like that in which I first saw WA-O. B-AW wintered. On March 22, 1953, its breast began to grow splotchy and it apparently went into a molt that it completed about April 22 but that left it in merely a cleaner-looking plumage of the dull, streaked type. (In the spring of 1952 a color-banded bird of the streaked type that had wintered went through such a molt between March 20 and April 3, ending with a throat only slightly whiter than before, and with a central breast spot still present, but with a fresher look. This bird did not return in later winters.) B-AW was present through April 29, and I saw it sing on March 24, April 2 and April 22.