

A STUDY OF THE ANNUAL CYCLE OF THE HOUSE SPARROW AT VARIOUS LATITUDES

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Because the House Sparrow (*Passer domesticus*) has a wide distribution and is numerous throughout the north-temperate and tropical zones, its annual gonad cycle has been repeatedly studied. Complete annual cycles are known for latitudes 34° 05' N (Pasadena, California; Davis and Davis, 1954), 35° 10' N (Norman, Oklahoma; Allender, 1936, *a, b*), 43° N (London, Ontario, Canada; Threadgold, MS), and 54° 35' N (Belfast, Northern Ireland; Threadgold, MS). In addition, an incomplete cycle, from October to April inclusive, is known from 45° N (Minneapolis, Minnesota; Kirschbaum and Ringoen, 1936).

These various researches provide a unique opportunity to compare the effect of latitudinal position on an avian annual cycle. Such a comparison may lead to some general conclusions on the important problem of the influence and relative importance of climatic factors on the timing and phasing of cycles. This is the principal object of this paper, but the comparison is not as complete as might be desired, mainly because of differences in technique and approach used by previous workers. Difficulty of this kind is especially true with respect to the cycle of the interstitial cell. For this reason quantitative data on interstitial cells cannot be compared, although those for London and Belfast are given, in the hope that they will stimulate research on this important feature of the avian testicular cycle.

MATERIALS AND METHODS

For Pasadena, Dr. John Davis supplied data on the testis volume of 63 birds and slides of the testes of 95 birds used in a previous study (Davis and Davis, 1954). For Norman, data on testis volume have been computed from Allender's original measurements (MS) based on 53 birds. An arbitrary short diameter, determined on the basis of the London and Belfast material, was assigned to the long axes given in her manuscript. Spermatogenetic stages have been deduced from a paper by Allender (1936*a*). For Minneapolis, details of testis volume and spermatogenetic stages have been abstracted from a study of 44 birds by Kirschbaum and Ringoen (1936). In addition Professor Kirschbaum kindly supplied slides for the author's use. For Belfast and London, data were taken directly from original studies by the author, based on 34 birds collected at Belfast and 68 at London. The birds were either shot and dissected in the field or netted and brought to the laboratory alive. The testes were measured to the nearest 0.5 mm. immediately upon dissection and were fixed in Zenker-formol. Subsequently the tissues were treated by method 1 of Threadgold (1957).

The six stages of spermatogenetic activity described for the House Sparrow by Bartholomew (1949) were used. These are:

- Stage 1. Resting spermatogonia only.
- Stage 2. Spermatogonia dividing, but only a few spermatocytes present.
- Stage 3. Many spermatocytes present.
- Stage 4. Spermatocytes and spermatids.
- Stage 5. Spermatids and a few spermatozoa.
- Stage 6. Full spermatogenetic activity with many spermatozoa.

Data on day length were obtained from the "Tables of Sunrise, Sunset and Twilight," published by the United States Naval Observatory, Washington, D.C. The sunrise and sunset times given in these tables are for local standard time and, for purposes of this study, day length was computed to within 15 minutes of latitude.

Temperatures for Pasadena, Norman, and Minneapolis were based on the data used by Davis and Davis (1954, fig. 10), and sunshine data were supplied by the National Weather Records Center, Asheville, North Carolina. Temperature and sunshine data for London were obtained from the Meteorological Division, Department of Transport, London Airport, Ontario. Details of temperature and sunshine for Belfast were obtained from the Meteorological Office, Air Ministry, and were for Aldergrove Airbase, Northern Ireland.

Before going into the details of the various cycles it must be emphasized that all interpretations of data, from whatever source, are the author's and in no way represent the opinions of the persons from whom the data were obtained. Furthermore, because all the testicular cycles show minimal conditions in August or September, it would appear reasonable to use this as a starting point. September 1 has therefore been taken as the date of commencement of the cycles. As will be seen, this system has the additional advantage of simplifying the cycle and dividing it into only two parts, a progressive phase and a regressive phase.

THE TESTIS VOLUME CYCLE

The overall outline of changes in testis volume is essentially similar in the four complete cycles (fig. 1). After the summer regression, which ends in September, there is a

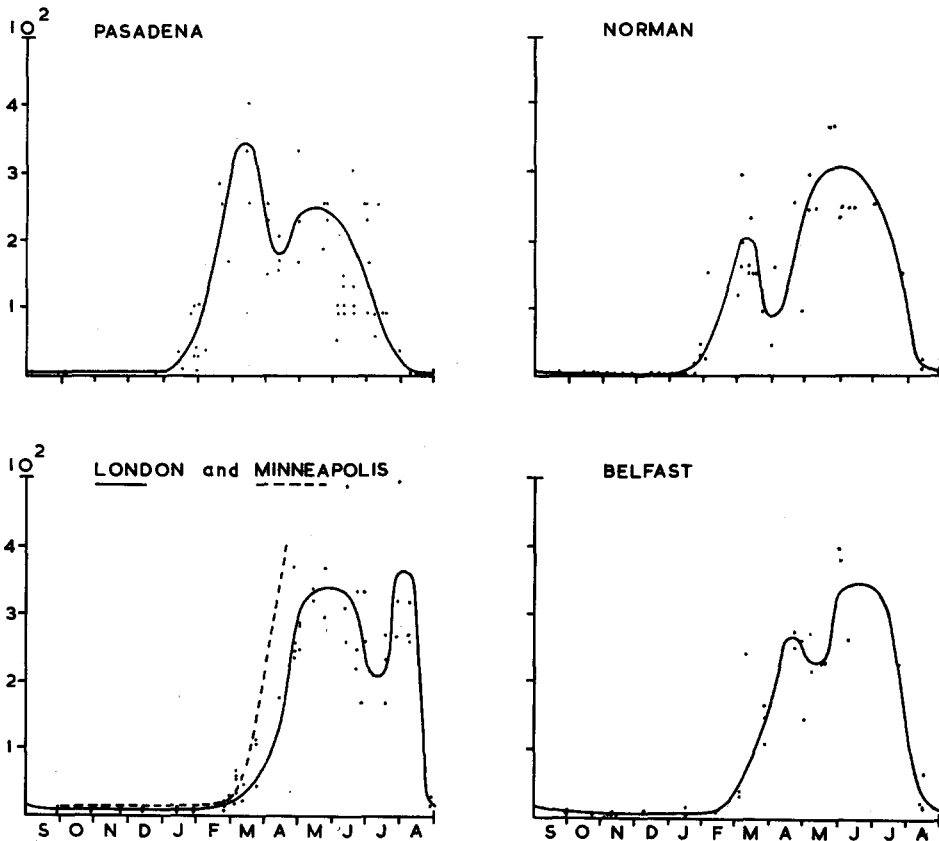


Fig. 1. Testis volume cycle. For clarity the points for Minneapolis (23 specimens) have not been included on the figure. Where two or more testes collected on the same date have identical volumes they are represented by only one point.

quiescent period of approximately 4 to 5 months and this is followed by rapid growth leading to the first volume peak. This peak gives way to a partial regression, to be followed by a second peak and the final rapid collapse, which is completed by the end of August. There is also little difference in the magnitude of the cycles, the maximum testis volumes being as follows: Pasadena, 400 mm.³; Norman, 368 mm.³ (probably underestimated); Minneapolis, 489 mm.³; London, 487 mm.³; and Belfast, 400 mm.³ Any differences are probably due to the uncertainty of obtaining specimens at the maximum for the latitude.

Despite overall similarity in the cycles, there are also essential differences. With September 1 as the starting date, the number of days taken to reach the first peak are: Pasadena, 196; Norman, 213; London, 284; Minneapolis, 227; and Belfast, 233. The dates on which testis volume was first over 50 mm.³ are: Pasadena, January 28; Norman, February 3; London, March 6; Minneapolis, February 19; and Belfast, March 3. There are also differences in the date of the first and second peaks and the time between them as shown in table 1.

Table 1
Dates of First and Second Peaks in Testis Volume

Locality	First peak	Second peak	Number of days between peaks
Pasadena	March 15	April 2	48
Norman	April 1	May 23	52
London	June 11	July 29	48
Minneapolis	April 15
Belfast	April 21	June 14	54

The length of time taken to complete regression, considered here to be the period between the second peak and the date when testis volume first falls below 20 mm.³, also varies, as follows: Pasadena, 89 days; Norman, 81 days; London, 29 days; and Belfast, 61 days.

It is clear, therefore, that the cycles are not uniformly retarded from south to north. The Minneapolis and London cycles, the latter especially, appear to be "held back" and are therefore "later" than would be expected.

THE SPERMATOGENETIC CYCLE

The four complete cycles show a general similarity (fig. 2), and they are broadly divisible into two parts. First, shortly after complete testicular collapse, there is a slight progressive spermatogenesis leading to a more or less pronounced quiescent period in early winter. Following this first phase there is rapid spermatogenesis giving a spring plateau of constant spermatogenetic activity and leading to the inevitable regression. Despite general agreement, however, there are differences in the timing of the two phases at the various localities as shown in table 2.

Table 2
Difference in Timing of Two Phases of Spermatogenetic Cycle

Locality	First date of regression stage	Date of Stage I	Date of Stage 6 for all specimens	Number of days at Stage 6
Pasadena	July 30	August 12	February 19	138
Norman	August 1	September 1	March 1	135
London	August 27	October 30	April 10	118
Minneapolis	October 30	March 31
Belfast	August 13	September 30	March 31	118

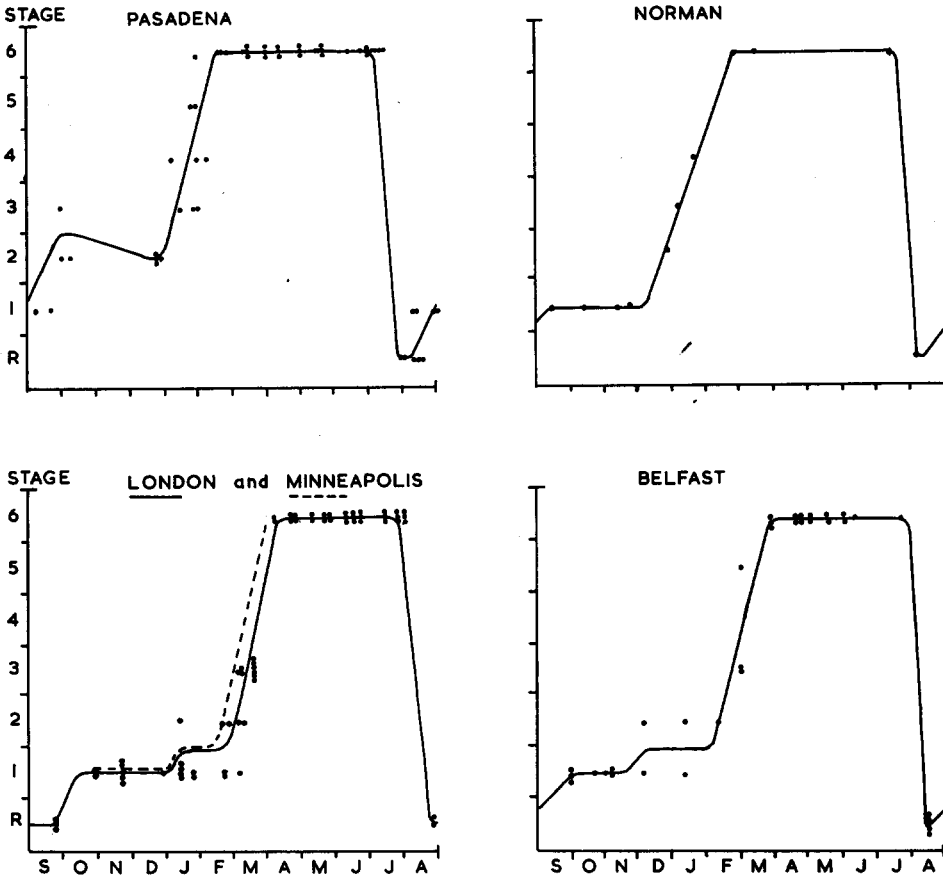


Fig. 2. Spermatogenic cycle. For clarity the points for Minneapolis (23 specimens) have not been included on the figure. R denotes regressed, steatogenous testes.

Clearly there is no uniform retardation of the spermatogenic cycle with latitude northward. The cycles of both Minneapolis and London are again noticeably displaced.

THE INTERSTITIAL CELL CYCLE

The cyclic fluctuations in the number of interstitial cells at Belfast and London are essentially similar (fig. 3). The low point of both cycles is in late summer and a gradual increase in cell numbers leads to a minor peak in mid-autumn. After a subsequent slight regression in mid-winter, a very rapid increase in the number of cells gives the first major peak in late winter or early spring. Another partial regression follows and there is finally a rapid rise and decline to form the final major peak of early summer.

Despite agreements between the Belfast and London cycles there are two essential differences between them. First, the magnitude of the London peak is generally greater than that of the Belfast peak. Second, the peaks for Belfast occur in early November, late March, and early June, whereas the corresponding peaks for London are in late December, mid-April, and late July. The London cycle, therefore, runs from approximately 2 to 5 weeks behind that of the Belfast cycle.

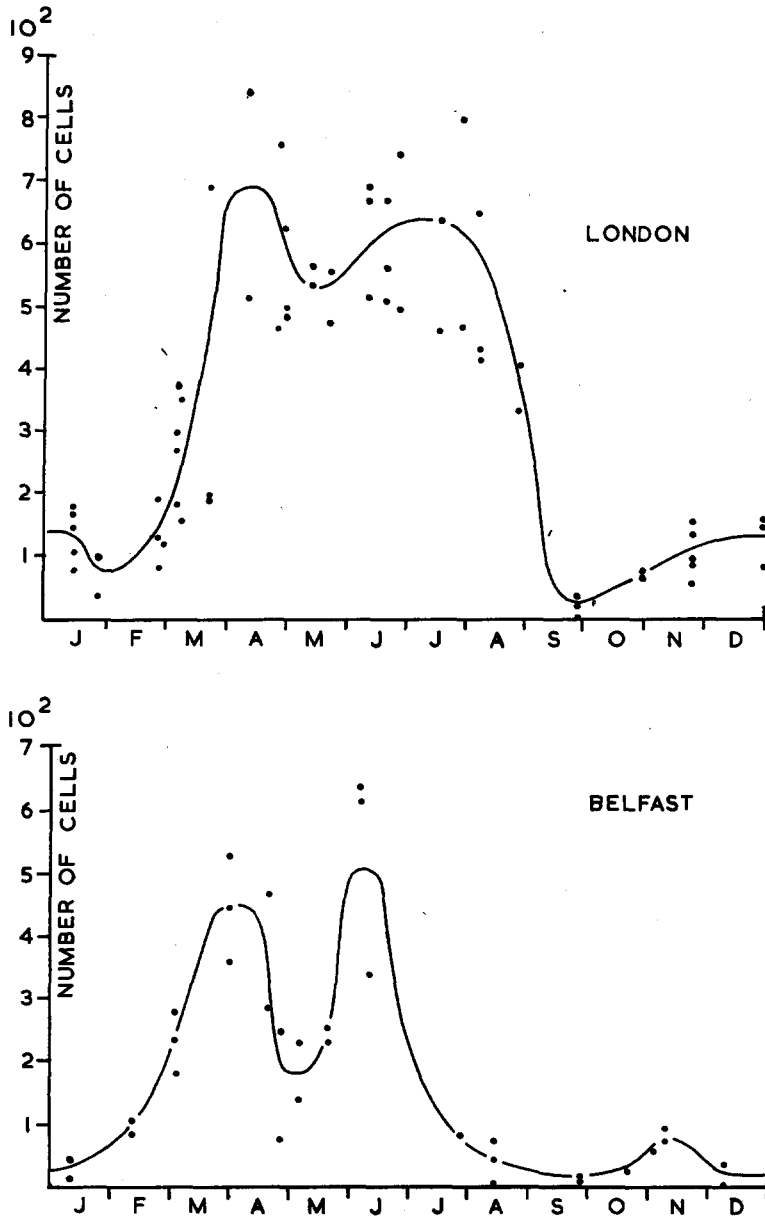


Fig. 3. Upper: Interstitial cell cycle for London.
 Lower: Interstitial cell cycle for Belfast.

DISCUSSION

The complete cycles of testis volume at Pasadena, Norman, London, and Belfast all have a bimodal form. It must be concluded, therefore, that this is normal for the House Sparrow, although it is in contrast to the single-peaked cycle of the Jackdaw (*Corvus*

monedulus; Threadgold, 1956). These two different forms probably reflect an essential distinction between single and multi-brooded species, the latter obviously requiring a longer period of testicular activity.

The partial regression in testis volume during the height of the breeding season, which gives the cycle its two-peaked form, can perhaps be accounted for in one or more of the following ways. First, either the transfer of mature spermatozoa produced in the spring to the seminal vesicles, or their use in copulation, would lead to a reduction in the volume of the seminiferous tubules and hence of the testis as a whole. Second, the sex hormones produced earlier in the season may inhibit the pituitary secretion of follicular stimulating hormone, with a consequent reduction in the rate of spermatogenesis and a decrease in testis volume. The remarkably constant interval between the two peaks at the various latitudes, 48, 48, 52, and 54 days, suggests that some internal mechanism may be responsible for the partial regression and recovery from it. Measurements of the specimens from Belfast and London show that a definite decrease in the average diameter of the tubules does occur, in April in the former, and in June in the latter (fig. 4), indicating that the decrease in tubule size is very probably responsible for the reduction in testis volume, although the actual factors involved are still not clearly known.

The final collapse of the testis is rapid in all cases but generally takes longer in more southerly populations. The southern cycles of Pasadena and Norman are subject to maximum day lengths of approximately 14.5 hrs., compared to approximately 15.5 hrs. at London and Minneapolis and 17.0 hrs. at Belfast. This would indicate that the timing and rate of regression is related to the previous exposure to light, thus agreeing with the findings of numerous photoperiodic experiments. Vaugien (1951) and Cowles and Norstrom (1946), however, have suggested that testicular collapse is due to heat

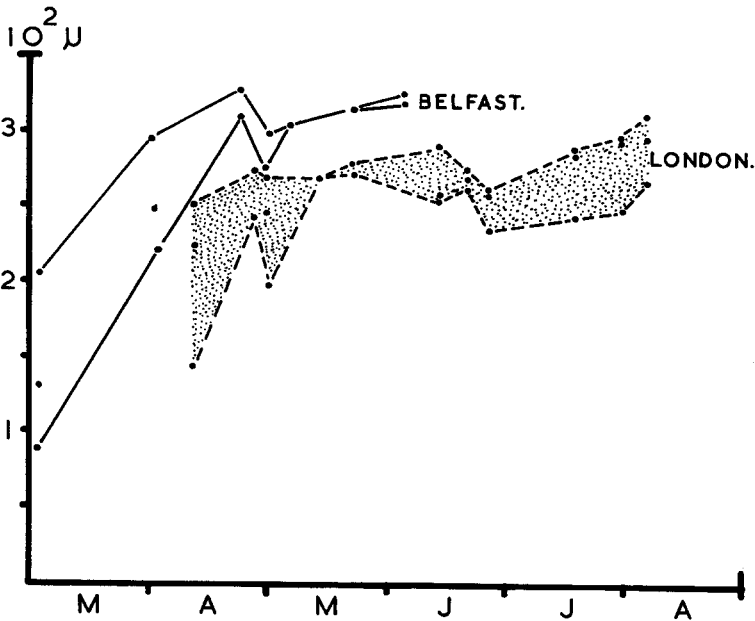


Fig. 4. Seminiferous tubule diameters for London (April to August, 1957 and 1958 combined) and for Belfast (March to June, 1956). Upper and lower lines join maximum and minimum diameters, respectively.

exhaustion. It is true that regression usually occurs not long after the weekly average temperature attains 60° F. for a few weeks at all the localities considered here. Perhaps high temperatures accelerate the effect of previous exposure to light and so both factors may work together.

In addition to the foregoing theories of the mechanism involved in testicular collapse, Davis and Davis (1954) have introduced new proposals. They consider that spermatogenetic activity may be retarded by an antagonism between the gonadotrophic and thyrotrophic functions of the pituitary. Their research shows relatively high thyroid activity during winter and also at about the time of regression, two periods of notable testicular inactivity. It is, however, possible to combine this idea with that of the effect of previous exposure to light, in the following manner. Low temperatures in winter may initiate active thyrotrophic function and consequently inhibit gonadotrophic secretion, thus slowing down the testicular cycle but not completely suppressing it. Toward the end of the breeding season previous light treatment brings about a decrease in pituitary gonadotrophic function with subsequent testicular collapse and an increase in thyrotrophic activity. Such a theory would explain both the peculiar occurrence of thyroid activity during the mid-summer period of high temperatures and also the slowing down, after its strong upsurge in autumn, of gonadal activity in the winter.

In the spermatogenetic cycles the existence of autumnal activity is well established, occurring, as it does to some extent, at all five latitudes, although it is most pronounced at the southern localities. Without doubt the testis of the House Sparrow is active over the whole autumn-winter period. The organ is therefore primed and only awaiting favorable environmental factors to burst into full activity. The rapid increase in testis volume and in the advance of spermatogenesis at the beginning of the breeding season is not then as remarkable as has so often been stated.

As previously indicated the length of time during which the testes were at Stage 6 is only weakly correlated with latitude, but it may be stated that there is a tendency for the breeding season to be progressively shorter with more northern latitude. This may be due to the more rapid rate with which spermatogenesis proceeds from Stage 1 or 2 to Stage 6 in the more southerly populations, as well as to the more obvious fact that environmental conditions are more favorable earlier in the year in such latitudes.

The testis volume and spermatogenetic cycles clearly show that uniform retardation of the breeding cycle with northern latitude does not occur. This indicates that the annual day length cycle is not the overriding influence in the timing of the gonad cycle of this species in the wild, despite the results of numerous photoperiodic experiments which have demonstrated the effectiveness of light and its importance in timing and activation of the gonads (Kirschbaum and Ringoen, 1936; Bartholomew, 1949). If this is true, it is necessary to look for other environmental factors capable of modifying day length effects.

Before it is possible to consider the influence of these other factors, it is important to have an accurate means of measuring differences in the timing of phases within the testis cycles. For this purpose, changes in the stage of spermatogenesis are superior to those of testis volume and have been used throughout. Second, it is essential to estimate the difference in days between gonad cycles which is due to the configuration of the day length cycles at the various latitudes, and by subtracting this from the total difference in days between cycles, eliminate the influence of day length. The remaining difference in days must then be due to the influence of other environmental factors.

Taking September 1 as the starting date of the annual gonad cycle, the total number of hours of daylight received at each locality up to the date of attaining Stage 6 is shown in table 3, column 1.

Table 3
Dates of Theoretical and Actual Attainment of Stage 6 in Annual Cycle

Locality	Column 1 Number of hours between Sept. 1 and date of Stage 6	Column 2 Difference in hours necessary to reach Stage 6 at Pasadena and other localities	Column 3 Theoretical date of attaining Stage 6, 1864.8 hrs. of daylight	Column 4 Actual date of Stage 6	Column 5 Difference in days between column 3 and column 4
Pasadena	1864.8	-----	-----	-----	---
Norman	1957.1	92.3	February 20	February 28	8
London	2377.8	513.0	February 27	April 10	42
Minneapolis	2217.5	352.7	March 2	March 31	29
Belfast	2078.3	213.5	March 13	March 31	18

If Pasadena is taken as the norm, then deducing the total number of hours which are required to induce Stage 6 at this locality from the number required at each of the other latitudes gives the "lateness" of the cycle at each place, as is shown in table 3, column 2. These "excess" hours can be used to count back to a theoretical date at which Stage 6 should have been reached at each latitude (table 3, column 3), and this naturally shows a progressive retardation north. The subtraction of the theoretical date of Stage 6 from that of the actual date of Stage 6 (column 4), gives a figure in days (column 5), which is "free" of latitudinal influences and hence day length.

It seems logical to consider the effects of temperature first, for it is known to influence the avian sexual cycle (Engels and Jenner, 1956; Farner and Mewaldt, 1952). It is difficult, however, to state whether high temperatures "boost" the effects of light, as appears to be the case in the experimental researches just cited, or whether low temperatures inhibit photoperiodic effects, perhaps due to the antagonism between the pituitary-thyroid and pituitary-gonad mechanisms, as proposed by Davis and Davis (1954). It is pertinent to note here that Vaugien (1954) showed that the injection of thyroxin appeared to stimulate the testis. This at first would appear to negate the idea of Davis and Davis, but it is very possible that exogenous thyroxin depresses the thyrotrophic function of the pituitary and hence allows uninhibited gonadotrophic activity. This response would agree with the theory of Davis and Davis (*op. cit.*). Perhaps both temperature effects, "boosting" with high temperatures and inhibition with low temperatures, are equally involved, for the two mechanisms are not mutually exclusive. For the present purposes, however, with Pasadena being used as the norm, low temperatures must be considered as inhibitory. In actual fact the cycle at Pasadena, with its high temperatures, may have been accelerated compared to that of Norman, for example, and thus account for the difference between the cycles at the two latitudes. This argument naturally applies to the difference between Pasadena and the other cycles.

Figure 5, which shows the average weekly temperatures for the five latitudes from September to April, clearly demonstrates that during this period the other four localities have a temperature which is generally lower than that of Pasadena. Furthermore, there is some correlation between the difference in days in reaching Stage 6 and the average weekly temperature, in general the greater the former the lower the latter. Nevertheless, temperature cannot explain the difference between the timing of the London and Minneapolis cycles; because although Minneapolis is 2 degrees farther north and has a lower temperature, its cycle is 13 days ahead of that of London, quite the reverse of what would be expected.

It becomes necessary, therefore, to look for yet another factor. Sunshine, in this respect, has been largely ignored in previous studies, although the author has shown (Threadgold, 1956) that it might have some influence on the interstitial cycle in the testis of the Jackdaw. Furthermore, Marshall (1952) has stated there is good evidence that prolonged sunshine stimulates the sexual cycle and breeding behavior of some birds.

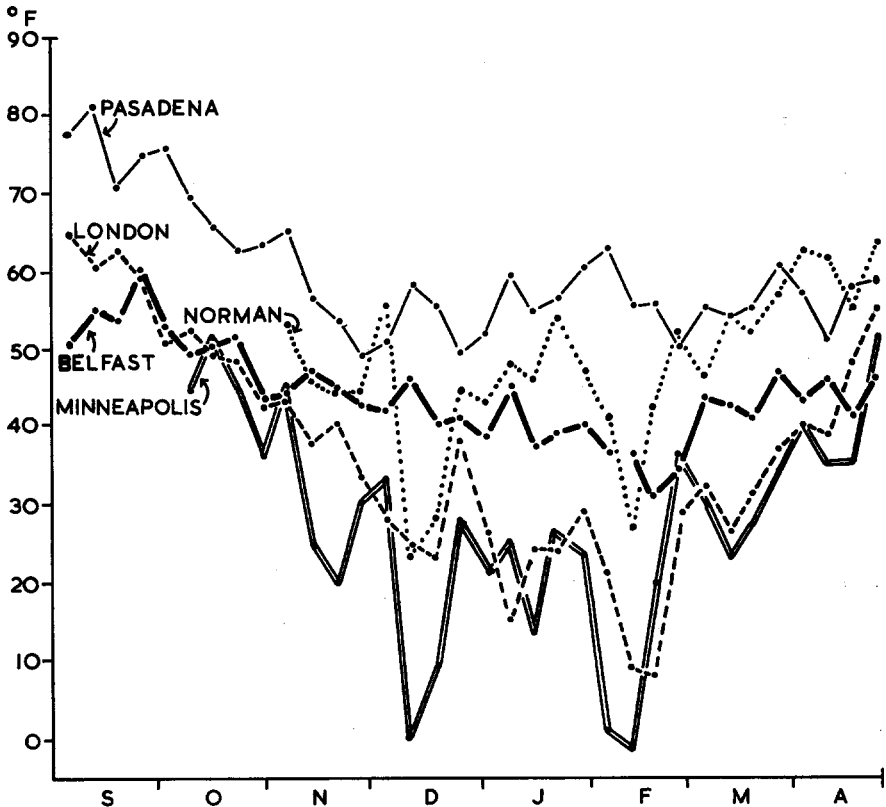


Fig. 5. Average of daily maximum and minimum temperatures for one-week periods at Pasadena (September, 1952, to April, 1953), Norman (November, 1932, to April, 1933), Minneapolis (October, 1932, to April, 1933), London (September, 1957, to April, 1958), and Belfast (September, 1955, to April, 1956).

Sunshine may be considered as one aspect of daylight, either with regard to increased intensity or as a change in the wave length composition of the natural light. There are inherent difficulties in these considerations, however. In nature light intensity is normally above the threshold level for stimulation of testicular activity in the House Sparrow except just before sunset and just after sunrise (Bartholomew, 1949). Continuous sunshine might therefore make little difference. Color composition could be more important, as yellow and red wave lengths are known to be more stimulatory than blue or green (Burger, 1949). But again the changes of color composition in natural daylight with and without sunshine are unknown. Perhaps more important than either of the two former factors is the possible psychic effect of bright sunshine.

Figure 6 shows that there is a marked difference between the monthly totals of bright sunshine for London and Minneapolis, the latter exceeding the former by an average of 61 hours per month in the period from October to April. Minneapolis itself

has an average of 92 hours per month less sunshine than Pasadena during the period from November to April, while compared to the latter place, Belfast has 175 hours per month less from September to April. It is clear, therefore, that lack of sunshine could account for temporal differences after temperature effects have been taken into account.

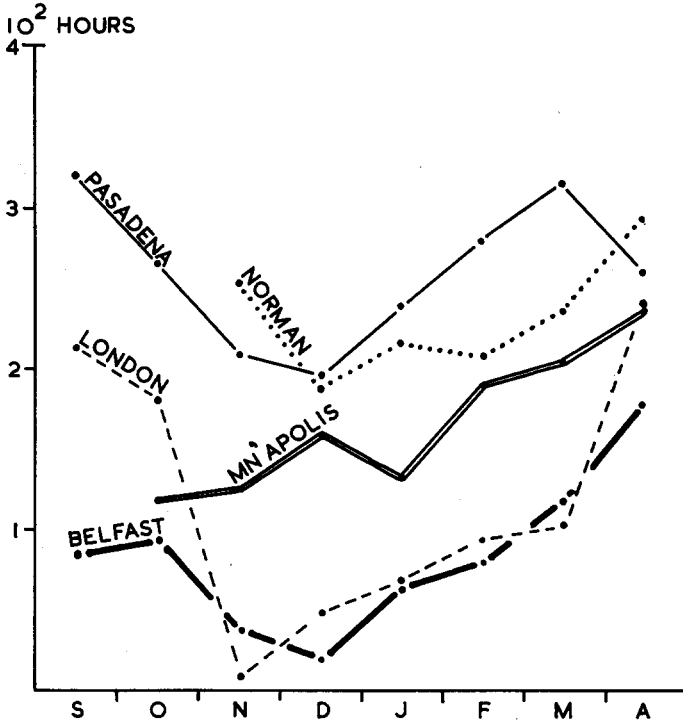


Fig. 6. Monthly totals of bright sunshine for Pasadena (September, 1952, to April, 1953), Norman (November, 1932, to April, 1933), Minneapolis (October, 1932, to April, 1933), London (September, 1957, to April, 1958), and Belfast (September, 1955, to April, 1956).

If both temperature and sunshine are factors which can alter the timing of the gonad cycle and modify the influence of the day length cycle, is there any indication of their relative importance? There are four combinations of these two factors among the localities.

Pasadena and Norman	High temperature	Many hours of sunshine
London	Low temperature	Few hours of sunshine
Minneapolis	Low temperature	Many hours of sunshine
Belfast	High temperature	Few hours of sunshine

From the last three combinations, it is possible to conclude that lack of high temperatures during the critical period of September to April results in a greater "retardation" than a lack of many hours of bright sunshine, for the Minneapolis cycle is more retarded than that of Belfast, 29 to 18 days (table 3). Combined low temperatures and few hours of bright sunshine are so "inhibitory" as to greatly retard the gonad cycle of London and place it later than a cycle approximately 12° farther north.

The findings presented here indicate that still further extensive research is necessary on even such a repeatedly investigated cycle as that of the House Sparrow. Studies of cycles in the wild and a comparison of them with the relevant climatic factors would

yield valuable evidence and a more complete understanding of the factors which control the timing of the avian cycle. The extensive study of a species of wide distribution, such as the House Sparrow, at different longitudes on the same latitude and at different latitudes, is becoming increasingly urgent and gives an opportunity for a cooperative project.

SUMMARY

The quantitative aspects of the annual testis cycle of the House Sparrow for the latitudes of Pasadena, Norman, and Minneapolis in the United States, London, Canada, and Belfast, Northern Ireland, have been compared and contrasted.

In all localities, the cycle commenced in late summer and had virtually only two parts, a progressive period from late summer to late spring and a regressive period during the major part of the summer. The testis volume and spermatogenetic cycles were essentially similar at all places. Interstitial cell cycles were established only for London and Belfast, but these also were similar in form if not in magnitude. Testis volume and interstitial cell cycles had a two-peaked form, while the spermatogenetic cycle had autumn and spring plateaus.

Differences between the cycles at the various localities occurred and were mainly concerned with the timing of the different phases within the annual cycle. There was no orderly progressive retardation of the phases with north latitude, as would be expected if day length were the environmental factor with overriding influence in the timing of the cycle. Other factors which were found to be capable of modifying the effect of day length were temperature and sunshine, the former having greater importance. The mechanisms whereby these factors might mediate their effects have been discussed.

It is concluded that the "out of latitude" commencement and sequence of the London and Minneapolis cycles, when compared to those of Pasadena, Norman and Belfast, is explicable on the basis of the different configurations of day length, combined with the temperature and sunshine cycles at the two localities.

ACKNOWLEDGMENTS

I wish to thank Professor A. J. Kirschbaum of Baylor University for kindly lending material from his own studies. I am especially appreciative of the help of Dr. John Davis of the University of California who not only generously lent slides and data relating to his study of the House Sparrow at Pasadena, but also supplied climatological data and read the manuscript, giving valuable criticism and advice. Part of this work was carried out while the author was a National Research Council Post-Doctoral Fellow at the University of Western Ontario.

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