A POPULATION STUDY OF SKYLARKS *ALAUDA ARVENSIS*

JUAN D. DELIUS

INTRODUCTION

In the summer of 1958 I colour-ringed a number of Skylarks *Alauda arvensis* to aid observation of their behaviour (Delius 1963 and in prep.). In the following years however, it became apparent that without much additional work the ringing could be extended and other data gathered to yield information on the dynamics of the population.

The study area chosen was in the Drigg Dunes and Gulleries Nature Reserve, commonly referred to as Ravenglass Gully, in northwest England ($54^{\circ} 21' N.$, $3^{\circ} 25' W.$, Fig. 1). It consisted of a 30 ha. strip of coastal dunes (only 10 ha. used in 1958) in a peninsula which projects off the Cumberland coast into the Irish Sea. The study area is isolated to some extent from neighbouring areas by high bare dunes and an estuary. It overlapped to only a very small extent the Black-headed Gull *Larus ridibundus* colony (Marchant 1952). The vegetation consists mainly of marram grass (*Ammophila* sp.) and is scarce. The Skylarks occupied mainly the lower valleys which have slightly more varied vegetation.

FIGURE 1. Part of the coast of Cumberland, England, to show the location of the study area which is marked in black.

METHODS

For ringing, the adult Skylarks were caught either with a clap-net baited with a stuffed Skylark which was either fought or courted and which, when touched, released the trap; or with a clap-net at a poppy-seed feeding-station; or, more often, with a door-trap on the nest which was actuated from a hide. They were then ringed with individual colour-ring combinations and, from 1959 onwards, with the British Trust for Ornithology aluminium rings. The young were taken out of the nest when about six days old and ringed with one colour-ring combination per brood. They were re-ringed with individual combinations if later they settled in the study area. The colour-rings used held their colour sufficiently well even after five years, but some rings by then had been lost and had to be replaced.

The adult birds were sexed according to wing length (Fig. 2) and this was then checked by watching their behaviour. In contrast to some other passerines, no differences of any kind could be found between one-year-olds and older birds; this was ascertained by recapturing

FIGURE 2. Wing-length distribution of male and female Skylarks *Alauda arvensis*, from 76 trapped individuals.

birds ringed as chicks. In a number of instances in this paper I have however compared one-year-old and older birds. Except in four cases in which one-year-old birds were known from being ringed as chicks, I have considered new settlers in the area as one-year-olds. This assumption is justified, at least for a good proportion of the new settlers, because (a) the strong site-tenacity of the adult birds makes it unlikely that many of the new settlers of the area were adults emigrating from surrounding areas; (b) the non-breeding population, whose age is unknown, was small and therefore only few settlers could stem from this group; (c) ringed first-year birds demonstrated that they can breed (six cases). These points will be substantiated later in this paper. Until their autumn moult in August, juveniles of the same season are easy to distinguish from adults by their striking plumage.

The population was kept under observation during the following periods: March–July 1958; March–August 1959; February–June 1960; during the second half of April 1961; during the second half of April, with short visits in March and June, 1962; during the

first half of May and a brief visit in July 1963; and in 1964, during a week in late April. Observations were made with a 10×50 binocular mounted with a ball-joint on a tripod. In 1962, 1963 and 1964 I also used a 25×60 telescope. Because of the sparse vegetation and the elevated points which could be used for observation, the reading of the colour-ring combinations was fairly easy. Nests were found by watching the birds or by searching the ground in likely places. A large proportion was found during nest-building and laying; almost all were known during early incubation and only a few were found later. The reader is referred to Delius (1963) for behavioural details such as anti-predator, incubation and parental care behaviour.

For the quantitative analysis non-parametric statistics (Siegel 1956) have been used except in a few cases where parametric ones were necessary (Weber 1961). In each case I give the test used and the probability obtained.

BREEDING SEASON

LAYING DATES OF FIRST CLUTCHES

Fig. 3 presents the distribution of the start of laying of all clutches over the breeding season, which, accordingly, can be taken to extend from the middle of April till the beginning of July. Two peaks, one at the end of April and one in the middle of May, are due to the relatively synchronized appearance of the first and second clutches respectively. The plateau from about the end of May till the middle of June, is mainly due to the third clutches, and tails off during the beginning of July. The data are from three breeding seasons with 5, 18 and 19 females respectively. Although the clutch distribution varies considerably from year to year the two peaks mentioned can be traced to some extent in each season.

FIGURE 3. Time distribution of Skylark *Alauda arvensis* clutches. Each point represents the number of clutches begun in a 5-day period. The line is a sliding average over 10 days. The two peaks are due to the relatively synchronized appearance of the first and second clutch respectively.

Fig. 4 shows the laying dates of the first eggs of the season for the females of the population in four different years. The beginning of the breeding season varied from year to year and, if one notes the number of clutches begun in the different years before 24 April, between 24 April and 1 May and after 1 May, it can be shown that these variations are significant (χ^2 , $p < 0.001$). The average date of the first eggs of the season was 3 May in 1958, 29 April in 1959, 30 April in 1960 and 17 April in 1961. The annual

FIGURE 4. Beginning of laying by Skylarks *Alauda arvensis* in the years 1958–1961. Each square represents the start of one clutch. The lines show the course of the mean daily temperatures.

difference can be related to the air temperature: the mean temperature in April 1958 was 0.6°C . below the April average for the four years, that of 1959 was 0.3°C . below, that of 1960 0.3°C . below, whilst that of 1961 was 1.3°C . above. In 1957, a year with an unusual warm spring, laying started strikingly early in Ravenglass (Beer, pers. comm.; see also Goodacre & Lack 1959). From Fig. 4 it would seem that the mean air temperature has to rise to about 10°C . before laying is initiated.

One-year-old and older birds show a difference in the onset of laying: only 1 one-year-old compared with 17 older birds laid before the median date, while 11 one-year-old compared with 7 older females laid after the median date (χ^2 , $p < 0.001$). The difference was seen in both years for which data were available and in both cases the average laying date for the one-year-old birds was seven days later than that of the older birds. The laying dates did not seem to be affected by whether or not the females had changed territory or mate from one season to the next.

CONSTANCY OF FEMALES' LAYING ORDER

There is a striking constancy in the laying order of the individual females of the population, irrespective of the starting date of the population as a whole (Fig. 5). The rank correlation coefficient τ is 0.76 ($p < 0.01$) for 1958/59; 0.72 ($p < 0.001$) for 1959/1960; and 0.68 ($p < 0.001$) for 1960/1961. There is even a correlation over three years: 1958/59/60, $W = 0.77$ ($p < 0.05$); 1959/60/61, $W = 0.92$ ($p < 0.001$). By dividing the groups of females into those which had the same mate in the two years considered (group a) and those which changed mates (group b), and in addition taking into consideration

FIGURE 5. Laying order of three groups of female Skylarks *Alauda arvensis* in two successive years, showing a constancy in the relative dates of the first laying of individuals. Dots: 7 females 1958/59; circles: 12 females 1959/60; crosses: 13 females 1960/61. The birds of a group were ranked twice according to the first laying dates in the two years considered, each point therefore indicates the ranks one individual occupied in the two years. If two or more birds of a group started laying on the same day, then they were all given the corresponding average rank.

the order of laying of the females of the males which were present for the two years but changed partners (group c), it can be shown that the constancy of the laying order is entirely due to the females, since the first two groups show similar correlation coefficients whereas group c shows no significant correlation. (r 's for (a) are 0.73 (1959/60) and 0.80 (1960/61), for both $p < 0.05$; for (b) 0.73 (1959/60) and 0.57 (1960/61), for both $p < 0.05$; for (c) 0.07 (1959/60) and 0.28 (1960/61), for both $p > 0.05$). In short, individual females rather than males tend consistently to be early, medium or late first-layers in successive years.

TEMPERATURE EFFECT ON LAYING OF FIRST CLUTCHES

Then arises the question of what determines the constancy of the individual females' rank in the laying order. It seemed possible that different females have different temperature thresholds and as the temperature rises in spring it would reach each of their thresholds successively, causing them to lay in a certain sequence. To test this one could calculate the mean temperature for, say, 10 days before laying for each female and see if these temperatures were related with their laying rank. Such a method is inconclusive, even if it gave a positive result, because one would expect such differences also if the laying order was determined by factors other than temperature, since on average the temperature rises during the course of spring. Another possible method would be to see if these mean temperatures before laying are consistent in the successive years for the individual females; but this is subject to the same sort of criticism just mentioned.

The method I finally used took this into account, and also catered for a possible additional complication which is that between the date the temperature reaches the

threshold for any given female to start laying there could be a definite time interval; in other words, that the mean temperature of only certain days is critical. The data used were the mean daily temperatures for 12 days before the laying in each of three or four years of 10 different females. For each day before laying the variance in the temperatures was analysed into the variance between individuals and that within individuals and between years. The ratio of these two variances gives the relative importance of the two components. If the quotient is low it means that there is little consistency in a given female to lay following the occurrence of a certain temperature and that the differences between the temperatures to which the different females responded are small. If it is high, it shows that there is a marked consistency in the temperatures to which the individuals respond by laying and marked differences between these temperatures for the different females. Fig. 6 shows these variance ratios for the different days before laying. It can be seen that on the 4th, 6th and 7th days such differences between individuals and consistencies within individuals are present to a significant degree (F-test, 4th day $p < 0.01$, 6th day $p < 0.01$, 7th day $p < 0.05$). Although the 5th day shows a non-significant quotient it seems likely that it belongs to this group of days which can be termed critical days.

FIGURE 6. Daily ratios of mean temperature variances before laying of the first egg of the season by Skylarks *Alauda arvensis*. (For explanation see text.) The higher values show where there is a marked consistency in the temperatures to which the individuals respond by laying and marked differences between these temperatures for the different females.

So far we have shown that it is likely that temperature plays a role in determining the differences in laying dates in different females, and that between the time the temperatures have an influence and laying there is an interval of four to seven days (compare below). To check if this influence can explain the laying order of the females I took the average temperature of the four critical days for each of the females and related them to their average rank in laying. There was a good agreement (Fig. 7 (a), $r_s = 0.95$, $p < 0.01$). Similarly I computed the average temperatures for the non-critical days and related them to the average rank but here the correlation is not significant (Fig. 7 (b), $r_s = 0.42$, $p < 0.05$).

Due to the existence of days in which the temperature is critical and days in which it is not, it is possible to counter the criticism that factors other than temperature determined the laying order because one would then not expect a difference between critical and non-critical days neither in variance ratios nor in correlation coefficients; in other words,

FIGURE 7. (a) Mean temperature of critical days for individual female Skylarks *Alauda arvensis* in relation to their average rank in the laying order, showing a good agreement. (b) Mean temperatures of non-critical days; there is no significant correlation.

the non-critical days provide a set of control data against which the critical ones can be compared. In both cases there are significant differences between the average variances of critical and non-critical days (F-test, variance within individuals, $p < 0.05$; variance between individuals, $p < 0.05$) and between the correlation coefficients just mentioned ($p < 0.05$, according to Kendall 1948).

From the evidence so far one could think that as the temperature rises in spring it reaches the different thresholds of the different females and after a delay of four to seven days causes them to lay. In fact inspection shows that it often happens that the temperature repeatedly reaches the threshold of any given female, sometimes up to a month before laying actually occurs. This suggests that some other factors play a role in releasing laying. It is known, of course, that daylength changes have an over-riding importance (Farner 1964), and even temperature may act not only in the way indicated but also in a more long term way (see above). It cannot yet be decided in what way the temperature effect described here interacts with these other factors. All that can be said is that it plays some role. It could be the sole factor which brings about the laying order previously described, while the other factors decide only the laying date of the population as a whole and are not responsible for the differences between the individuals.

Some further points may be mentioned here. In the preceding analysis I have always used the mean daily temperatures obtained by averaging the maximum and minimum daily temperatures. It could be that either of these latter two are more important than their average in determining the initiation of laying. I therefore did two sample analyses of variance in the way described above but using respectively the maximum and the minimum temperature for only the 4th day before laying. In both cases the variance ratio obtained was not significant (F-test), suggesting that it is the mean temperature or some related temperature measure which is critical.

To see whether the females were reacting just to a temperature level or additionally to a temperature change (rise), I examined the course of the mean daily temperatures in the days before laying obtained by averaging for each day the temperatures related with the 10 females in all the years (Fig. 8). It seems that they react to a temperature-rise as well as to a temperature level since the rise in temperature after the 7th day is steeper than the rise that, on average, takes place during the period of first laying (end of April).

FIGURE 8. Average temperature course of daily mean temperatures before and after laying of the first egg of the season by Skylarks *Alauda arvensis*. Straight line: long term average temperature course for the end of April. (For explanation see text.)

I examined my data for one possible interaction between temperature and other factors regulating the beginning of laying suggested by the findings of Nice (1937) in the Song Sparrow *Melospiza melodia*. She found a lowering of the temperature thresholds for song with the advance of the breeding season, probably due to the concurrently increasing daylength. To do this, I made use of the fact that the dates of first laying for each female varied from year to year (see above). I compared within each female the temperature thresholds (namely the mean temperatures in the critical days) in the years with early beginning of laying with those in years with late beginning. No consistent differences in thresholds could be found.

LAYING DATES OF SUBSEQUENT CLUTCHES

This date is dependent on the stage at which the previous clutch or brood is lost. Fig. 9 shows that the interval between losing a clutch (or brood) and the laying of the next is about four days if the loss occurred during egg-laying or just after it, six days if it was during the incubation period and between five and six days—depending on the nestlings' age—if it was during the nestling stage. The difference between the intervals after loss at the egg-laying stage and those at the incubation plus nestling stage is significant (Mann Whitney, $p < 0.01$). If the previous brood disappears after having left the nest, the interval decreases steeply with increasing age of the young lost and becomes zero on the 17th to 18th day after hatching. Beyond that age the intervals are negative; in other words, the females lay again before the young have been lost or have reached independence. The points of this part of the graph seem to fit a straight line, which is the line they would follow if there is no inhibition of re-laying beyond 17 days after hatching.

This makes possible the occurrence of "telescoped" broods and may be related with the fact that after they leave the nest the share of the female in feeding the young decreases rapidly. In fact the inhibiting effect of previous broods must stop sometime before 17–18 days after hatching since it takes a Skylark at least four days to get physiologically ready for laying judging from the four days it takes a laying female to lay again (Fig. 9.), though a laying female may not be quite comparable physiologically to one feeding

FIGURE 9. Time intervals between the loss of a clutch (or brood) of Skylark *Alauda arvensis* and the laying of the next. Sliding average over three days. The straight line is explained in the text.

young. Possibly then the inhibition is relaxed even earlier, say, five to six days before re-laying, that is 11–13 days after hatching. (For discussion on the causal background of this problem see Lehrman 1959). This picture, of course, is only true for the “average” female; there are plenty of exceptions, as can be seen in the graph. No other factors could be found which affected the laying date of these subsequent clutches.

TERMINATION OF CLUTCH LAYING

It is not clear what inhibits a Skylark from laying at the end of the breeding season. Fig. 10 compares the time distribution of the start of laying of the last clutches of the breeding season for 46 females with the time distribution of the laying of the first clutches by the same birds (data from three seasons). It shows that the spread is much larger for the end of the season than for the beginning. There is no correlation between the date at which different females began the season and that at which they ended it. Nor is there a difference in the final date in old and one-year-old Skylarks, nor any consistency in individual females in the laying date of the last clutch from season to season.

In the literature there are two reports of autumn broods of Skylarks: Hardy (1939) found a nest with eggs in October and Thorburn (1954) one with eggs in December (see also Hachisiuka (1924) for *Alaemon alaudipes*), which in each case coincided with abnormally warm periods (see Snow 1955). Physiologically these broods have to be considered as "early" ones of the following season (Marshall 1961).

FIGURE 10. Comparison of the time distribution of first (circles) and last (dots) Skylark *Alauda arvensis* clutches of the season, showing a much wider spread for the end of the season than the beginning. Each point represents the number of clutches begun in a 5-day period.

It would be interesting to know the pattern of the breeding season of Skylarks in other habitats. I observed that Skylarks outside the study area with territories in corn-fields and in bracken abandoned their territories in early June when the vegetation became high, but I do not know if they took up new territories elsewhere and continued their breeding there.

TABLE 1. *Geographical variations of the breeding season of the Skylark Alauda arvensis.*

Locality	% of clutches found in				Total number of clutches
	April	May	June	July	
England	3	57	33	7	120
France	10	41	32	17	83
Germany	25	38	31	6	55

Table 1 compares the breeding season of populations from different geographical areas, England (own data for 1958, 1959 and 1960), Germany (Haun 1931, data from an unspecified number of years) and France (Labitte 1957, data from an unspecified number of years). The comparison suggests that the English population has a rather short season while the French season seems to be later than the German one (compare also Pätzold 1963). The suggestion is supported by a statistical test on the homogeneity of the figures in the table (χ^2 , $p < 0.001$), but it is questionable if this means very much, as data of this kind are very dependent on equal effort in searching for clutches throughout the breeding season.

CLUTCHES

NUMBER OF CLUTCHES PER SEASON

On average a female lays 2.7 clutches per breeding season (1959, 2.6; 1960, 2.8, difference not significant). Fig. 11 shows a frequency distribution of the number of clutches laid by single females; many were replacement clutches, but re-laying often

FIGURE 11. Distribution of number of clutches laid by individual female Skylarks *Alauda arvensis* in any one season ($N=34$, data from 1959 and 1960).

FIGURE 12. Distribution of clutch sizes of Skylark *Alauda arvensis*. (89 clutches, data from 1959 and 1960).

follows "successful" broods, i.e. after at least one chick has been reared to independence (see above). One pair reared 3 broods successfully, in a season; at least four pairs successfully reared 2 broods and did not lay any further clutches; and one pair laid only one clutch and reared that with success. There is therefore considerable variation in the number of broods Skylarks "normally" undertake in one season. No significant differences in the number of clutches laid could be found between one-year-old and older Skylarks, nor could I find any constancy in the number of clutches laid by the same female in two different years.

CLUTCH SIZE

During 1959 and 1960 all the nests of 18 and 19 females respectively were carefully searched for and no more than about 5% of their nests can have been missed. The average clutch size, taking the years together, was 3.69. Fig. 12 shows the distribution of the clutch sizes. Two clutches of two eggs were also found, but circumstantial evidence suggested that they were incomplete clutches due to egg-robbing while laying. Some of the clutches included in Fig. 12 might have been similarly affected, but judging from cases in which the nest was kept under observation from before the laying of the first egg and onwards, it is unlikely that it affected more than 5% of the clutches. Three clutches had to be omitted because they disappeared before they were completed. Comparing the averages for 1959 (3.75) and 1960 (3.62), there is no significant difference between the two years; nor is there a significant difference between these averages and that of 1958 (3.40), based on a smaller and incomplete sample. (This is at variance with a statement in Delius (1963) based on an erroneous calculation.) The clutch size range of 3 to 5 eggs agrees well with published data (Witherby *et al.* 1938), but exceptional clutches of 6 and 7 eggs (Brown 1945, Wörner 1931) have been reported.

Fig. 13 shows that the clutch size does not remain constant throughout the breeding season, but that after remaining constant initially it increases steadily and then drops steeply at the end of the season. Haun (1931) and Kalitsch (1930) report similar findings in German Skylark populations. While the increase is certainly significant, the later drop is based on a few clutches and is not significant. A closer analysis reveals that the

FIGURE 13. Seasonal clutch size variations and variations between successive clutches of Skylarks *Alauda arvensis*. Each circle gives the average size of the clutches begun in a 10-day period, these periods shifting by 5 days. Each point gives the average size of early and late first-, second- and third-clutches respectively. The figures indicate the number of clutches on which the averages were calculated.

increase is due to a difference in the size of the successive clutches of any one female in any one year (Table 2). The difference in size of first and second clutches is significant with $p < 0.001$ (χ^2), while the difference between second and third clutches is not significant. There are not enough data for fourth clutches to make a reliable comparison. Subdividing the groups of first, second and third clutches according to the laying dates into early and late, there is no significant difference between early and late clutches in any of the clutch groups (Table 3). Also the size of the successive clutches remains surprisingly constant from year to year (Table 4); none of the differences between the years are significant.

Since it was thought that each female might lay clutches of individually characteristic size an analysis of variance was made. For this one source of variance, the different size of subsequent clutches discussed above was allowed for and the resulting data then transformed to obtain normality by means of a square root transformation. The analysis then showed that the variation within individuals was less than the variation between individuals (F-test, $p < 0.005$), thus confirming that individual clutch size did in fact occur in the Skylark, as it does also for example in the Blackbird *Turdus merula* (Snow 1958) and Pied Flycatcher *Ficedula hypoleuca* (Curio 1959).

There is no significant difference in clutch size between one-year-old and older birds (Table 5), though age differences of this kind are known in other birds (Curio 1959). Further, by comparing the average clutch size of 19 females in successive years, I found that there was no systematic change in this average with increasing age.

An examination of the data for a possible influence of the male on the clutch size of the female was inconclusive.

The possibility that clutch size is affected by the site-attachment of the females was then examined. Changes in average clutch size in successive years of females which had kept the same territory throughout were compared with those of females which had changed territory from one year to the other. While there was no significant difference in the means, the scatter of the two groups was different, being larger in the females which

TABLE 2. *Difference in size of first, second and third Skylark Alauda arvensis clutches.*

Clutch size	First clutch	Second clutch	Third clutch
3	35	6	1
4	13	21	16
5	0	1	2
Average	3.3	3.8	4.0

TABLE 3. *Difference in size of first, second and third Skylark Alauda arvensis clutches in relation to laying date.*

Clutch size	First clutch		Second clutch		Third clutch	
	laid early	laid late	laid early	laid late	laid early	laid late
3	26	16	4	3	1	1
4	11	8	16	7	8	8
5	0	0	0	1	2	9
Average	3.3	3.3	3.8	3.8	4.1	3.9

TABLE 4. *Difference in size of first, second and third Skylark Alauda arvensis clutches in different years.*

Clutch size	First clutch			Second clutch		Third clutch	
	1959	1960	1961	1959	1960	1959	1960
3	10	13	12	1	5	0	1
4	4	5	4	11	10	8	8
5	0	0	0	0	1	2	0
Average	3.3	3.3	3.3	3.9	3.7	4.2	3.9

TABLE 5. *Comparison of clutch size of one-year-old and older female Skylarks Alauda arvensis.*

Clutch size	Clutches laid by	
	one-year-old females	older females
3	11	20
4	11	18
5	0	2
Average	3.50	3.55

changed territories. This was tested by comparing the changes in the two groups, disregarding whether they were increases or decreases (Fig. 14). The significance is $p < 0.02$ (Mann Whitney), suggesting that changes of territory cause an increased variability in the clutch size of individual females. It would be interesting to know whether particular territories consistently affect the clutch size in the same way by either increasing or decreasing it, but I have insufficient data to examine this.

In Table 6 I have compared the clutch sizes of four European populations of Skylarks, namely from Ravenglass, from France (Labitte 1957), from Germany (Haun 1931) and from Estonia (Randla 1963). The overall differences are significant (χ^2 , $p < 0.01$). The

averages seem to indicate that the clutch size increases from northwest to southeast. If this cline is a real one, it would be similar to that found in a number of other birds (see Lack 1954). The effect does not seem to be due to uneven sampling over the season; splitting the data into successive months and comparing the monthly average clutch sizes gives the same picture.

FIGURE 14. Variation in yearly average clutch size in two successive years for female Skylarks *Alauda arvensis*, which kept the same territory (a) and females which changed it (b). There is greater variation in those which changed territories. The individual clutches were corrected for the effect of successive clutches.

TABLE 6. *Geographical variation of clutch size in the Skylark Alauda arvensis.*

Clutch size	England	France	Germany	Estonia
3	33	27	17	8
4	51	52	28	21
5	5	6	10	7
Average	3.69	3.75	3.87	3.97

Clutch size does not seem to be affected by air temperature judging from the results of a number of different analyses relating air temperature to clutch size. The clutch size of replacement clutches is not affected by the stage at which the previous clutch was lost (see above).

As to the determination of the clutch size (Eisner 1961), my experiences—three clutches which remained incomplete after the removal of the first egg and the inability to suppress laying by putting eggs into two nests before laying started—are in contradiction to that of Chappel (1948) who induced a Skylark to lay ten eggs by repeatedly removing the fourth egg of the clutch.

With reference to the adaptiveness of the clutch size, I did two experiments in which I added two eggs to clutches of four. Although they all hatched normally, only five young survived in each case. The sixth chicks were continuously being trampled under by the others due to lack of space in the nest and were consequently underfed.

EGG SIZE

In the course of two breeding seasons I took the measurements of 21 clutches. There is a good deal of variation in the shape of the eggs as shown by the rather low correlation between egg width and egg length ($r = +0.51$, Fig. 15); and indeed, even eggs of the same measurements can differ in shape. There is also a large variation in the colour of eggs, not only in the intensity but also in the patterning.

FIGURE 15. Correlation graph for length and width of Skylark *Alauda arvensis* eggs. Straight lines are the regression lines.

An analysis of variance of measurements showed that any given female tended consistently to lay eggs of similar size (F test, width: $p < 0.005$; length: $p < 0.01$) and that eggs of the same clutch tended to be even more similar among themselves (F test, width: $p < 0.005$; length: $p < 0.01$). The same must have been true for colouration although this was only obvious in one exceptional case in which a female consistently laid particularly pale eggs, the degree of paleness being more uniform in eggs of any one clutch. Within a clutch there is a tendency for egg width to increase, by 0.2 mm. on average, with successive eggs (Sign-test, binomial, $p < 0.05$), probably due to a widening of the uterus or shell-gland of the female during egg formation; but there is no increase from clutch to clutch. No such effect can be traced in the egg length (compare Preston & Preston 1953).

CLUTCH AND BROOD MORTALITY

As would be expected in a ground nesting bird with an open nest, Skylarks have a strikingly high clutch and brood mortality. To assess this mortality, the fate of practically all clutches of 17 females was followed up during two seasons. This was relatively simple when eggs and nestlings were involved, but once the chicks had left the nest the task was much more difficult. The technique was to observe the feeding behaviour of the parents and infer from that the number of young still alive, but the method is very time consuming and it can, at best, yield only approximate results.

TABLE 7. Annual variation in survival rate and clutch sizes in the Skylark *Alauda arvensis*.

Year	Clutch size	Eggs laid	% eggs hatched	Young leaving nest % of eggs laid
1959	{ 3	39	77	61
	{ 4	104	72	56
1960	{ 3	54	55	28
	{ 4	76	71	42
Total	{ 3	93	64	32
	{ 4	180	72	50

EGG LOSSES

From a total of 319* eggs laid, 216† hatched, i.e. 68% (69% in 1959, 66% in 1960; less reliable data for 1958 gives 80%). Of the remaining 103 eggs, five did not hatch because of slight damage to the shell, such as cracks and small holes, produced by the females leaving the nest precipitately in fright; four were infertile or their development was arrested by unknown causes; four were abandoned by the female, three because the female was caught for ringing too early in the incubation period, and one after all the other eggs of the clutch had been robbed; four were covered by sand in a gale. The other 86 eggs which did not hatch disappeared without known cause, but from the fact that whole clutches disappeared at once, and from circumstantial evidence one can safely conclude that the vast majority of them were lost through predation. In about half the cases the nest-lining had been pulled out and from observations on the feeding habits of Carrion Crows *Corvus corone* it is probable that they were the predators involved; the study area was one of their regular feeding grounds. The nests in which the nest material had been left undisturbed probably had been robbed mainly by Hedgehogs *Erinaceus europaeus* judging from the number of cases in which their tracks lead up to the robbed nests, and possibly also Weasels *Mustela nivalis*, Stoats *M. erminia*, Foxes *Vulpes vulpes*, shrews *Sorex* spp., fieldmice (Murinae) and voles (Microtinae). Predation accounted for some 85% of the egg losses.

Cold weather and rain did not seem to affect egg survival, even if the incubating female was kept off the nest for quite long periods because of trapping and ringing. Rain did not produce flooding in the sandy soil of the study area, but this might be an important factor in other habitats.

BROOD LOSSES

Of the 215† young which hatched, 144 left the nest, i.e. 67% (73% in 1959, 59% in 1960—difference not significant; less reliable data for 1958 gives 80%). Of the 71 chicks which died before leaving the nest, one died due to an eye-tumour, two due to under-nourishment caused by the disappearance of the male during their first days of life, and three because they were trodden on by man. The remaining 65 nestlings disappeared under similar circumstances to the eggs. Hedgehog teethmarks were found on rings of some of the dead young, but the condition of the robbed nests indicated that Carrion Crows were again responsible for about half the losses. Predation accounted for some 90% of the losses.

The degree of cold and rain resistance of the nestlings was similar to that of the eggs. I found no signs of food deprivation in any of the young of this sample (except in the desertion case) nor in any of the further 150 or so which I saw in the course of the whole six years. With the exception of the tumour I did not detect any diseases. Pätzold (1963) mentions parasites attacking young Skylarks and also quotes a case in which a brood died of heat. He also discussed the risk for clutches and broods arising from agricultural work.

BREEDING SUCCESS

From 312* eggs laid, 144 young left the nest, i.e. 46% (52% in 1959 and 39% in 1960—differences not significant). This compares with 47% which Pickwell (1931) found for the Horned Lark *Otocoris alpestris*, and 48% which Coulson (1956) found for the Meadow Pipit *Anthus pratensis*. As all the eggs or nestlings of a clutch or brood were

Note. * † Apparent disagreement in these numbers is due to the fact that the fate of a few nests could not be followed up through all phases.

almost always taken from a nest at once and not singly, it is not surprising that the average number of eggs per clutch (3.55) is not very different from that of hatched nestlings per nest (3.60), nor from the average number of nest-leaving young per nest (3.50). The apparent contradiction in the number of hatchlings being larger than that of the eggs per nest is due to differences in egg mortality in the different sizes of clutches.

A comparison of c/3 and c/4 (I have not enough data for c/5) reveals a striking difference: only 32% of the eggs laid produced nest-leaving young in c/3 compared with 50% in c/4 (Table 7). However, the difference is entirely due to the 1960 season when there was increased mortality (increased loss) at the beginning of the season, and, as 3-egg clutches are more common early in the season they were more affected. The increased mortality was undoubtedly due to predation tests which were being carried out in the study area in the early spring of 1960 (Tinbergen *et al.* 1962). Carrion Crows were the predators involved in the tests and it was obvious from my own observations that the crows became conditioned to the area and preferentially searched for food there. Under normal conditions I would expect that there would be no difference between c/3 and c/4 in nest-mortality and in fact in 1959 there was no significant difference.

The above incidental observation suggests a mechanism for density-dependent nest mortality. In the tests mentioned, hens' eggs were laid in a scattered fashion over the study area, and it can be imagined that a similar increased risk from predators would result from an increased number of Skylark nests in the area.

A clearcut difference in nest mortality is found between one-year-old and older females. The older birds hatched 97% of their eggs and 51% of their eggs produced young of nest-leaving age, while the corresponding figures for the one-year-old birds are 42% and 15% respectively. In the statistical comparison of old and young birds the fact that the mortality of an egg or a nestling is not independent of that of other members of the clutch or brood was taken into account, and the difference in success of raising nest-leaving young is then significant at $p \approx 0.03$ (Mann Whitney). I could not find any consistent seasonal differences in nest mortality, nor could I find a consistent difference between first, second and third clutches; but the data are difficult to interpret in this respect because of the predation experiment described above. The degree of site-tenacity and faithfulness of the pair did not affect success, nor did the age of the males, even though they take part in the feeding of the nestlings. I can find no consistent individual differences in success among females.

In Fig. 16 I have plotted cumulatively the daily disappearance of 88 clutches during the laying, incubation and nestling periods, and similarly, the fate of the broods after leaving the nest on the eighth day of life judged by whether or not the parents showed feeding behaviour. The interpretation of this last part of the graph is difficult because it has to be considered that the losses of the different young from a brood are more or less independent of one another, and that the parents only stop feeding when all the young have disappeared. I had time in only a few cases to record regularly how many young were being fed. On the other hand, the feeding behaviour of the parents becomes rather intermittent as the number of young decreases and their age increases. Without doubt, I have plotted some broods as lost before the last young had in fact died. The two sources of error tend to cancel each other out to some extent, but nonetheless this method of estimating mortality is rather crude, and beyond the 25th day of life of the young it becomes completely useless because the young start to become independent. There is an interesting kink in the curve on the 16th day (Fig. 16), which probably correlates with the fact that at that age the young start to fly and this probably reduces their mortality rate. If the graph is taken as reliable 25% of young survive to flying age and 10% reach independence.

It is no more easy to estimate the causes of mortality of the young once they leave the nest, than the mortality rate itself. There is some circumstantial evidence that crows

FIGURE 16. Survival of 88 clutches and broods of the Skylark *Alauda arvensis*. The line gives the number of clutches or broods still alive at the different stages of incubation and parental care.

continue to take young as long as they are unable to fly, but I am not sure what part the Hedgehogs play at this stage. Weasels seem to play a greater part in predation once the young leave the nest, but again the evidence is only circumstantial.

SITE-TENACITY AND MATE-FAITHFULNESS

Site-tenacity is important in two respects in the context of this paper. Together with agonistic behaviour it is an essential element of territorial behaviour, which I shall discuss under Territoriality; and its existence makes it possible to assess mortality rates of adult Skylarks, as discussed further on. Site-tenacity is widespread among birds and has been recorded for Skylarks (Makowski 1953) and for Woodlarks *Lullula arborea* (Koch 1936, Koffan 1948/51).

Site-tenacity was measured here by noting the distance between the centres of the territories of the same individuals in successive years. For this part of the work an area around and up to 1.5 km. from the centre of the study area was checked for ringed birds, in parts of which there were Skylark populations of similar size to the one studied. Fig. 17 gives the distribution of these distances for 55 males and 64 females, and shows that there is a strong tendency for Skylarks to return to the same area from year to year. Observations showed that returning birds almost always try to settle in the territory of the year before. Thus site-tenacity would be even greater if returning birds always found their previous territory unoccupied, either by one-year-old settlers or birds which had settled there having themselves been displaced from their previous territory.

The difference in the settling distance (Fig. 17) of males and females is significant (χ^2 , $p < 0.01$), and may be explained by the fact that a returning female not only may find her previous territory occupied by another female, but even when it is not, she still has to come to terms with the male in the territory, for males regularly return earlier than females. That this is not always easy for the female was made apparent in two closely observed cases, in which the females were eventually rejected.

FIGURE 17. Distances between the centres of the two territories which individual Skylarks *Alauda arvensis* held in any two successive years. The frequency of occurrence of the different distances is plotted separately for males and females in percentages of the total number of cases recorded. Data from 7 years.

There were large and significant, as well as unexplained, differences in site-tenacity of the population as a whole from year to year, but they did not affect males and females consistently in the same way. I was unable to detect any consistency in the site-tenacity of individuals. Breeding success of the previous year does not affect the site-tenacity of males or females (but see below). No changes in site-tenacity were found with increasing age.

During the breeding season site-tenacity is even more pronounced than that observed from one season to the next. Of about 100 cases in which territory-owners were observed over three months of the breeding season, only one female changed territory (after having been trapped on the nest too early in the incubation period), some 10 or 15 birds shifted their territory boundaries slightly, and a further three abandoned their territories in the course of the season, probably because they remained unmated.

It is not only adult Skylarks that show site-tenacity, for one-year-old birds also have the tendency to return to the region of their birthplace. Of the 171 nestlings that I ringed, about 25 (15%) should still have been alive in the following year (see later). In fact 15 birds were seen in the study area and the additional surrounding region, nine of these in the study area itself. Only six of these took up territories in the study area, and a further four had territories in the surrounding area; the remainder wandered in the general area as non-breeders.

Associated with site-tenacity is mate-faithfulness. Of 36 pairs, the members of which were alive for over two years, 17 (47%) remained faithful to each other. One pair remained faithful over four seasons and another over three seasons. In all cases mate-faithfulness was coupled with site-tenacity, but in five cases the pairs shifted the borders of their territory to some extent after they had paired up. In two closely observed cases, the females visited, but did not pair up with their males of the previous year, which had changed territories but were still unpaired. There might have been many more such cases which passed unobserved. All this seems to suggest that mate-faithfulness depends on site-tenacity. However, there is also evidence that mate-faithfulness affects site-tenacity. This is borne out by examining the location of the territories in a given year of males and females which in the previous year were the partners of a pair, and therefore also shared a territory. For the understanding of what follows it is necessary to remember

that the females arrive in the study area after the males are already established. Let us first consider (*a*) those 20 cases in which the males stay settled in the same territory as in the previous year. We find that 12 (60%) of the female ex-partners settled in the same territory they held in the previous year, and consequently paired with the same partners. The other 8 (40%) settled elsewhere and therefore paired with new males. Now we consider (*b*) those 16 cases in which the males changed territories and we find that only 3 (19%) of their female ex-partners returned to the territories of the previous year, and they of course paired with new males, and that all the other 13 (81%) settled in territories other than those of the previous year; but since they never in fact settled in the same territories as their male ex-partners had done, they also always paired with new males. The difference in the site-tenacity of the females of the two groups is significant (χ^2 , $p \approx 0.02$). On this basis one would conclude that for the females the attractiveness of their previous year's territory is diminished if they do not find their previous male partner established there. However, if we now consider (*c*) the location of the territories of the females whose male partners of the previous year had meantime died (by the criteria used in the section "Mortality") we find that of 25 cases, 14 (56%) settled in the territory of the year before now occupied by a new male, while the other 11 (44%) settled elsewhere. Statistical comparison shows a difference in the site-tenacity of the females of group *c* and group *b* (χ^2 , $p \approx 0.02$), but there is no difference between group *c* and group *a*. The explanation indicated above obviously does not cope with this since it would predict that group *c* and group *b* would not be different. It now seems that only the males who have changed territories (*b*) exert an influence on their female partners of the previous year when they return by making them also abandon the territory of the previous year but not in such a way as to attract them to the mates' new territories (the females never settled in these) but just by making them move elsewhere. A tentative explanation for this might be that the females in such situations vacillate between old territory and old male and eventually miss both because other females have taken the places and partners, forcing them to settle elsewhere.

There is a striking correlation between the breeding success of a pair in a given year and the likelihood of its remaining a pair in the following year. Twenty pairs were divided into two equal groups according to their breeding success in a given year, measured in terms of percentage eggs laid producing nest-leaving young: one group with above median breeding success the other with below median breeding success. In the following year out of the first group nine pairs remained faithful and one broke up, while out of the second group only two pairs remained faithful and the other eight broke up. The difference between the two groups is significant (Fisher's Exact Test, $p < 0.01$). Remembering that mate-faithfulness is associated with site-tenacity, it is surprising that breeding success, as mentioned previously, does not seem to have an effect on site-tenacity. However, the effect may in fact have been masked in the data used here because the pairs of birds which could have exhibited the phenomenon just described were in a minority. If one only considers the site-tenacity of only those Skylarks which were used in the analysis of the effect of breeding success on mate-faithfulness, then breeding success is shown to affect site-tenacity as well. But it seems that the primary effect of breeding success differences is to change the degree of mate-faithfulness and only secondarily that of site-tenacity; otherwise, whatever the samples used, they would show an effect of breeding success on site-tenacity.

There are great fluctuations in the proportion of faithful to non-faithful pairs from year to year, but no adequate explanation could be found for this. No difference was found in comparing the faithfulness of old and young birds, but there were few data for such an analysis. It is worth mentioning that new settlers in the study area, probably one-year-olds, did not show any particular preference either for old birds or for other new settlers when pairing up. I could not find any consistency in the tendency to mate-

faithfulness in individual Skylarks. During the breeding season all but one of the 49 pairs stayed together, the exception being the female, already mentioned, caught too early on the nest.

MORTALITY OF ADULTS AND JUVENILES

Examination of Fig. 17 shows that due to the high site-tenacity exhibited by the Skylarks the probability of a breeding bird from the study area returning to and settling in an area outside the study area is extremely low (less than 1%) unless we assume a non-monotonic distribution, an assumption for which there are no good reasons. It is therefore justified to equate the non-return rate of birds with their mortality rate.

Of 200 Skylarks alive on any 1 May of one year, 133 were still alive on the following 1 May, while 67 did not return. The figures therefore give a mean annual mortality rate of 33.5%.

TABLE 8. *Mortality of adult Skylarks Alauda arvensis in different years.*

	1958/59	1959/60	1960/61	1961/62	1962/63	1963/64
Birds alive on 1 May of first year	20	41	42	41	34	22
Birds alive on 1 May of next year	14	29	29	28	18	15
Birds missing on 1 May of next year	6	12	13	13	16	7
Mortality	30%	29%	31%	32%	47%	32%

The mortality rate varied little from year to year except in 1962/63 (Table 8). It seems likely that the higher mortality in that year was due to the unusually cold winter (Dobinson & Richards 1964, compare Jourdain & Witherby 1918). A comparison of the 1962/63 period with all the other years taken together gives a significant difference in the mortality rate (χ^2 , $p < 0.05$). There is a difference in the mortality rate of males (30%) and females (38%), but it is far from significant. The mortality rate does not change with the age of the Skylark, once it has reached its first year, at least not over the age range examined (1–5 years).

I made a rather limited comparison of the mortality during the three months of the breeding season with that during the other nine months. Eighty birds were observed closely for three months, during which 76 remained alive and 4 died. This gives a trimestral mortality of 5%, which approximates to a yearly mortality of 20%. If a small sample can at all be relied upon, this suggests a seasonal fluctuation in the mortality rate, in that during the other nine months of the year the mortality must be higher in order to make up the annual mortality rate of 33.5%. In fact, it is probable that this increased mortality occurs during the two or three winter months, as the high mortality in 1962/63 seems to suggest.

Accepting that the average yearly mortality of adult Skylarks was 30% (omitting the unusual period 1962/63), the mean further life expectancy works out at 2.8 years (for comparison with other species see Lack 1954). Assuming also that the population remained constant (which seems to be approximately true for the population studied) and that the adults dying were replaced by an equal number of one-year-old birds each breeding season, the average age of the breeding population is calculated as 3.3 years.

It is less easy to assess the mortality of Skylarks during their first year of life. Again assuming that the population remains constant, although it could be that either emigration to or immigration from surrounding areas kept the numbers unchanged, let us consider a population of 100 Skylarks. Ninety are breeding birds, since some 10% remain non-breeders (see later). Each of the 45 females lays an average of 2.7 clutches per year with an average of 3.69 eggs. Therefore each female lays an average of 10 eggs per year, so

that 45 females would lay 450 eggs. Of these eggs 46% (207) produce young of nest-leaving age, of which 10% (45) reach independence (some 30 days after hatching). By the next year 30% of the adults of the population have died and they have to be replaced by 30 one-year-olds; so that a further 15 young have to die in the 10½ months between becoming independent and replacing the adults. If we consider a Skylark is born when the egg is laid, then the mortality during the first year of life is 93%; if we consider it born with hatching, the mortality rate is 90%; and finally if we consider the mortality of the young after they have become independent, it is 33%, or 38% if allowance is made for the 1½ months from laying to independence. This figure is still slightly higher than that of adult Skylarks. The graphical integration of the above figures (Fig. 18), gives the "life expectancy" of an egg as 3½ months, and of a newly-hatched young as 5 months. For comparison, wild Skylarks are known to have reached the age of 6 years (own data, several individuals), and 7 years (Burckhardt 1957); and caged birds 10 years (de Radigues 1939) and 12 years (Weber 1956).

FIGURE 18. Survival of Skylarks *Alauda arvensis*. Points give the percentage of birds still alive at the different stages of life. The figures were arrived at by different methods which are described in the text.

I have direct evidence for only two sources of mortality of adult Skylarks, Merlins *Falco columbarius*, which in my population caught three birds, and Weasels which caught one. I did not observe any disease or injury except two or three cases in which Skylarks limped for one or two months but were not seriously hampered, one case of a drooping wing, which the bird survived with for at least two years, one case of a one-eyed bird which was observed over one month and one case of a bird unable to fly for unknown reasons, and which disappeared the following day. In one case a bird strained its wing while being trapped and was unable to fly; released in its territory just after the accident it survived and recovered in one week. I did not observe any case in which birds damaged each other in intra-specific fights (Darling (1950) reports this for the Horned Lark). During the periods of observation there was certainly no food shortage. (See Pätzold 1963 for a detailed discussion of the causes of mortality.)

TERRITORIALITY

Skylarks display well developed territorial behaviour. Site-tenacity during the breeding season has already been discussed and details of agonistic behaviour are given by Delius (1963). The reader is also referred to Tinbergen (1957) whose argumentation I follow closely.

The number of pairs in the study area hardly varied: about 21 in 1958, 20 in 1959, 21 in 1960, 21 in 1961, 22 in 1962. There is little doubt that territorial behaviour limited the number of birds breeding (Fig. 19). This was shown particularly by observations of birds or pairs of birds trying to settle in the area after the number already settled had reached or approached the figures given. Fights with these newcomers were intense and intruders were regularly fought not only by nearby territory owners but also by larks from further afield. Newcomers elicited the same behaviour even late in the season when hostility was otherwise declining. That this behaviour deterred a good proportion of newcomers from settling was obvious. The argument that such newcomers might not have settled anyway, even if they had not been molested is difficult to counter, but in one case at least, such a pair was observed to settle elsewhere in the neighbourhood.

This last observation leads to the question whether territoriality merely ensured dispersal with its obvious advantages, such as lessening density-dependent predation, avoiding food shortage, "overgrazing" of food sources, etc.; or whether, in fact, it also

FIGURE 19. Territories of Skylarks *Alauda arvensis* in the study area in 1960 to show the limiting effect of territories on the population density. Thick lines: coast at spring tide; thin lines: approximate contours; spaces between territories represent disputed areas. Territories with broken boundaries were only held temporarily. Numbers denominate the individually marked birds.

played a role in the actual regulation of breeding numbers. To answer such a question it is necessary to find out what happens to birds which do not manage to settle in the area considered. If all settle elsewhere as the pair mentioned above, then the only effect of the territorial behaviour is an even and wider dispersal; but there is good evidence that the case observed was not a typical one in the population studied. Most birds which did not manage to settle did not move away, but tended to remain in the study area and its closer surroundings constituting the non-territorial non-breeding population. I estimated this at some 10% of the total population, but it is difficult to be at all exact because of the mobility of non-breeding birds.

The non-breeding population consisted mainly of birds which did not possess a territory and which wandered over an apparently large area. Occasionally there were pairs which did not breed though they had territories, or, more often, males which had territories but failed to get females; but even these birds gave up their territory in the course of the season and became non-territorial non-breeders. Males seemed to predominate in this population but their behaviour is more conspicuous than that of the females, and the sex-ratio estimate may have been biased. On the other hand this may support the earlier evidence of a higher mortality rate for females. That the members of the non-breeding population were not inherently unable to breed was shown by a number of cases in which males of this group successfully replaced breeding males which had disappeared. A similar case was recorded for a female.

The age structure of this non-breeding population was difficult to assess. Most of its members were unringed, i.e. came from neighbouring populations and so there was no way of estimating their ages. However, I suspect that it was composed mainly of one-year-old birds, for I observed only one older bird (which had already bred) among the non-breeding population, compared with four one-year-old birds which had been ringed as chicks the year before. The predominance of the one-year-olds must be even greater than the figures reflect since, due to their weak site-tenacity, they are less likely to be observed in the area than adults with their strong site-tenacity (compare Wynne-Edwards 1962).

The fact that birds unsuccessful in establishing territories in the study area did not settle elsewhere might be due to one, or a combination, of several factors, for all of which I have incidental evidence. They might have been unsuccessful wherever else they tried to settle; habitat conditions may not have been suitable in surrounding areas and this may have deterred them; the attraction to available places may have been outweighed by their site-tenacity, either in relation to their birthplace or previous territory; and finally, alternative territories may have lacked the attraction of other Skylarks settled nearby. The last factor amounts to a tendency to clump, i.e. to form colonies (cf. Patterson 1965). Thus, the Skylark's territorial behaviour in conjunction with the other factors mentioned seems to be a powerful density regulating mechanism, which can, when the population reaches or approaches a maximum density, exclude a proportion of birds from breeding and therefore can adjust the reproductive rate of the population as a whole.

In an adjacent area, in contrast with the study area, the main factor holding numbers down seemed to be the unsuitability of the habitat, which deterred Skylarks from settling there. It is also possible that the population had too low a reproductive rate and an immigration rate too low to compensate for losses. The territories were about three times the size (15,000 sq. m.) of those in the study area, but there is evidence that here territory size was passively adjusted to density and not actively regulating it. In other words, I believe that territoriality increasingly checks density as this becomes higher (Huxley 1934).

In the 1963 breeding season the number of Skylarks in the study area, 16 pairs, and in the neighbouring areas, was lower than normal, probably as a result of the high mortality during the previous hard winter. The average territory size was somewhat larger than

usual but it was striking that there seemed to be no non-breeding birds around, suggesting that there was now space for them. It is obvious that in this way the population was making use of its maximum reproductive rate.

Territorial behaviour can also affect population numbers without the existence of a non-breeding population. If all birds which cannot settle because of territoriality in the area they stem from find elsewhere to settle, then, in the case of an increasing population, at some point these emigrants will have to start settling in sub-optimal habitats in which breeding success will consequently be low. As the population continues to increase an increasing proportion of it will have a low reproductive rate and this will in turn check the total numbers of the population. It is clear that the two mechanisms by which territoriality can regulate numbers, although different, can operate simultaneously in any given population. However, due to the lack of pertinent information it is not clear if the last mentioned mechanism does play a role in the Skylark population studied.

Finally, both mechanisms might not only affect the reproductive rate but also the survival of the adult birds themselves. The restless behaviour of the non-breeding population, arising from the fact that they are chased continuously by territory-holding birds, may produce the so-called Selye stress syndrome (Barnett 1958), with an increased mortality rate in both breeding and non-breeding individuals. The emigration to sub-optimal habitats may also affect the mortality rate of adults due, for example, to lack of adequate food or to insufficient cover from predators, etc., two factors which might besides also affect the non-breeding birds (cf. Jenkins, Watson & Miller 1963).

ACKNOWLEDGMENTS

I wish to thank Dr. N. Tinbergen, F.R.S., for supervision in this work, Prof. G. Birukow for seconding it, my colleagues in the Ravenglass camp for help and discussion in many matters, my wife for painstaking statistical calculations, Dr. J. M. Cullen for criticising the draft, Mrs. J. McFarland for preparing the manuscript and drawings, Sir W. Pennington Ramsden Bart. and the Cumberland County Council for permission to work in Ravenglass, Prof. G. Birukow, Göttingen, and Prof. J. W. S. Pringle, F.R.S., Oxford, for providing facilities in their departments and the Deutscher Akademischer Austauschdienst for a grant. Part of my equipment was supplied from funds which the Nuffield Foundation and the Nature Conservancy had put at Dr. Tinbergen's disposal.

SUMMARY

A population of colour-ringed Skylarks *Alauda arvensis* was studied intensely over two and less thoroughly over another five breeding seasons in Ravenglass, Cumberland.

The breeding season extends from mid-April to early July, but the onset, which is well synchronized, varies from year to year, probably depending on the spring temperature. One-year-olds lay the first clutch about a week later than older birds. Within a group of females there is a constancy in the laying order of first clutches from year to year. The rank of any given female seems to depend on an individual temperature threshold, which is reached four to seven days before laying, but other factors must play a role. The interval between the disappearance of a clutch or brood and the laying of the next clutch varies from four to six days depending on the stage at which the previous brood was lost. Beyond the 17th or 18th day of life the chicks of one brood no longer prevent the laying of a new clutch. No factors influencing the end of the season could be found. On average, Skylarks lay 2.7 clutches per year (range 1-5). Three successful broods seems to be the maximum.

Average c/sizes are 3.69 eggs (range 3-5). The c/sizes vary with successive clutches, from 3.3 for first, to 4.0 for third clutches. Individual females tend to lay clutches of a characteristic size. No difference could be found between the clutches of one-year and older birds. Females which retain the same territory from year to year show more consistency in clutch size than those which change territories. Data from different geographical locations in Europe suggest a cline from northwest to southeast of increasing clutch size. Clutch size does not seem to be affected by temperature. The variability of egg size and shape is discussed.

68% of the eggs laid hatched (incubation period 11 days) and 67% of the young hatched left the nest on the 8th day. About 90% of the eggs and young lost were taken by predators. No consistent seasonal differences in nest mortality could be found, nor between c/3 and c/4. An incidental experiment suggests that predation of Skylark nests is density dependent. The success of one-year-old females in rearing nest-leaving young is lower than that of older birds (15% compared with 51%). From observations of the feeding behaviour of the parents it is estimated that about 25% of the young survived to flying age (16th day of life), and about 10% reached independence (30th day).

Skylarks, males more than females, exhibit a strong site-tenacity. One-year-old birds tend to return to the birthplace area. Associated with site-tenacity the Skylarks show mate-faithfulness.

Of 36 pairs 17 remained faithful from one year to the next. During a breeding season mate-faithfulness is practically absolute. There is a correlation between the breeding success of a pair and the likelihood of the pair remaining together the following year.

Mean annual adult mortality was 33.5%, with little variation except in 1962/63 (47%—the result of a hard winter). After reaching independence, the first-year mortality of juveniles was estimated to be 38%, on the assumption that the population remains constant in numbers. The average "life-expectancy" of a newly laid egg is about 3½ months and that of a newly hatched young about 5 months. The mortality sources for adult Skylarks are briefly discussed.

Skylarks have a well-developed territorial behaviour which is an important mechanism in regulating the maximum breeding density. In conjunction with site-tenacity, habitat preferences and social attraction, it is capable of regulating the reproductive rate of the total population by excluding a proportion of birds from breeding when the population numbers are high.

REFERENCES

- BARNETT, S. A. 1958. Physiological effects of social stress in wild rats. *J. Psychosomat. Res.* 3: 1–11.
- BROWN, R. H. 1945. Large clutches of Skylark, Meadow Pipit and Yellow Bunting. *Brit. Birds* 39: 53.
- BURCKHARDT, D. 1957. Hohes Alter einer beringten Feldlerche. *Orn. Beob.* 45: 174.
- CHAPPEL, B. 1948. The dissimilar egg and other problems. *Ool. Rec.* 22: 1–6.
- COULSON, J. C. 1956. Mortality and egg production of the Meadow Pipit with special reference to altitude. *Bird Study* 3: 119–132.
- CURIO, E. 1959. Beiträge zur Populationsökologie des Trauerschnäppers (*Ficedula h. hypoleuca* Pallas). *Zool. Jahrb. Syst.* 87: 185–230.
- DARLING, G. 1950. Death of a Horned Lark in territorial combat. *Wilson Bull.* 62: 134.
- DELIUS, J. D. 1963. Das Verhalten der Feldlerche. *Z. Tierpsychol.* 20: 297–348.
- DOBINSON, H. M. & RICHARDS, A. J. The effect of the severe winter of 1962/63 on birds in Britain. *Brit. Birds* 57: 373–434.
- EISNER, E. 1960. The relationship of hormones to the reproductive behaviour of birds referring especially to parental behaviour. *Anim. Behav.* 8: 155–179.
- FARNER, D. S. 1964. The photoperiodic control of reproductive cycles in birds. *Amer. Scientist* 52: 137–156.
- GOODACRE, M. J. & LACK, D. 1959. Early breeding in 1957. *Brit. Birds* 52: 75–83.
- HACHISUUKA, K. 1924. Notes on birds collected in Egypt. *Ibis* 6: 771–773.
- HARDY, E. 1939. Skylark nesting in October in Lancashire. *Brit. Birds* 33: 198.
- HAUN, M. 1931. Statistische Untersuchungen über die Eierzahl in den Gelegen der 3 Lerchenarten (*Alauda arvensis*, *Galerida cristata*, *Lullula arborea*) sowie des Goldammers (*Emberiza citrinella*). *Z. Fortpfl. Vögel* 7: 135–138.
- HUXLEY, J. 1934. A natural experiment on the territorial instinct. *Brit. Birds* 27: 270–277.
- JENKINS, D., WATSON, A. & MILLER, G. R. 1963. Population studies on Red Grouse *Lagopus lagopus scoticus* (Lath.) in North East Scotland. *J. Anim. Ecol.* 32: 317–376.
- JOURDAIN, F. C. R. & WITHERBY, H. F. 1918. The effect of the winter of 1916–1917 on our resident birds. *Brit. Birds* 12: 26–35.
- KALITSCH, L. von. 1930. Eierzahl der Feldlerche. *Z. Fortpfl. Vögel* 6: 213.
- KENDALL, M. G. 1948. 'Rank Correlation Methods.' London: Griffin.
- KOCH, J. 1936. Eenige biologische gegevens van den boomleuwerik *Lullula arborea* (L.). *Org. Cl. Ned. Vogelk.* 9: 76–79.
- KOFFAN, K. 1948/51. Preliminary report on my studies of *Lullula arborea*. *Aquila* 55–58: 292.
- LABITTE, A. 1957. Notes biologiques sur l'alouette des champs (*Alauda arvensis* L.) dans le centre nord-ouest de la France. *L'Oiseau* 27: 59–71.
- LACK, D. 1954. 'The Natural Regulation of Animal Numbers.' Oxford: University Press.
- LEHRMAN, D. S. 1959. Hormonal responses to external stimuli in birds. *Ibis* 101: 478–496.
- MAKOWSKI, H. 1953. Notizen über Vogelalbinos. *Orn. Mitteil.* 5: 130.
- MARCHANT, S. 1952. The status of the Black-headed Gull colony at Ravenglass. *Brit. Birds* 45: 22–27.
- MARSHALL, A. J. 1961. Breeding season and migration. In 'Biology and Comparative Physiology of Birds' (Ed. A. J. Marshall) 2: 307–339. New York & London: Academic Press.
- NICE, M. M. 1937. Studies on the life history of the Song Sparrow I. *Trans. Linn. Soc. N.Y.* 4: 1–247.
- PÄTZOLD, R. 1963. Die Feldlerche (*Alauda arvensis* L.). Wittenberg: Ziemsen.
- PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. *Ibis* 107: 433–459.
- PICKWELL, G. 1931. The Prairie Horned Lark. *Trans. Acad. Sci. St. Louis.* 27: 1–153.
- PRESTON, F. W. & PRESTON, E. J. 1953. Variation of the shapes of birds eggs within the clutch. *Ann. Carn. Mus.* 33: 129–139.
- RADIGUES, X. de. 1939. L'âge d'une alouette des champs en cage. *Gerfaut* 29: 58.
- RANDLA, T. 1963. Andmed Mõningate värvuliste pesitsemise matsalu lahe Ääres. *Orn. Kogumik* 3: 69–75.
- SIEGEL, S. 1956. 'Nonparametric Statistics for the Behavioral Sciences.' New York: McGraw-Hill.
- SNOW, D. W. 1955. The abnormal breeding of birds in the winter 1953/54. *Brit. Birds* 48: 120–126.

- SNOW, D. W. 1958. The breeding of the Blackbird *Turdus merula* at Oxford. *Ibis* 100 : 1-30.
- THORBURN, N. 1954. Skylark's nest with 2 eggs in turnip field. *Field Naturalist* 1954 : 4.
- TINBERGEN, N. 1957. The functions of territory. *Bird Study* 4 : 14-28.
- TINBERGEN N., BROEKHUYSEN, G. J., FEEKES, F., HOUGHTON, J. C. W., KRUUK, H. & SZULC, E. 1962. Egg shell removal by the Black-headed Gull *Larus ridibundus* L.; a behaviour component of camouflage. *Behaviour* 19 : 74-117.
- WEBER, E. 1961. 'Grundriß der biologischen Statistik.' Jena : Fischer.
- WITHERBY, H. F. JOURDAIN F. C. R., TICEHURST, N. F. & TUCKER, B. W. 1938. 'Handbook of British Birds.' London : Witherby.
- WÖRNER, E. 1931. Große Eierzahl im letzten Brutjahr. *Z. Fortfl. Vögel* 7 : 62.
- WYNNE-EDWARDS, V. C. 1962. 'Animal Dispersion in Relation to Social Behaviour.' Edinburgh & London : Oliver & Boyd.

Dr. J. D. Delius, Department of Zoology, University Museum, Parks Road, Oxford.