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BREEDING BIOLOGY OF THE SPOTTED FLYCATCHER.*

BY

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INTRODUCTION

THE information on the breeding of the Spotted Flycatcher (*Muscicapa striata*) which is analysed in this paper has been obtained from a number of sources, the most important being the British Trust for Ornithology. Altogether some data on 548 nests were available as shown below:

Before 1939 1939 1940 1941 1942 1943 1944 1945 1946 1947 1948 1949 1950 Totals British Trust for Ornitbology

Totals		86	6	8	τO	12	26	21	26	26	77	81	100	120	# 18
Riviere (1949)								-		-			4		4
1950)	•••		_	_			I							2	3
	and														•
Lewis (1937)		3		_										_	3
1948-1950)		4	•	-			_				_	50	55	78	187
	and														
1946)	·	76	5	3	2	2	2	4	5	2	-				101
Whitaker (189	3-	-		-			<i>v</i>	•				Ĵ			Ū
(1933-50)	•••	3	I	5	8	10	23	17	21	24	17	31	41	49	250
Ornithology															

The Nest Records Scheme organised by the British Trust for Ornithology was begun in 1939 though there are a few records for earlier years; in this members of the Trust fill in a card for each nest they discover giving details of dates of laying, hatching, numbers of eggs, etc., and these are subsequently deposited at the Edward Grey Institute. By far the greatest number of Spotted Flycatcher nests recorded in this scheme have been found in gardens or near by and so have been discovered early in the nesting cycle and the subsequent operations noted in some detail. The late A. Whitaker deposited a copy of his personal records in the Edward Grey Institute, and though these include details of one hundred Spotted Flycatcher nests the information given is much less detailed and only a limited number of nest records could be used. In addition Mr. J. H. Owen has very generously supplied data on nests he has recorded in Montgomeryshire from 1948 to 1950. The other information noted above has been obtained from published literature.

Where there is any ambiguity in the data the information has not been used in the analysis. For example where there is only one visit to a nest the clutch size cannot be known with certainty; this is also the case where the nest has not been found until after the beginning of incubation or during the nestling period, as eggs or young may have disappeared prior to discovery. Again unless a visit is paid to the nest at least once per day during hatching or when the young are leaving the nest the uncertainty in the time that this occurs becomes too great. This means that the actual number * A Publication of the British Trust for Ornithology. of nests on which information is available for each of the following sections is somewhat reduced; for instance in the analysis of the breeding season 397 records have been used and in most of the other sections the number has been further reduced. The method adopted in choosing suitable data is discussed in each section with an indication of the errors that are likely to be introduced.

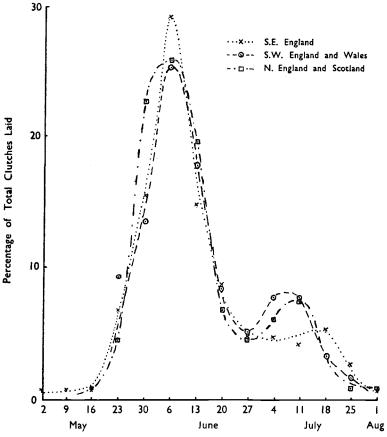
BREEDING SEASON

In the analysis of the breeding season the date of completion of the clutch has been used. The numbers of clutches completed in seven day periods from the beginning of May onwards are shown in Table I. The records have been divided into three regions :— South-east England; South-west England and Wales; and North England and Scotland, each region accounting for about one third of the records. The boundary between North and South has been chosen as the southern boundaries of Cheshire, Derby, Notts. and Lincs. and the boundary between South-east and South-west as the eastern boundaries of Warwick, Glos., Wilts. and Dorset.

			T/							
Clutch con	nplete	d	S.E.		S.W		Ν.		Tota	1
	-		clutches	%	clutches	%	clutches	%	clutches	%
April 30-May	75	.,.	I	0.7					I	0.3
May 6-12			I	0.7					I	0.3
May 13-19			I	0.7			I	o.8	2	0.5
May 20–26	•••		10	6,8	11	9.3	6	4.5	27	$6.\bar{8}$
May 27-June	2		23	15.6	16	13.5	30	22.7	69	17.4
June 3-9	•••		43	29.2	30	25.4	34	25.8	107	27.0
June 10-16	• • • •		22	14.9	21	17.8	26	19.7	69	17.4
June 17-23			13	8.8	10	8.5		6.8	32	8.0
June 24-30	•••		7	4.8	6	5.Ĭ	6	4.5	19	4.8
July 1-7	•••		7	4.8	9	7.8	8	6.1	24	6.0
July 8-14			6	4.2	9	7.8	10	7.6	25	6.3
July 15-21			8	5.4	4	3.4			12	3.2
July 22-28			4	2.7	2	1.7	I	0.8	7	1.8
July 29-Aug.	4	•••	Ĩ	0.7			I	0.8	2	0.5
Totals			147		118		132		397	

In the case of the Nest Record cards and also of records from other sources the actual date of completion of clutch is not always known. In including these data the following steps have been employed: (i) if a record is given of the incomplete clutch together with the subsequent size of the complete clutch then the date of completion has been obtained by assuming an egg-laying rate of one per day; (ii) if the date of hatching or departure of young from the nest is given then the clutch completion date has been obtained by subtracting thirteen or twenty-six days respectively; (iii) in cases where the nest was found with eggs or young but no information is available about hatching or time of leaving nest then the completion date has been obtained by subtracting six or nineteen days respectively from the date of finding, though where some indication of the state of incubation or age of young is given this

has been taken into account. The estimated dates are probably correct to within a day or two and as seven day totals are used in the table very little error is introduced in this way, which eliminates personal bias towards any period. The information in Table I is shown graphically in Figure I:



Two interesting points emerge from this :

(i) The curves from the different regions are all bimodal; the first peak occurs during June 3rd-9th, 25-30% of all nests being completed at this time. The second peak is much less marked and occurs during the first half of July. This shows that while the Spotted Flycatcher may be double-brooded in Britain this probably only occurs with about 20% of pairs. It should however, be pointed out that the enthusiasm for nest finding is greatest early in the season and thus a smaller proportion of late than of early nests may be recorded. About 50% of all clutches are laid

between May 27th and June 16th.

(ii) There is no evidence to show that there is any difference in the breeding season between the different regions of the country selected (except possibly that a very few nests may occur in the South-east region in early May before nests are found in the West and North). This is not surprising with such a late arrival as the Spotted Flycatcher; conditions cannot be much less favourable in the North than in the South by the time that breeding begins.

The Spotted Flycatcher seems to be very susceptible to adverse weather conditions (Ryves & Ryves, 1950) and it would be interesting to see if this would show in the records for any one year; unfortunately there are, as yet, insufficient data to test this point. The rather flatter first peak for the North region suggests a high proportion of repeat clutches and this may be due possibly to desertion caused by adverse weather conditions which are more probable in the North at the end of May and the beginning of June.

CLUTCH SIZE

For the determination of clutch size and its variation with the season only those clutches known to have been completed have been used; i.e. clutches in which the same number of eggs has been recorded on two visits separated by more than twenty-four hours. The effect of the loss of odd eggs due to predation before the discovery of the nest has been ignored and all clutches, whether fresh or partly incubated, have been included. Lack (1948) has shown in the case of the Robin (*Erithacus rubecula*) that this makes only a negligible difference. The date of clutch-completion was derived as already indicated. As before, the records have been divided into three regions; the seasonal variation in clutch size is shown in Table II.

 TABLE II.
 Seasonal variation in clutch size

 (a)
 South-east England

Clutch			(Clutc	hes o	of			Average
completed		Ι	2	3	4	5	6	Total	clutch size
April 29-May 5					I			I	
May 6-12						r		I	
May 13-19						I		I	
May 20-26				I	- 6	4		11	4.3
May 27-June 2					7	цi	ĩ	19	4.7
June 3-9				4	16	20	I	41	4.4
June 10-16				3	11	8		22	4.2
June 17-23				2	7	3		12	4.1
June 24-30					6	-		6	4.0
July 1-7		2	τ	1	2			6	2.5
July 8-14				2	5			7	3.7
July 15-21			2	2	3			7	3.1
July 22–28	•••			2				2	
Total No.		2	3	17	64	48	2	136	4.17*
	%	1.5	2	13	47	35	1.5		• •
	Sta	Inda	rd ei	ror o	of me	ean -	-0.0	77.	

	South-west En Clu		D AN	ID V			hes o	f		1
	comp				2	3	4	5	Total	Average clutch size
	May 20-26						3	4	7	4.6
	May 27–June	2.	••				6	8	14	4.6
	June 3-9	•	••	• • •		3	10	9	22	4.3
	June 10–16	•	••	• • •		I	9	- 9	19	4.4
	June 17–23		••	• • •		I	4	2	7	4.1
	June 24–30		••		1	I	3		5	3.4
	July 1-7					I	3		4	3.8
	July 8-14	•	••			2	4		6	3.7
	July 15-21					I	2		3	(3.7)
	July 22-28			•••	I				Ĩ	
	Total No %		••	•••	2	11 10	44 50	32 36	88	4.21*
		Stand				mea	in ±0	0.075	j.	
) 1	North Englane Clutcl		Sco	OTLA		itche	s of			Average
	complet			2	3	4	5	6	Total	clutch size
	May 20-26									
	May 20-26 May 27-Jupe		•••			I	2		3	(4.7)
	May 27-June		•••		- ·	9	12	I	22	4.6
			•••		1	2	17	I	21	4.6
		•••	•••		I	8	7		16	4.4
	5 1 5	• • •	•••		I	2	1		4	4.0
	June 24-30 .					5			5	4.0
						9			2	4.0
	T 1			I	I	3	2		7	3.9
	July 1-7			I I	I I		2 I			
	July 1-7 July 8-14 Total No.	•••	•••	1 2	1 5	3 4 34	1 42	2	7	3.9
	July 1-7 July 8-14		···· ···	1 2 2	I 5 6	3 4 34 40	1 42 50	2	7 7 85	3.9 3.6
	July 1–7 July 8–14 Total No. %		···· ···	1 2 2	I 5 6	3 4 34 40	1 42	2	7 7 85	3.9 3.6
) •	July 1-7 July 8-14 Total No. %		···· ···	I 2 2 d eri	1 5 6 ror (3 4 34 40 of me	1 42 50 ean =	2	7 7 85	3.9 3.6 4.44*
) (July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch	*Sta	 ndar	I 2 2 d eri C	I 5 6 ror c	3 4 34 40 0f me	$\begin{array}{c} 1 \\ 4^{2} \\ 5^{0} \\ ean \\ = \\ of \end{array}$	2 ±0.0	7 7 85 77.	3.9 3.6 4.44*
) (July 1-7 July 8-14 Total No. %	*Sta	···· ···	I 2 2 d eri	1 5 6 ror (3 4 34 40 of me	1 42 50 ean =	2	7 7 85 77.	3.9 3.6 4.44*
) (July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed	 *Sta:	 ndar	I 2 2 d eri C	I 5 6 ror c	$ \begin{array}{r} 3 \\ 4 \\ 34 \\ 40 \\ 0 \\ f \\ m \\ hes \\ 4 \end{array} $	$\begin{array}{c} 1 \\ 4^{2} \\ 5^{0} \\ ean \\ = \\ of \end{array}$	2 ±0.0	7 7 85 77. Total	3.9 3.6 4.44*
) (July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch completed Apr. 29-May	*Sta:	 ndar	I 2 2 d eri C	I 5 6 ror c	3 4 34 40 0f me	$\begin{array}{c} 1 \\ 4^{2} \\ 5^{0} \\ ean \\ = \\ of \end{array}$	2 ±0.0	7 7 85 77.	3.9 3.6 4.44*
) (July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12	 *Sta: 5	 ndar	I 2 2 d eri C	I 5 6 ror c	$ \begin{array}{r} 3 \\ 4 \\ 34 \\ 40 \\ 0 \\ f \\ m \\ hes \\ 4 \end{array} $	$ I \\ 42 \\ 50 \\ ean = 2 0 f \\ 5 \\ I \\ I $	2 ±0.0	7 7 85 77. Total	3.9 3.6 4.44*
) '	July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19	*Sta:	 ndar	I 2 2 d eri C	I 5 6 ror c	$ \begin{array}{r} 3 \\ 4 \\ 34 \\ 40 \\ 0 \\ f \\ m \\ hes \\ 4 \end{array} $	$ \begin{array}{c} 1 \\ 4^2 \\ 50 \\ ean \\ 5 \\ \hline 5 \\ \hline 1 \\ I \end{array} $	2 ±0.0	7 7 85 77. Total	3.9 3.6 4.44* Average clutch size
) (July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26	*Sta 5	 ndar	I 2 2 d eri C	I 5 6 ror c lutc 3	$ \begin{array}{r} 3\\ 4\\ 34\\ 40\\ 56\\ 6\\ 6\\ 4\\ 1\\ 10\\ 10\\ 10\\ 10\\ 10\\ 10\\ 10\\ 10\\ 10\\$	$ I \\ 42 \\ 50 \\ 2 \\ 5 \\ 5 \\ 5 \\ 5 \\ 1 \\ 10 $	2 ±0.0 6	7 7 85 77. Total I I I 21	3.9 3.6 4.44* Average clutch size
) '	July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June	*Sta 5	 ndar	I 2 2 d eri C	I 5 6 ror c lutc 3	$3 \\ 4$ 34 40 of models hes of 4 1 10 22	$ \begin{array}{c} 1 \\ 4^{2} \\ 5^{0} \\ 2^{f} \\ 5 \\ 1 \\ 10 \\ 3^{0} \end{array} $	2 E0.0 6 2	7 7 85 77. Total I I 21 54	3.9 3.6 4.44* Average clutch size
) '	July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9	 *Sta: 5 2 	 ndar	I 2 2 d eri C	I 5 6 ror c lutc 3 I 8	3 4 34 40 of me hes c 4 1 10 22 28	$ \begin{bmatrix} I \\ 4^{2} \\ 50 \\ ean \\ 5 \\ $	2 ±0.0 6	7 7 85 77. Total I I 21 54 84	3.9 3.6 4.44* Average clutch size
) (July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16	 *Sta: 5 2 	 ndar	I 2 2 d eri C	I 5 6 for (1 lutc 3 I 8 5	3 4 34 40 of me hes c 4 1 10 22 28 28	$ \begin{bmatrix} I \\ 4^{2} \\ 50 \\ ean \\ 5 1 $	2 E0.0 6 2	7 7 85 77. Total I 1 21 54 84 57	3.9 3.6 4.44* Average clutch size
) '	July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16 June 17-23	 *Sta: 5 2 	 ndar	I 2 2 d err 2 2	I 5 6 for (1 1 1 8 5 4	$ \begin{array}{r} 3 \\ 4 \\ 40 \\ $	$ \begin{bmatrix} I \\ 4^{2} \\ 50 \\ ean \\ 5 \\ $	2 E0.0 6 2	7 7 85 77. Total I I 21 54 84 57 23	3.9 3.6 4.44* Average clutch size
) (July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 17-23 June 24-30	*Star 5 2 	 ndar	I 2 2 d err C 2	$\begin{bmatrix} I \\ 5 \\ 6 \\ ror \\ 1 \\ 1 \\ 1 \\ 8 \\ 5 \\ 4 \\ 1 \end{bmatrix}$	$ \begin{array}{r} 3 \\ 4 \\ 40 \\ $	I	2 E0.0 6 2	7 7 85 77. Total I I 21 54 84 57 23 16	3.9 3.6 4.44* Average clutch size
	July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16 June 24-30 July 1-7	*Sta:	 ndar	I 2 2 d err 2 2 C 2	I 5 6 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7	$ \begin{array}{r} 3 \\ 4 \\ 40 \\ $	I 42 50 ean = 0f 5 1 10 30 46 24 6 2 2	2 ±0.0 6 2	7 77 85 77. Total 1 1 21 54 84 57 23 16 17	3.9 3.6 4.44* Average clutch size
) •	July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16 June 17-23 June 24-30 July 1-7 July 8-14	 *Sta: 5 2 	 ndar	I 2 2 d err 2 2 C 2 2	I 5 6 for c 1 1 8 5 4 1 3 5	3 4 34 40 0f me 4 1 10 22 28 28 13 14 8 13	I	2 ±0.0 6 2	7 77 85 77. Total 1 1 1 21 54 84 57 23 16 17 20	3.9 3.6 4.44* Average clutch size
)	July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16 June 24-30 July 1-7	*Sta:	 ndar	I 2 2 d err 2 2 C 2	I 5 6 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7	$ \begin{array}{r} 3 \\ 4 \\ 40 \\ $	I 42 50 ean = 0f 5 1 10 30 46 24 6 2 2	2 ±0.0 6 2	7 77 85 77. Total 1 1 21 54 84 57 23 16 17	3.9 3.6 4.44* Average clutch size
)	July 1-7 July 8-14 Total No. % GREAT IBRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16 June 17-23 June 24-30 July 1-7 July 8-14 July 15-21 July 22-28	 *Stat	 ndard I	I 2 2 d ern C 2 2 I 2 I 1	I 5 6 7 0 7 0 7 0 7 0 7 0 7 0 7 0 7 0 7 0 7	3 4 34 40 0 0 f m 4 1 1 22 8 28 13 14 8 13 5	I 42 50 ecan =	2 ± 0.0 6 2 2 2	7 7 85 77. Total 1 1 21 54 84 57 23 16 17 20 11 3	3.9 3.6 4.44* Average clutch size
)	July 1-7 July 8-14 Total No. % GREAT BRITAIN Clutch completed Apr. 29-May May 6-12 May 13-19 May 20-26 May 27-June June 3-9 June 10-16 June 17-23 June 24-30 July 1-7 July 8-14 July 15-21	 *Star 5 2 	 ndar	I 2 2 d err C 2 I 2 I 2	I 5 6 for c 1 1 8 5 4 1 3 5 4	3 4 34 40 0f me 4 1 10 22 28 28 13 14 8 13	I 42 50 ecan =	2 ±0.0 6 2	7 77 85 77 77 1 1 1 1 1 21 54 84 57 23 16 17 20 11	3.9 3.6 4.44* Average clutch size 4.4 4.5 4.5 4.5 4.5 4.5 4.5 3.8 3.4 3.7 3.7 3.3

The average clutch size is plotted as a function of the seven day periods in Figure 2. It remains at about 4.5 from May 20th to June 9th and then decreases steadily to a value below 3 by the end of July. 85% of the clutches recorded had four or five eggs; out of over 300 clutches only four had six eggs, two one egg and seven two eggs; small clutches all occurred late in the breeding season.

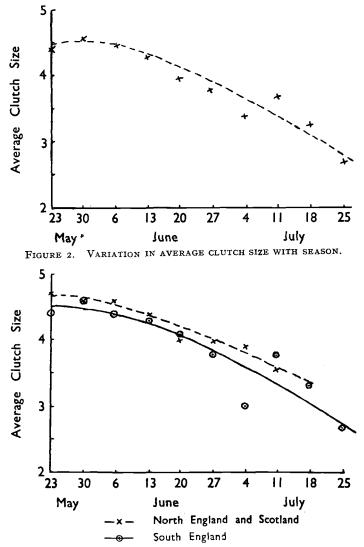


FIGURE 3. REGIONAL VARIATION IN AVERAGE CLUTCHSIZE WITH SEASON.

While there is no significant difference in clutch size between South-east and South-west England, the average clutch size is significantly larger in the North. This is clearly shown in Figure 3

where the seasonal variation in average clutch size is plotted for the North and the combined South regions. Owen's (1948-50) data from Montgomeryshire for 1949 and 1950 (not included in the above analysis) give an average clutch size of 4.1 (55 nests) and 4.2 (78 nests) respectively; these agree closely with the value for Southwest England and Wales derived in Table II(b).

By assuming that most first clutches are complete by the end of June and that most second clutches are laid after this as is indicated in Table I (d), we can derive an average value of 4.4 eggs for first clutches and 3.5 eggs for second clutches.

NESTING SUCCESS

Complete data are available for 267 clutches and 197 broods; 819 eggs hatched out of 1,052 laid, and from 749 eggs that hatched 609 young flew. This means that 78% of eggs hatched and that 81% of the young that hatched flew from the nest. An alternative method of estimating success is by complete nests; in this case we get closely comparable figures for the percentages of clutches and broods that were more than 50% successful, which are respectively 81% and 82%. The figures for the success of nestlings may be a slight overestimate as the nests are in most cases not visited more than once per day and it is assumed that, if on one visit the young are almost ready to fly and on the next the nest is empty, then the young have flown successfully. This is necessary, as so few records are available of young birds being seen actually leaving the nest, though it may result in the inclusion of some young which subsequently failed to do so.

The data can be analysed in more detail so that we can examine nesting success in relation to season and clutch size; this is shown in Tables III and IV respectively:

	TABLE III	. Effec	T OF SEASOR	N ON NESTING	G SUCCES	ss
	s of Eggs					
Clutch		Total	Total		% of c	lutches which
completed	Clutches	eggs	hatched	l % Hatche	d failed	completely
May	. 46	208	150	72		17
June	. 164	711	560	79		13
July	. 40	133	109	82		15
(b) Succes	S OF YOUNG			% succ including/ex		% of broods
Clutch		Total	Total to	broods whic	h failed	which failed
completed	Broods	young	leave nest	complet	ely	completely
May	35	143	121	85	93	9
June		502	403	80	93	14
July	-	104	85	82	<u>9</u> 6.5	15
(c) OVERAL	LL SUCCESS					
	Clutch	1 complet	ed	% Success		
		May		61		
		June		63		
		July		67		
		J J				

The hatching success appears to show a significant increase with advance of season. There is no doubt that this is connected with robbing of eggs by small boys which takes place principally in May whereas later in the season interest in "bird-nesting" has waned : however, this effect may obscure the effect of chilling of eggs which is more probable early in the year and might also account for a lower success at this period. The position of young is rather more obscure. Percentage success is shown in Table III (b) for the total young hatched both including and excluding the figures for broods which failed completely. Excluding the effect of predation (almost all cases of total failure are due to predation) the success is the same for May and June and apparently increases for July; this, however, may not be a seasonal effect per se, but could be due to the different distribution of brood sizes in the three monthly periods, if there is a correlation between brood size and success (this point is discussed later). The effect of brood size can be eliminated by considering the success of individual brood sizes. There is no significant variation of success with season for b/3 and b/4, but the figures available are rather small so that this point cannot be settled without further information.

TABLE IV. EFFECT OF CLUTCH AND BROOD SIZE

		TUPPE IA	. LIFEUI	OF CLUICE	I AND BROOM	D SIZE
(a)	SUCCESS OF	Eccs			uccess	0/ of alutabag
	Clutch size	Total eggs	Total hatched	clutches v	% of clutches which failed completely	
	I	2	I			
	2	10	8	(80)		_
	3	81	54	67	90	26
	4	496	394	79	92.5	14
	5 6	445	349	78	88	II
	6	18	13	(72)		
(b)	SUCCESS OF	F YOUNG			uccess /excluding	% of clutches
	Brood size	Total young	Total to leave nest	clutches v	which failed pletely	which failed completely
		3 38	3			
	2		32	(84)		
	3	123	93	76	94	19
	4	344	284	83	96	14
	5	235	191	81	91	11
	6	6	6			

Table IV shows that both hatching and nestling success is apparently greater for clutches and broods of three and four than for those of five. In the case of eggs this may reflect a greater proportion of infertile eggs in c/5, while in the case of young it would seem that in Britain broods of five can only be reared successfully when the conditions are very favourable. To eliminate any seasonal effect the success of the different brood sizes can be examined for a restricted period. This is shown in Table V for the period June 1st to 13th when a maximum amount of information is available.

TABLE V. RELATION BETWEEN BROOD SIZE AND SUCCESS. CLUTCHES COMPLETED JUNE I-13

Brood size	Total young	% Success including/excluding broods that failed completely				
3	51	78	95			
4	96	81	97			
5	110	74	90			

Again a lower success is shown for b/5.

It is of some interest to investigate the cause of failure in both eggs and young. This is known for only a proportion of cases. However, we can get some idea of the frequency of the various causes by using reduced totals as shown in Table VI.

Clutch _ size/ month complete	eggs	No. in which cause	% in which cause	Total eggs	se of fair Reduced total			EGGS Hui interfe		Preda	tors
4 5	102 96	74 62	72 65	496 445	360 290	No. 30 31	% 6 10	No.	%	No. 	%
June	58 151 24 233	37 109 11 157	72 72 46 67	208 711 133 1052	150 510 65 700	11 43 7 61	7 8 10 9	12 17 	8 3 4	14 49 4 67	9 10 6 10

The table clearly shows the effect of egg robbing by boys which accounts for 8% of eggs laid in May but for none of those laid in July. There is little to show that the proportion of infertile eggs is related to the season, though it does seem possible that the proportion is higher in c/5 than in c/4. Predation seems to be somewhat reduced in July. Apart from human beings the following have been recorded as predators of eggs and young in the nest. Birds: Magpie (*Pica pica*), Jay (*Garrulus glandarius*), and Little Owl (*Athene noctua*); mammals: Grey Squirrel (*Sciurus carolinensis*), Rat (*Rattus norvegicus*), and Stoat (*Mustela erminea*). Other causes of loss of young are due to drowning and to overcrowding in the nest resulting in birds either falling out or being squashed.

RATE OF LAYING

Most records show that eggs are laid at the rate of one per day, with usually an interval of 24 hours. There are, however, a few cases where apparently a day has been missed though it is possible in these that an egg may have been stolen without the observer's knowledge. On the other hand there is one record of an interval of only 17 hours between the laying of two eggs. We have only records of the actual time of laying in eight nests; in six of these the eggs were laid before o6.30 G.M.T., in one about 09.00 and the other about 16.00.

INCUBATION AND NESTLING PERIODS

Moreau (1946) has indicated the difficulties in estimating the incubation and nestling (fledging) period when visits are paid to the nest only once per day as is usually the case with observers completing Nest Record cards. It is possible in this way that an error of \pm 1 day may be introduced. Many records show that incubation begins before the last egg is laid. It is possible in most cases that this is only casual and it is thus not possible to determine the exact start of incubation without more extensive field observation. For this reason it is more satisfactory to choose arbitrarily the day of completion of the clutch as the start of incubation. In many cases hatching takes place over two days; where this occurs it is reasonable to assume that the last egg laid is the last to hatch (Gibb (1950) has established this for the Great Tit (Parus major) : in these nests the period from the clutch completion date until the last egg has hatched, which gives an accurate period for the last egg, has been used. Provided a large enough sample is available reasonably accurate incubation and nestling periods should be obtained in this way, and, of course, the possible error of + 1 day for any individual record will be greatly reduced. Table VII gives the incubation data for the three monthly periods as well as for the different clutch sizes.

TABLE VII. INCUBATION PERIOD

No.	of n	ests							Av. incub.	
10	11	12	13	14	15	16	17 days	Total	period	
	2	2	10	6			. I	21	13.2	
	2	10	27	15	3	3	I	63	13.2	
		4	6	2	1			13	13.0	
				~	I			r		
		2	3	2		I		8	13.4	
	2	9	24	8	2	I		46	13.1	
2	2	5	16	13	I	I	2	42	13.3	
2	4	16	43	23	4	3	2	97	13.2	
	No. 10 2 	No. of normalized number $10 ext{ II}$ $2 ext{ 2 } $	No. of nests 10 11 12 -2 2 2 2 10 4 2 -2 9 2 2 5	No. of nests with 10 11 12 13 -2 2 10 2 2 10 27 	No. of nests with incu 10 11 12 13 14 -2 2 10 6 2 2 10 27 15 4 6 2 2 3 2 2 9 24 8 2 2 5 16 13	No. of nests with incubati 10 11 12 13 14 15 -2 2 10 6 $2 2 10 27 15 34$ 6 2 1 2 3 2 2 3 2 2 9 24 8 2 2 2 5 16 13 1	No. of nests with incubation p 10 11 12 13 14 15 16 -2 2 10 6 $2 2 10 27 15 3 3$ 4 6 2 1 $-$ 2 3 2 $-$ 1 2 3 2 $-$ 1 2 9 24 8 2 1 2 2 5 16 13 1 1	No. of nests with incubation period of: 10 11 12 13 14 15 16 17 days -2 2 10 6 $$ 1 2 2 10 27 15 3 3 1 4 6 2 1 $$ 1 2 3 2 $-$ 1 $$ 2 9 24 8 2 1 $2 2 5 16 13 1 1 2$	No. of nests with incubation period of: 10 11 12 13 14 15 16 17 days Total -2 2 10 6 $$ 1 21 2 2 10 27 15 3 3 1 63 4 6 2 1 $$ 13 2 3 2 $-$ 1 $-$ 13 2 3 2 $-$ 1 $-$ 8 -2 9 24 8 2 1 $-$ 46 2 2 5 16 13 1 1 2 42	

There is no variation in incubation period either with the time of year or with clutch size. The mean value of 13.2 days agrees well with the figure of 12-14 days given by Jourdain (1938). 15%of nests lie outside the limits he gives, extending from as few as ten to as many as seventeen days, but in most cases these are almost certainly due to the imperfect method used in recording the start of incubation.

It is less easy to determine the nestling period; in 38% of the nests hatching is recorded as taking place over two days (in three nests over three days), whereas in 15% of nests the young did not all fly on the same day. We can thus choose as the nestling period in these cases either a mean period or the maximum or minimum number of days, which are also accurate for certain of the nestlings. The data for the mean nestling period is given in Table VIII. In addition the figures for the minimum and maximum averages are also shown. Data from nests where it is known that the young

flew prematurely, due to the presence of the observer, have not been included, though, of course, this is not known for all the nests in which it occurred.

TABLE VIII. NESTI No. of nests with nestling	ING PERIOD (period of : Av. Nestl. Per.
10 11 12 13 14 15	16 17 days Total Mean Min. Max.
$ \begin{array}{c} \hline Clutches \\ completed \\ in \\ \end{array} \begin{cases} May - 0.5 & 4 & 9.5 & 3 \\ June & 2 & 6 & 8 & 15.5 & 28.5 & 8 \\ July - 2 & I & 4.5 & 8 & I.5 \\ \end{array} $	1 1 22 13.5 13.4 13.6
completed { June 2 6 8 15.5 28.5 8	3 — 71 13.4 13.2 13.6
in [July - 2 I 4.5 8 I.5	— —
ſ I — — — — I ·	
2 - 2 3 2 5.5 0.5	1 — 14 13.2 13.1 13.3
Brood 3 I 0.5 4.5 4 II.5 3	0.5 — 25 13.4 13.2 13.6
size 4 0.53.5 2 11.5 16.5 7.5	
5 - 2 3.5 12 6 0.5	0.50.5 25 13.1 12.9 13.4
[6 0.50.5 — — — —	I
All nests 2 8.5 13 29.5 39.5 12.5	4 1 110 13.4 13.2 13.6

There is apparently no variation in the nestling period with the time of year, nor does it appear that there is any correlation between brood-size and nestling period, though the figure for b/5 may be shorter than for any other brood size.

Jourdain (1938) gives 12-13 days for the normal nestling (fledging) period with occasional cases of 11 or 14-15 days. The overall average found here is 13.4 days, about a day greater than the value quoted above. The maximum and minimum average values of 13.6 and 13.2 days respectively differ very little from the mean value. The long records of 16 and 17 days may have been due to unfavourable weather conditions and the attendant difficulties of obtaining food. The nestling period was 12-13 in only 39% of the cases recorded; in 6% of the nests the period was outside the limits given by Jourdain.

We can consider in more detail those nests where the hatching or the departure of the young from the nest took place over more than one day, though of course it must be emphasized that where a period of two days is recorded this may in fact be because the nest was only visited once during the day. The data is summarized in Table IX. From this it appears that prolonged hatching is more

TABLE	IX.	Cases	OF F	ROLONGED	HATCHING	AND	DEPARTURE	OF YOUNG
				Clut				oods
			Tota	al Prolonge	d Hatching	Total	Prolonged	Departure
								· · · · · · · · · · · · · · · · · · ·
				No.	%		No.	%

			No.	%		No.	%
Clutches	(May	21	4	19	22	3	14
laid in	{ June	63	27	43	71	10	14
laid in	July	13	Ĝ	46	17	4	24
	(1				I		
Clutch	2	I	r		14		0
Clutch/ brood	3	8	2	(25)	25	2	8
size	4	46	20	43	44	7	16
SIZC	5	42	14	33	25	7	28
	6				I	I	
Total		97	37	38	110	17	15

frequent in the later nests; on the other hand there does not seem to be any dependence on clutch size. Cases of prolonged departure of young from the nest are much less common. This is probably because the departure of some members of the brood stimulates the others to leave the nest; however, the frequency with which this occurs does seem to increase with the size of the brood. It is probable that prolonged hatching occurs more often in the nests where incubation begins before the last egg is laid and suggests that this may occur more frequently with later clutches. It is of interest to notice that Gibb (1950) has found for the Great Tit, that, whereas incubation begins earlier, relative to the time of clutch completion, with the advance of the season, it is not dependent on clutch size.

Nests

The sites for 197 nests were as follows:

Against walls				117	60%
Trees, in holes	•••		•••	25)	
in ivy				$[17]{63}$	32%
in fork		•••		13	J-70
on stum	P	•••	•••	87	
Nest Boxes	•••		•••	10	5% 3%
Old nests of oth	her sp	pecies		6	3%

By far the greatest proportion of nests are on walls, usually in ivy or creepers or bushes trained against walls. The only other important site is in trees. Because of the method of obtaining the results (most records coming from gardens and the neighbourhood of houses) these figures are probably biased in favour of walls. The use of old nests of other species has been noticed quite frequently; the nests of fourteen different species have been reported as used for this purpose (Jourdain (1917) and this investigation). The same nest is not infrequently used for a second clutch though this is not invariably the case.

The distribution of nests at various heights above the ground is given in Table X. The greatest number occur at 5-7 feet.

	TABLE	: X.	HEI	GHTS	OF N	ESTS	5 ABOV	E GROU	IND		
Height above	ground	in ft.	1-3	3-5	5-7	7-9	9-11	11-13	13-15	15-17	> 17
No. of nests			7	25	33	27	16	8	5	3	8
This may	be rat	her a	alo	w va	hne	as	lower	nests	bein	g easie	er to

This may be rather a low value as lower nests, being easier to observe will be recorded more frequently.

DISCUSSION OF RESULTS

In species which are regularly double-brooded it has been found in Britain that there is a tendency for clutch size to rise to a maximum in early June and then to decrease (Lack, 1947). This has been shown for the Yellow Bunting (*Emberiza citrinella*) (Parkhurst and Lack, 1946), the Robin (Lack, 1946 and 1948) and the Song-Thrush (*Turdus ericetorum*) (Silva, 1949). According to Lack (1947) this is connected with the day length which, being at a maximum in June, enables sufficient food to be collected to feed a larger brood, assuming of course that suitable food is available in plentiful supply

at this period. The Spotted Flycatcher is a late nester, clutches not being completed in the majority of cases till late May or early June, so that we do not find an increase in clutch size to a maximum at the beginning of June; Fig. 2 and Table II indicate that clutches completed from May 20-26th may be slightly smaller than those completed from May 27th to June 9th though the values are not significantly different; after this period, however, the average clutch size decreases steadily as happens with the other species mentioned above. The other influence of day length, the increase of clutch size with latitude, is also found; the overall average clutch size in the north of England and Scotland being 4.4 eggs against a value of 4.2 for the south. That this is not merely the effect of a larger proportion of second clutches in the south, is indicated in Fig. 3, which shows that a higher average clutch size is maintained throughout the breeding season in the north. This increase is shown in Table II as an increase in the proportion of c/5's in the north; there is nothing to show that c/6's are more common in the north than in the south; clutches of this size are, however, extremely rare throughout the country, though according to Lövenskiold (1947) they are not infrequent further north in Norway.

The successes of both eggs and young are appreciably higher than the values obtained for the Robin and Song-Thrush in Britain:---

	Succ	ess of	Overall	
	Eggs	Young	success	
	 78% 71%	81% 77%	63% 55%	
Song-Thrush (Silva, 1949)	 71%	78%	55%	

It may be that the sample used is biased in favour of successful nests, though this is unlikely as it has been obtained in the same way as that for the Song-Thrush, investigated by Silva, so it is possible that this is a genuine result. It is tempting to relate this higher success to the shorter breeding period of the Spotted Flycatcher, but there are insufficient data for all three species to determine whether there is a real variation of success within the normal breeding season.

Both Lack (1948) and Silva (1949) found an apparent decrease in the nestling period for larger broods in the Robin and Song-Thrush respectively, though they consider that this was not a real effect but due to the seasonal distribution of larger broods. The same tendency has been found for the Spotted Flycatcher, and, though the results are not statistically significant, it seems possible that the nestling period does in fact decrease for larger broods; the effect in the present case cannot be explained as a seasonal one. The reason for such an effect, if it is proved, is somewhat obscure, though it may possibly be connected with the greater activity that presumably occurs in nests with large broods.

The amount of data on a particular species that is made available

by a co-operative inquiry, such as the Nest Records Scheme of The British Trust for Ornithology, opens up a new field in the attainment of comprehensive information. Not only can records be obtained on a scale beyond that of individual resources, but also they are received from all parts of the country and, because of the large number of observers concerned, are largely free from bias. It is to be hoped that inquiries of this nature will receive greater support in the future, because it is only with the accumulation of data that information of real value is obtained. In spite of there being records available on over five hundred nests of the Spotted Flycatcher it is clear that still more records are required to clear up some of the more subtle points, such as the effect of annual variations in weather conditions, the influence of brood size and season on nestling success, and the influence of brood size on nestling period.

Detailed factual information of this sort also provides a yardstick whereby long-term changes may be evaluated in the future. It is possible for instance that, if the present amelioration of climate continues, changes may occur in clutch size; this effect would probably only be small and might not be detected without accurate information being available over a period of several years.

Summary

1. The normal laying period for the Spotted Flycatcher in Britain extends from mid-May to the end of July, a small number of pairs being double-brooded.

2. The average clutch size decreases from about 4.5 eggs at the end of May to less than 3 eggs by the end of July. A slightly, but significantly, higher average clutch size occurs in North England and Scotland than in the rest of England and Wales throughout the breeding season.

3. It is probable that the Spotted Flycatcher can only successfully rear a brood of five young in Britain when the conditions are very favourable.

4. No significant variation in nesting success with season has been detected.

5. The average incubation period is 13.2 days and the nestling period 13.4 days; this latter figure is about one day greater than that given in *The Handbook*.

6. The situation of nests is discussed briefly.

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