

CLUTCH-SIZE, INCUBATION AND HATCHING SUCCESS IN THE HOUSE SPARROW AND TREE SPARROW *PASSER* SPP. AT OXFORD

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INTRODUCTION

The present paper on clutch-size, incubation and hatching success in the House Sparrow *Passer domesticus* and Tree Sparrow *P. montanus* describes part of a study the aim of which it was to assess the factors influencing recruitment to the population; the breeding season has already been described (Seel 1965, 1968). The main observations were made in 1961 and from 1963 to 1964 in the city of Oxford and its surroundings, but a few extra data for *P. domesticus* were collected from 1957 to 1959 at Pinner, Middlesex, by myself, and for *P. montanus* from 1951 to 1954 and in 1962 at Oxford by J. L. Boldero.

METHODS

An account of the study areas and definitions relating to the methods of analysis of data on breeding seasons will be found in Seel (1968).

DETERMINATION OF CLUTCH-SIZE

When eggs were discovered, they were usually numbered with red nail varnish and inspected daily until the clutch was complete, that is, when successive inspections showed it unchanged in size and also warm. Warm clutches of four or more eggs were inspected on the day of completion and on the following day, but an extra visit was paid to nests with clutches of two and three eggs in case the day following the day of apparent completion of the clutch represented a break in the laying sequence. All clutches which were cold when apparently complete were also inspected on the next two days for the same reason. In a few instances, clutch-size was determined from a single inspection made several days after the beginning of incubation. Though numbering the eggs helped to avoid inaccuracies due to the loss of eggs during the laying period, slight inaccuracies due to loss of eggs between laying and the first inspection cannot be ruled out, but, as Snow (1955) has pointed out, such errors should not affect measurements of seasonal, annual and specific differences in clutch-size.

DETERMINATION OF THE INCUBATION PERIOD

Following Moreau (1946), the incubation period is taken as the time between the laying and hatching of the last egg laid in each clutch. Incubation periods were calculated from data for the following clutches: (i) clutches of all sizes in which numbering was begun before all the eggs were laid: in these the last egg laid could be readily identified; (ii) those un-numbered clutches of four eggs laid between successive four-day inspections made for new clutches, and in which the last egg laid could be distinguished from the other eggs in the same clutch by its appearance (in *P. domesticus* the most recently laid egg was usually brighter, paler and cleaner than the older eggs: this distinction generally lasted less than 24 hours; in *P. montanus* the final egg only was often paler than the others at the time of laying and this appearance persisted throughout the incubation period); (iii) other un-numbered clutches of four eggs whose dates of laying were known (as above) and in which all the eggs hatched between two successive daily inspections.

To determine the dates of hatching, clutches of from two to four eggs were inspected daily, beginning on the tenth day after completion and larger clutches daily from the tenth day after the fourth egg was laid. The daily inspections continued until all the eggs had hatched, or could reasonably be expected to have hatched. The later young to hatch were commonly smaller than their fellows; where hatching was spread over two or more days, this effect was marked because from nestling day $\frac{1}{2}$ to $1\frac{1}{2}$, young birds approximately doubled their weight. Late-hatched young frequently died at a very early stage, some even within a few hours of hatching. During the hatching period, eggs in some clutches disappeared without increase in number of young; in these cases it was assumed that the young birds had died and had been removed by the parents soon after hatching. Once a parent bird of *P. domesticus* was seen removing a corpse from its nest (Seel 1966).

CLUTCH-SIZE

The frequency distribution of clutch-size was similar in both *P. domesticus* and *P. montanus*, though there was a difference between the mean clutch-size of each species (Table 1). The total weight of eggs per clutch was equal to about 40–50% of the adult body weight in both species; the eggs of *P. domesticus* are relatively larger than those of *P. montanus*. After various losses during incubation, the total weight of nestlings immediately after hatching corresponded to about 30% of the adult body weight.

TABLE 1. Clutch-size in *Passer domesticus* and *P. montanus* at Oxford.

CLUTCH-SIZE	<i>P. DOMESTICUS</i>		Clutches	<i>P. MONTANUS</i>	
	No.	%		No.	%
c/2	40	5		2	1
c/3	158	19		3	1
c/4	429	52		42	16
c/5	189	23		156	60
c/6	14	2		44	17
c/7	1	0		12	5
Total	831			259	
Mean	3.98			5.05	
S.D.	±0.83			±0.79	

Evidence presented elsewhere (Seel 1968) suggests that first-year individuals of *P. domesticus* start breeding later in the season than older birds. Since the mean size of the first clutch of the early-starting birds was slightly larger ($P < 0.01$) than that of the birds starting later (Table 2), it seems likely that first-year birds laid on average slightly smaller clutches than older birds (cf. Great Tit *Parus major* (Kluijver 1951); Redstart *Phoenicurus phoenicurus* (Ruiter 1941)).

TABLE 2. Clutch-sizes of "early-" and "late-starting" birds of *P. domesticus* at Oxford.

CLUTCH-SIZE	* BIRDS WHICH BEGAN LAYING:	
	EARLY IN THE SEASON	LATE IN THE SEASON
	NO. OF CLUTCHES	
c/2	8	21
c/3	54	51
c/4	136	156
c/5	83	66
c/6	8	3
c/7	1	
Total	290	297
Mean	4.11	3.93
S.D.	±0.76	±0.85
Difference between means	0.18, $P < 0.01$	

Note. * Since there is seasonal variation in clutch-size, the only valid comparison is that between clutches laid during the same periods. Thus only those clutches laid between 29 April and 6 August in 1961 and 1964, and between 9 May and 6 August in 1963, have been used in the Table. "Early starters" are the birds which first started laying early in the season. (See Seel 1968.)

ANNUAL AND LOCAL VARIATIONS IN CLUTCH-SIZE

In *P. domesticus* there was no significant variation in the mean clutch-size in 1961, 1963 and 1964 in any given study area at Oxford (Table 3). Because of this, the data for all years were combined; a slight but significant variation ($P < 0.05$) between the mean clutch-size of different localities was then detected, due to the low mean value for a colony nesting in Ivy *Hedera helix*. Exclusion of the latter value eliminated the significant variation with respect to locality. Hence, it may be concluded that *P. domesticus* showed no appreciable annual or local variation in its mean clutch-size at Oxford.

TABLE 3. Clutch-size in *P. domesticus* and *P. montanus* in different years and different localities at Oxford.

LOCALITY	MEAN CLUTCH-SIZE (AND NO. OF CLUTCHES EXAMINED)							
	1951	1952	1953	1954	1961	1962	1963	1964
<i>P. domesticus</i>								
Headington					3.94 (31)		3.89 (84)	
Summertown—nest-boxes					3.98 (63)		3.98 (102)	4.09 (111)
Summertown—"ivy colony"					3.74 (42)		3.72 (53)	
Wytham village					3.88 (41)		4.01 (144)	4.09 (160)
<i>P. montanus</i>								
Summertown—nest-boxes					5.00 (10)			
Stanton St. John	4.75 (4)	4.57 (7)	4.90 (10)	5.00 (15)		4.67 (15)	5.60 (20)	5.29 (17)
Wytham village					4.67 (15)		5.00 (16)	5.07 (14)
Wytham woods					4.78 (18)		5.09 (55)	5.23 (43)

In *P. montanus* there was significant annual variation ($P < 0.01$) in mean clutch-size at Stanton St. John, for which a longer series of values was available than elsewhere. Two groups of clutch-sizes were also analysed for variation with respect to year and locality: there was significant annual variation ($P < 0.05$) but no significant local variation between the clutch-sizes for Wytham village and woods in 1961, 1963 and 1964; and secondly, there was no significant variation between the years or between the localities in the clutch-sizes for Stanton St. John and Wytham village and woods in 1963 and 1964.

Thus, there was evidence of annual variation in the clutch-size of *P. montanus* but not of local variation; such annual variations as occurred differed between localities, sometimes being in opposite directions. Creutz (1949) also found appreciable annual variations in the clutch-size of *P. montanus*.

If one assumes that the mean clutch-size anticipates the average amount of food available to the nestlings (see Lack 1954), then the absence of appreciable annual and local variations in the clutch-size of *P. domesticus* suggests that there was likely to be no predictable variation in the abundance of food between places or years. In *P. montanus* the existence of annual variations of clutch-size suggests that for this species there may be predictable variation in food abundance from year to year. Since *P. montanus* appeared to include a large proportion of caterpillars in the food given to its nestlings (D. C. Seel, in prep.), it may be significant that the annual variation in clutch-size of *P. montanus* in Wytham woods in 1961, 1963 and 1964 and the annual variation in total numbers of caterpillars of all species feeding on oak leaves in the same years in the same locality were in the same direction, though they were not of the same order of magnitude (Seel 1965).

SEASONAL VARIATIONS IN CLUTCH-SIZE

In both species the mean clutch-size rose and then fell as the season progressed (Fig. 1), suggesting a correlation with the seasonal variation in day-length (see Lack 1947). The peak of clutch-size was reached about 21 days before the longest day in *P. montanus* and about 19 days in advance in "early-starting" birds of *P. domesticus*. In "late-starting" *P. domesticus*, however, the maximum clutch-size (excluding the high point at the very beginning) was reached about four days after the longest day. In *P. montanus* and "early-starting" *P. domesticus*, the shape of the curve for mean clutch-size plotted against date corresponded closely with the curve for day-length; the curve for the clutch-size of "late-starting" *P. domesticus* showed a considerable initial deviation from that of day-length in that it decreased markedly during May, but subsequently it corresponded moderately well with day-length.

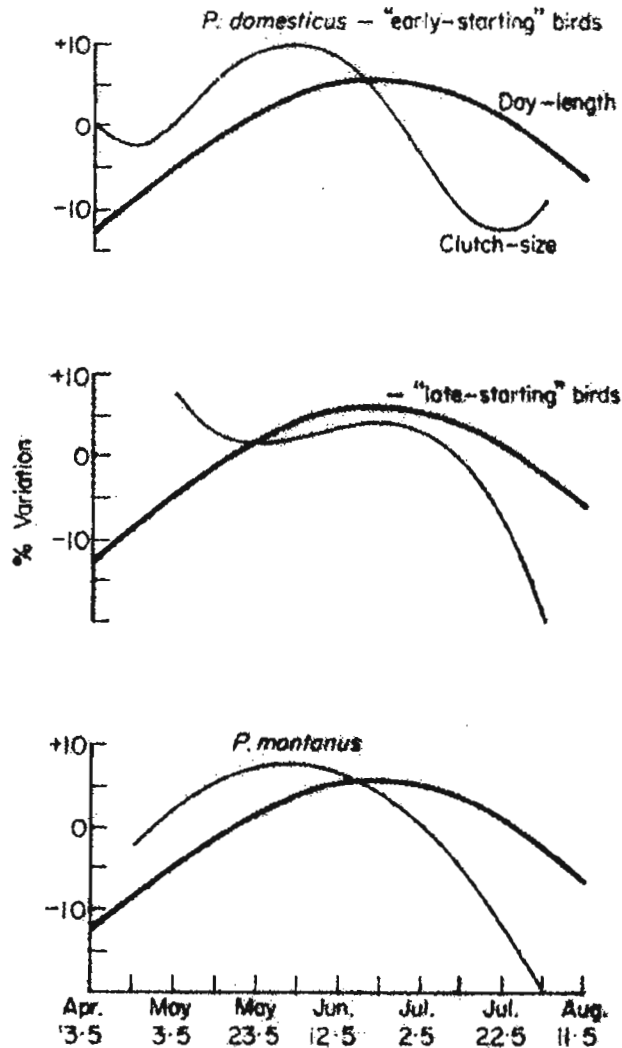


FIGURE 1. Variation in mean clutch-size and day-length during the breeding seasons of *Passer domesticus* and *P. montanus*.

Assuming average clutch-sizes of four and five eggs in *P. domesticus* and *P. montanus* respectively, average incubation periods of 11 days in both species, and average nestling periods of about 15 and 13 days respectively (or seven and six days to the mid-points of the nestling periods), the approximate interval between the date the first egg is laid and the middle of the nestling period is 22 days. This length of time corresponds closely with the observed interval between the peak of clutch-size of *P. montanus* and "early-starting" *P. domesticus* and the longest day. Thus, the seasonal variation in clutch-size satisfies Lack's (1954) condition that for the clutch-size to be effectively

adapted to the food supply the relationship must be to the food supply at the time the young require it, that is several weeks after the eggs are laid. In this case, the relationship may well be with the length of time for which food can be collected.

Lack (1947: 321) also stated that "it is . . . the quantity . . . of food brought to the nest which matters, and day-length is only one factor affecting this . . . For this reason, one would not expect too exact a correlation between clutch-size and day-length in any species. . . ." In *P. montanus* the close correspondence between the shapes of the curves of mean clutch-size and the variation in day-length plotted against date not only indicates the existence of a correlation between them, but suggests that other factors, also varying seasonally, were relatively unimportant. The same also seems to be true for "early-starting" *P. domesticus*. As the family-size varied in parallel with day-length, it may be concluded that no intrinsic variation in the availability of the food for the nestlings of either species was anticipated, other than that governed by day-length. The differences in the seasonal variation of clutch-size of "late-starting" *P. domesticus* may possibly be related to their supposed difference in age (see above).

INCUBATION

At Pinner, Middlesex, *P. domesticus* laid its eggs between about $\frac{1}{2}$ and $1\frac{1}{2}$ hours after sunrise throughout the breeding season (Table 4).

TABLE 4. Recorded times of egg-laying by *P. domesticus* at Pinner, Middlesex.

NEST	CLUTCH	DATE	TIME (G.M.T.) WHEN FEMALE:		MEAN TIME OF EGG-LAYING AFTER SUN-RISE (MIN)
			ENTERED NEST TO LAY	LEFT NEST AFTER LAYING	
A	1st	24.iv.57	05.10	05.36	35
B	1st	24.iv.58	05.03	05.53	40
B	1st	26.iv.58	05.28	05.59	59
A	2nd	31.v.57	04.45	05.38	80
C	1st	15.vi.58	05.01	05.41	97
D	2nd	17.vi.59	04.25	04.53	55
D	2nd	18.vi.59	04.10	04.56	49
D	2nd	19.vi.59	04.10	04.50	46
A	3rd	10.vii.57	04.20	04.57	42

At Oxford each nest was inspected at the most once per day, at about the same time on each occasion. Consequently, it was not possible to determine the precise interval between the laying of consecutive eggs in the clutch. From inspections made on successive days, beginning before the appearance of the first egg in each pair of eggs concerned, the rate of increase in number of eggs was found, and from this the approximate interval between the laying of each egg.

In no case were two eggs laid in a day. In 476 (98%) out of 487 intervals in *P. domesticus* and 137 (99%) out of 139 in *P. montanus*, the rate of increase in number of eggs was one per day, while in the few remaining cases intervals of more than one day were recorded, implying that in nearly all instances the interval between the laying of consecutive eggs was approximately 24 hours in both species. At Pinner two intervals of about 24 hours each were recorded for *P. domesticus* with an observation nest-box (see data for nest D in Table 4).

During the laying period the temperature of the clutch was estimated as "cold", "warm" or "intermediate" by holding an egg against the cheek. Observations were made in the afternoon, that is, long after the time each egg was laid. "Warm" eggs were assumed to have been heated by the parents, for all eggs were well insulated from the sun. Though some subjectivity is inevitable in this method of estimating the temperature of the eggs, the temperature of untended eggs was probably about 10–15° C compared

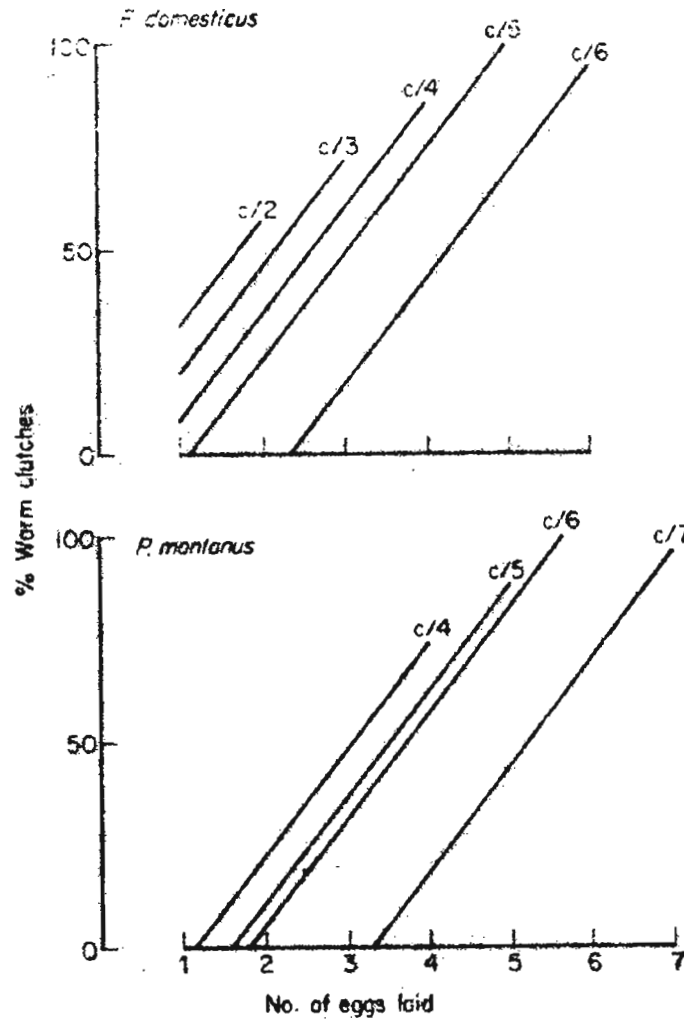


FIGURE 2. Incubation during the laying period in *Passer domesticus* and *P. montanus*.

with about 34° C for incubated eggs (Huggins 1941), so there is little likelihood of bias from this source. Indeed, only 8.8% of 1,727 observations fell in the "intermediate" category.

Some clutches were found to be warm during the laying period, the proportion increasing steadily with the laying of each egg (Fig. 2). The rate of this increase (which did not differ significantly in the two species nor in different clutch-sizes) was 25.74%

TABLE 5. Proportion of warm clutches observed during the laying period in *P. domesticus* and *P. montanus*.

CLUTCH-SIZE	NO. OF OBSERVATIONS	% OF WARM CLUTCHES *	S.E.
<i>P. domesticus</i>			
c/2	26	5.45	± 8.45
c/3	167	6.89	± 3.33
c/4	840	17.16	± 1.49
c/5	460	28.29	± 2.01
c/6	38	60.07	± 6.99
c/7	1	—	—
<i>P. montanus</i>			
c/3	1	—	—
c/4	21	29.29	± 9.40
c/5	119	40.34	± 3.95
c/6	37	46.36	± 7.08
c/7	17	84.43	± 10.45

Note. * % of warm clutches at start of laying, that is when the number of eggs laid = 0, extrapolated from successive observations made during the laying period (see Fig. 2).

Regression coefficient of percentage of warm clutches on number of eggs laid for all clutches of both species = +25.74, S.E. ± 0.95.

TABLE 6. *Incubation periods of P. domesticus and P. montanus at Oxford.*

Clutch-size	(a) PERIOD IN DAYS* BETWEEN LAYING OF LAST EGG AND HATCHING OF FIRST YOUNG			(b) INCUBATION PERIOD IN DAYS* OF LAST EGG LAID IN EACH CLUTCH			DIFFERENCE BETWEEN MEAN PERIODS FOR (a) AND (b)
	No. of clutches	Mean	S.D.	No. of clutches	Mean	S.D.	
<i>P. domesticus</i>							
c/2	8	11.50	±0.76	6	11.84	±0.73	0.34
c/3	58	11.24	±0.91	40	11.53	±0.60	0.29
c/4	304	10.80	±0.86	246	11.46	±0.70	0.66
c/5	152	10.67	±1.01	124	11.40	±0.80	0.73
c/6	12	10.42	±1.09	9	11.22	±0.46	0.80
c/7	1	(9)	—	—	—	—	—
Total	535	10.81	±0.91	425	11.45	±0.72	—
Regression coefficient:		-0.259 ± 0.054, <i>P</i> < 0.001		-0.085 ± 0.050, <i>P</i> > 0.05			
<i>P. montanus</i>							
c/4	8	11.38	±1.06	6	12.17	±0.77	0.79
c/5	61	10.90	±1.13	35	11.46	±0.71	0.50
c/6	19	10.32	±0.82	14	11.22	±0.58	0.90
c/7	6	10.50	±1.37	4	11.75	±1.50	1.25
Total	94	10.80	±1.08	59	11.49	±0.77	—
Regression coefficient:		-0.382 ± 0.160, <i>P</i> < 0.05		-0.185 ± 0.137, <i>P</i> > 0.05			

Note. * The error on each original observation was ± 1 day; but since *P. domesticus* lays its eggs in the early morning and since the nests at Oxford were examined between 14.00 and 18.00 G.M.T., the observations are probably accurate to within half a day.

(s.e. ± 0.95) for each egg laid. Furthermore, for any given number of eggs laid, the proportion of warm clutches was less for large than for small clutches (Table 5). It is assumed that the proportion of clutches found warm in the daytime during the laying period provides a measure of the amount of time spent in incubation.

THE INCUBATION PERIOD

The period between the laying of the last egg and the hatching of the first young was used as a further measure of the extent to which incubation took place before the clutch was complete. It was calculated for all those clutches in which the date of laying of the last egg and the date of hatching of the first young were known and in which at least one egg, other than the last to be laid, hatched. It was difficult from one inspection per day to determine the exact order of hatching of those eggs preceding the last one laid; in some clutches these eggs hatched in order of laying, in others out of order. Certainly, the first egg to be hatched was not necessarily also the first to be laid. In both species the period between the laying of the last egg and the hatching of the first young was shorter (*P. domesticus*, $P < 0.001$; *P. montanus*, $P < 0.05$) for larger clutches than for small ones (Table 6). For any given clutch-size, there was no significant difference between the species in the length of this period.

TABLE 7. Variation in incubation period of *P. domesticus* and *P. montanus* during the breeding season.

CLUTCH-SIZE	MEAN INCUBATION PERIODS IN DAYS (\bar{x}) AND NUMBER OF OBSERVATIONS (n)			
	"EARLY-SEASON" (up to 13 May)	"MID-SEASON" (14 May-22 June)	"LATE-SEASON" (23 June onwards)	
<i>P. domesticus</i>				
c/2	\bar{x}	12.33	11.33	
	n	3	3	
c/3	\bar{x}	11.81	11.57	
	n	16	7	
c/4	\bar{x}	11.68	11.41	
	n	85	100	
c/5	\bar{x}	11.56	11.30	11.57 (11.15)
	n	36	74	14 (13)
c/6	\bar{x}	11.33	11.00	
	n	3	5	
<i>P. montanus</i>				
		(up to 18 May)	(19 May-17 June)	(18 June onwards)
c/4	\bar{x}	12.67		11.50
	n	3		2
c/5	\bar{x}	11.67	11.50	11.09
	n	18	6	11
c/6	\bar{x}	11.38	11.00	
	n	8	5	
c/7	\bar{x}		11.00	
	n		3	

Notes. The divisions of the breeding season correspond with the normal dates of 1st, 2nd and 3rd clutches of "early-starting" birds in *P. domesticus* and the "main group" of birds in *P. montanus*.

Figures in parentheses exclude one example of a period of 17 days (see text).

The incubation period, that is the period from laying to hatching of the last egg in each clutch, was determined in each instance to the nearest whole day (see note to Table 6). In both species the incubation period for clutches of any given size appeared to decrease slightly as the season progressed and large clutches had shorter incubation periods than small ones throughout the season (Table 7). The only marked exception to this trend was a late clutch of five eggs of *P. domesticus* which appeared to have a quite exceptional incubation period of 17 days; when this example is omitted, the mean

value for clutches at this stage of the season fits the general trend. The combined data for the whole season (Table 6) show more fully the inverse relationship between the decrease in incubation period and the clutch-size, though the decrease in incubation period was significant in neither species. The data in Table 6 also show that there was no significant difference between the species in the length of the incubation period for any given clutch-size.

The difference between the two periods measured from the date the last egg was laid (i.e. the periods up to the hatching of the first and last egg respectively) increased with clutch-size, which indicates a greater spread of hatching in larger clutches (Table 6). Close examination of the hatching period shows that in clutches of three or more eggs of *P. domesticus* hatching of all eggs except the last one laid occurred more or less together and occupied a similar amount of time to that occupied by the hatching of a clutch of two eggs; the spread of hatching was due to the last egg to be laid, but only in clutches of four or more eggs was hatching on average spread over two days (Table 8). The data for *P. montanus* were fewer and less clear-cut, but the situation appeared to be similar to that in *P. domesticus*.

Despite the fact that one egg is laid per day, the hatching of all eggs, except the last to be laid in each clutch, is synchronised in *P. domesticus* and *P. montanus*. Lillie (1952) stated that the latent period of the eggs, that is the time required for the resumption of

TABLE 8. *The spread of hatching of whole clutches and parts of clutches in P. domesticus and P. montanus.*

Clutch-size	Part of clutch (eggs)	No. of examples	<i>P. DOMESTICUS</i>		No. of examples	<i>P. MONTANUS</i>	
			Mean hatching spread (days) Part-clutches	Whole-clutches		Mean hatching spread (days) Part-clutches	Whole-clutches
c/2	1-2	18		1.17			
c/3	1-2	51	1.20				
	1-3	75		1.49			
c/4	1-2	219	1.15		7	1.00	
	1-3	221	1.30		6	1.00	
	1-4	273		1.70	7		1.71
c/5	1-2	100	1.12		40	1.15	
	1-3	96	1.18		40	1.35	
	1-4	97	1.27		39	1.46	
	1-5	134		1.74	44		1.68
c/6	1-2	6	1.00		12	1.08	
	1-3	6	1.00		11	1.27	
	1-4	5	1.20		10	1.30	
	1-5	5	1.20		10	1.40	
	1-6	9		2.00	13		1.92
c/7	1-2				3	1.00	
	1-3				3	1.00	
	1-4				3	1.00	
	1-5				3	1.00	
	1-6				3	1.00	
	1-7				5		1.80

Note. Significant differences:

		<i>P. domesticus</i>	<i>P. montanus</i>
c/3,	e 1-2/e 1-3	$P < 0.01$	
c/4,	e 1-3/e 1-4	$P < 0.001$	
c/5,	e 1-4/e 1-5	$P < 0.001$	$P < 0.05$
c/6,	e 1-5/e 1-6	$P < 0.05$	$P < 0.01$

With one exception (c/4, e 1-2/e 1-3 : $P < 0.001$), which is apparently of little practical importance, there is no significant difference between one part clutch and another in any clutch-size.

development after cooling following laying, is longer in eggs left untended than in newly laid eggs. By inducing development earlier in the older eggs and thereby offsetting their greater latent period, incubation during the laying period may be a means of synchronising the development of the eggs, for without such incubation they might hatch in reverse order of laying (cf. Vince 1964).

The temperature of the clutch during the laying period suggests that by the time the clutch was completed incubation was most intense in nests with the largest clutches. Hence, the shortest mean incubation period of 11.2 days (Table 6) probably most closely represents the normal minimum incubation period of both *P. domesticus* and *P. montanus*. Comparison of this figure with the period between the laying of the last egg and the hatching of the first young indicates that, on average, full incubation began after the completion of the clutch in clutches of two and three eggs in *P. domesticus* and clutches of four eggs in *P. montanus*, but before the clutch was completed (by up to one day) in larger clutches. The greater spread of hatching in larger clutches also supports this interpretation. The delayed hatching of the last egg laid in large clutches was presumably due to the fact that full incubation began before this egg was laid. Bearing in mind Kendeigh's (1952) criterion that incubation behaviour is fully developed when the attentive period of the adults in the nest exceeds the inattentive period, it will also be noticed (Fig. 2) that warm "clutches" first became in the majority in each clutch-size as follows: when the last egg had been laid in clutches of two or three eggs in *P. domesticus* and in clutches of four in *P. montanus*; but prior to the laying of the last egg in larger clutches of both species—as a rule, following the laying of the penultimate egg.

In summary, both species possessed a combination of synchronous and asynchronous hatching. Asynchronous hatching has been ascribed to the need for a rapid means of adjusting the family-size to a (variable) food supply at the possible expense of part, but not all, of the family (Lack 1954).

The decrease in the length of the incubation period with the passing of the season may possibly be linked with the rising air temperatures during that time.

HATCHING SUCCESS

The number of clutches which were fully incubated in each nest (as opposed to the number actually laid) is given elsewhere (Table 4 in Seel 1968): a similar proportion in each species failed to survive the incubation period.

Clutches were deserted in a variety of circumstances. An important cause was trapping at the nest: thus, at six out of seven nests of *P. domesticus* where incubating females were caught in the nest during the day, the eggs were found cold the following day and were never observed to be incubated further. Similarly, most adult *P. montanus* caught in the nest for ringing deserted apparently as a consequence. When adults were frightened out of their nests, desertion rarely followed. A few other clutches were found deserted even though the adults had not been present at these nests during the inspection of the eggs. Desertion of the nestlings—and therefore probably of eggs, too—sometimes follows the death of one member of the pair in *P. domesticus* (Summers-Smith 1963).

Subsequent events in deserted nests of *P. domesticus*, at least, appeared to depend somewhat on the circumstances of desertion. Thus, after desertion due to trapping and sometimes frightening, the nests were not used for the rest of the breeding season. In most cases of desertion, either due to disturbance by frightening or to unknown causes, the eggs disappeared from the nest, sometimes within 24 hours of the disturbance, but more commonly after several days. The eggs were sometimes found broken on the ground beneath their nests and in these cases had almost certainly been ejected by the

owners of the nests. After a few days another clutch was laid, indicating that, although the previous clutch might have been deserted, the nest itself had not. In several instances, the new clutch was added to the remaining eggs of the old clutch, which did not hatch.

On rare occasions single eggs in a clutch were found punctured, or the nest-material was found disturbed and the whole clutch gone. In no instance in *P. domesticus* was either situation apparently due to predation; the eggs were never found eaten (practically every nest-box erected for sparrows in the city of Oxford and Wytham village was so sited, e.g. on a wall, that it was inaccessible to ground-moving predators), so it seems more likely that the breakages were caused by movements of the adults themselves in their own nests and by the possible intrusion of other sparrows. Occasional clutches of *P. montanus* breeding in Wytham woods were found apparently part-eaten, possibly by Weasels *Mustela nivalis*.

THE SURVIVAL OF EGGS

Both species lost about 1% of their eggs between laying and hatching (Table 9), and such loss occurred evenly in all clutch-sizes. The loss may be attributed to accidental breakage of the eggs by the parents in the nest. Some eggs in particular were found to have thin, fragile shells. Such actions do not appear to have been an important source of loss of eggs. Damaged eggs were rarely found in the nests; they had almost certainly been removed by the adults. On one occasion I saw *P. domesticus* remove a damaged egg from its nest (Seel 1966).

TABLE 9. *Survival of eggs to the day of hatching in P. domesticus and P. montanus.*

INITIAL CLUTCH-SIZE	NO. OF EGGS LAID	NO. SURVIVING	
		No.	%
<i>P. domesticus</i>			
c/2	72	72	100
c/3	405	400	99
c/4	1576	1561	99
c/5	870	848	97
c/6	78	75	96
c/7	7	7	
Total	3008	2963	98.50
<i>P. montanus</i>			
c/2	2	2	
c/3	9	9	
c/4	152	152	100
c/5	705	699	99
c/6	228	223	98
c/7	77	76	99
Total	1173	1161	98.98

Note. Losses due to destruction or desertion have been omitted from this Table.

HATCHING SUCCESS

A nestling was regarded as being "hatched" when it was completely free of the egg shell. In *P. domesticus* about 12% of all surviving eggs failed to hatch; in *P. montanus* about 7% failed to do so, that is significantly fewer ($P < 0.001$) (Table 10). There was no consistent variation in the proportion of eggs hatching over the range of clutch-sizes of either species.

Fully incubated eggs which failed to hatch were opened in the field. Some (category 1) contained no visible embryo, so were either infertile or contained an embryo which had died at a very early stage; others (category 2) contained a visible embryo which had died during incubation and which had not begun to hatch. Finally, some (category 3) contained an embryo which had died during hatching—the criterion for this was the

TABLE 10. *The hatching success of eggs which survived to the day of hatching in P. domesticus and P. montanus.*

CLUTCH-SIZE AT TIME OF HATCHING	NO. OF EGGS SURVIVING	EGGS HATCHING	
		No.	%
<i>P. domesticus</i>			
c/1	1	1	
c/2	86	71	83
c/3	441	371	84
c/4	1564	1378	88
c/5	765	684	89
c/6	66	57	86
c/7	7	6	
Total	2930	2568	87.65
<i>P. montanus</i>			
c/1	—	—	—
c/2	2	1	
c/3	15	15	
c/4	156	145	93
c/5	705	649	92
c/6	204	195	96
c/7	63	60	95
Total	1145	1065	93.01

Note. All eggs which survived to the expected day of hatching are included as are eggs of failed but fully incubated clutches (i.e. in which no egg hatched), because the reasons for failure appeared to be the same as those for partial failure of surviving eggs in any other clutch.

presence of broken shell around or attached to the embryo. The proportion of eggs falling into each of the three categories listed above was similar in the two species, there being no significant difference between them with respect to the proportion in each category (Table 11).

The data for the eggs in which embryos were observed can be used to obtain an approximate measure of the fertility of the eggs in the two species. Of 2,930 eggs of *P. domesticus*, which survived to the end of the incubation period, 2,706 (92%) were fertile. Of 1,145 eggs of *P. montanus* which survived to the end of incubation, 1,102 (96%) were fertile. The difference is statistically significant ($P < 0.001$) and suggests that the lower hatching success in *P. domesticus* is mainly due to the lower proportion of fertile eggs.

Sparrow embryos which died during hatching did so at a variety of stages from pipping to complete splitting of the shell: premature exhaustion of the food reserves seems a possible cause. Whatever the causes of mortality, at this or earlier stages of incubation, they seem to be quite random in occurrence and are probably due primarily to inherent variation in the structure and physiology of the embryo rather than to the

TABLE 11. *Sources of failure in eggs which survived the incubation period but failed to hatch.*

NATURE OF FAILURE	<i>P. DOMESTICUS</i>		<i>P. MONTANUS</i>	
	No. of eggs	%	No. of eggs	%
Eggs containing no visible embryo	214	62	29	54
Eggs containing visible embryos which died during incubation	108	31	17	31
Eggs containing embryos which died during hatching	24	7	8	15
Total	346		54	

circumstances of incubation. If deficiencies of incubation were important, several eggs would tend to fail in each clutch, but this was rarely observed. Furthermore, no tendency was observed for the embryo in the last egg laid to die more frequently just before hatching than the embryos in the other eggs.

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SUMMARY

Clutch-size, incubation and hatching success were studied in *P. domesticus* and *P. montanus* in 1961 and 1963-64 at Oxford. The most frequent clutch-size was four eggs in *P. domesticus* and five eggs in *P. montanus*. With one exception, colonies of *P. domesticus* showed no significant annual or local variations in its mean clutch-size; in *P. montanus*, however, there were significant annual variations in the mean clutch-size. Both species showed a seasonal increase followed by a decrease in their mean clutch-sizes.

Partial incubation occurred during the laying period of the clutch; sufficient incubation for continuous development of the embryo was apparently achieved when the last egg had been laid in clutches of two and three eggs in *P. domesticus* and in clutches of four eggs in *P. montanus*, but when the penultimate egg had been laid in larger clutches of both species. On average, hatching in *P. domesticus* occurred more or less synchronously in all eggs in clutches of two and three eggs, and in all eggs except the last one laid in larger clutches; the last egg in the larger clutches hatched up to a day after the others. It is suggested that this pattern of hatching was brought about by the pattern of incubation during the laying period.

P. domesticus had a lower hatching success than *P. montanus*, probably because fewer of its eggs were fertile.

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