Seasonal and geographical variation in the clutch size of the Common Treecreeper *Certhia familiaris*

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The clutch size of the Common Treecreeper (n = 299 clutches) was studied in southern Finland in 1974–1983. The mean clutch size was 5.43±0.71(SD) and the mean date of laying was 27 April. One-third of the pairs also laid a second clutch. The seasonal variation in clutch size was peak-shaped. Age and size of the female did not correlate with clutch size. Seasonal variation in clutch size followed the same relation to calendar date in different years. The early breeding attempts produced more young to the next generation than expected. The strategy to start breeding early and to lay also a second clutch allowed the parents to produce more offspring than did those breeding only once in the middle of the season. The geographical variation is analyzed on the basis of literature and nest cards.

The importance of three hypotheses (Food availability, Day-length, Reproduction effort) explaining the peak-shaped seasonal variation in clutch size is discussed. A combination of the "Food availability hypothesis" and the "Day-length hypothesis" was most supported. Calendar effect and geographical variation in the clutch size gave evidence for the "Day-length hypothesis", but the "Food availability hypothesis" may still be more important.

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Introduction

Two different patterns emerge in the seasonal variation of clutch size in temperate-zone passerine birds (Klomp 1970). The more common pattern is a continuous decrease in clutch size during the course of the breeding season. The alternative pattern involves an initial increase to a peak, followed by a decrease. Traditionally the explanations for the seasonal variation have dealt exclusively with declining trends. Three main hypotheses (Fig. 1) are as follows.

The seasonally decreasing food supply has been assumed to be the most important reason for the declining trend (Snow 1955, Lack 1966, Perrins 1969, Hussell 1972, Slagsvold 1975, 1982, Murphy 1978). This hypothesis will be called the *food availability* hypothesis. Lack's (1947) general theory on the determination of the clutch size includes food as a central factor. Lack (1966) also proposed that natural selection in species which only have one brood in a season, has produced a mechanism, which ensures that nestlings are raised when the food supply is at its maximum. Also, Ashmole (1963) proposed that food availability is the major factor creating geographical variation in clutch size (see also Ricklefs 1980). According to this hypothesis it is also possible to explain the peak-shaped seasonal variation in clutch size, if birds begin to breed before the seasonal peak in food abundance.

Another hypothesis, named here as the *reproductive effort* hypothesis, which implies that birds vary clutch size seasonally irrespective of available resources. The reproductive effort is changed much in the way as proposed in Cody's (1966) general theory of clutch size. The trade-off between the available resources and the effort to use them could be connected to the avoidance of the risk of predation (see Slagsvold 1982), or the risk of adults to stay alive at the end of the breeding season or at the following breeding season (cf. Bell 1984, but see Boyce & Perrins 1987). Likewise, Orell & Ojanen (1983) have emphasized that this could be an adaptation to the start of moulting. Moreover, Tiainen (1983) has suggested that the decreasing trend depends on the energetic compromise between breeding and moulting. This hypothesis also includes Hussell's (1972) idea that offspring in broods laid in the beginning of the breeding season have more time to

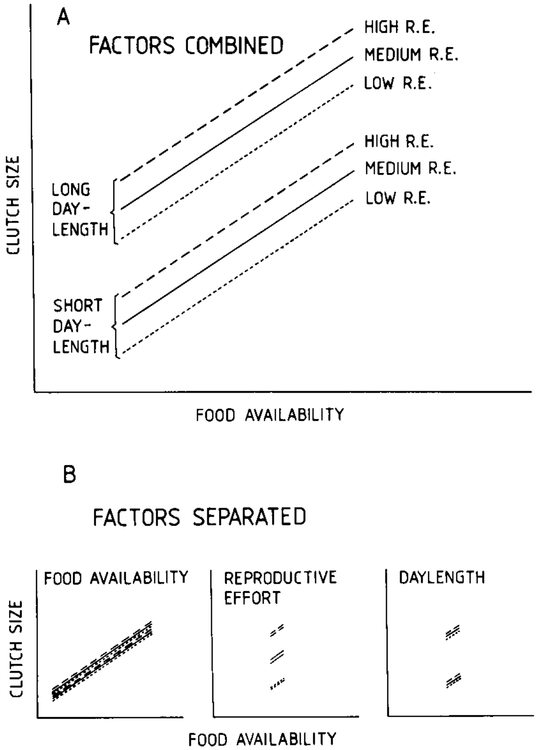

Fig. 1. A graphical illustration of the three alternative hypothesis to explain seasonal variation in clutch size. In the upper figure (A) the effect of the three factors have been combined, clutch size increases with increasing food availability, reproductive effort (R.E.) and daylength. In the lower figure (B) the hypothesis are presented in a pure form, only one of the factors in question influencing clutch size in each case.

collect winter reserves. Clutch size is larger early, because the value of the offspring is higher the earlier laid (see Ekman & Askenmo 1986).

Finally, the *day-length* hypothesis proposes that the time available for feeding limits clutch size (Lack 1966). This time varies with season and latitude. After Lack the hypothesis has largely been neglected (but see, e.g., v. Haartman 1971, Murphy 1978, Yom-Tov & Hilborn 1981).

The Common Treecreeper, *Certhia familiaris* (below: Treecreeper), offers good opportunities for obtaining information on the importance of the above alternatives. This species has a clutch size peak long after the laying of the earliest clutches, a pattern that often has been neglected in the discussion of the proposed explanations. The ecology of the Treecreeper includes features different from the enormously studied and ecologically related tits, *Parus* spp. Unlike tits exploiting the larva peak the Treecreeper, a microhabitat specialist (e.g. Gibb 1954, Nilsson & Alerstam 1976, Alatalo 1980), uses especially spiders as nestling food (Kuitunen & Törmälä 1983).

I will attempt to test the proposed hypotheses using data collected mostly in southern Finland. The three hypotheses can be distinguished by their predictions. The *food availability* hypothesis predicts that the clutch size peak should occur simultaneously with the food maximum, taking into account the delay to the nestling time. The *reproductive effort* hypothesis could apply if predation is strongest at the beginning and at the end of the breeding season. The moult can explain only the end part of the peak-shaped seasonal variation. A seasonal decrease in offspring value predicts a monotonically decreasing clutch size. The *day-length* hypothesis predicts a close connection with clutch size and seasonal, as also geographical variation, in daylength.

Study area and methods

The study area (7.0 × 20.5 km) is situated in Hauho, southern Finland (about 61°10´N, 24°40´E). The area includes 5870 ha of forest growing mostly Norwegian spruce (*Picea abies*), and it belongs to the south-boreal vegetation zone.

The breeding ecology of the Treecreeper was studied using 156 special nestboxes (for details, see Moilanen & Kuitunen 1976, Kuitunen 1985). The fieldwork lasted from the end of March to the end of July in 1974–1979 and 1981–1983 (some additional material for 1984–1986 has been included). The nestboxes occupied were visited weekly, or more frequently if necessary between 15 April and 15 June. Three ornithologists worked separately and about 7000 hours of field work was spent on the study.

Laying date, clutch size, the number of hatchlings and the number of fledglings were registered for each breeding attempt (n = 506, the basic observation units in the analysis carried out). All the breeding females and nestlings and about half of the males were ringed. Wing length was measured using the maximum chord method and birds were weighed to the nearest 0.1 g with a spring balance.

The Treecreeper starts building its nest by placing thin, dry twigs of spruce and spider webs on the bottom of a hole. One single pair often carries twigs into several boxes but the one which is selected for

Table 1. Mean date of laying for the first and the second clutches, the interval between them and the percentage of Treecreeper pairs that laid second clutches in southern Finland in 1975–1978 and 1982–1983. ANOVA between years. Number of cases in parentheses.

Year	First clutch (April or May)	Second clutch (June)	Interval Days	%
1975	24.4. (48)	4.6. (2)	41	24
1976	24.4. (63)	6.6. (9)	43	37
1977	1.5. (56)	18.6. (3)	48	39
1978	8.5. (17)	19.6. (5)	42	62
1982	22.4. (15)	–	–	62
1983	22.4. (28)	6.6. (10)	45	41
Mean	27.4. (236)	10.6. (29)	44	37
P <	0.001	0.002		
F	56.3	8.3		

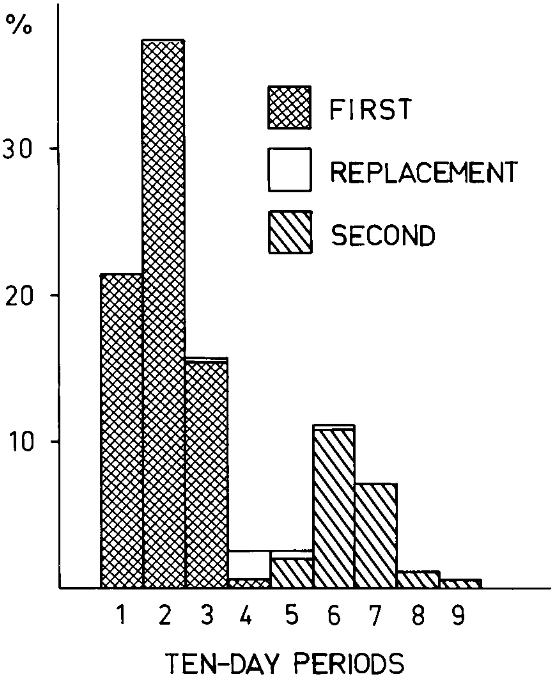

Fig. 2. Start of laying the first, replacement and second clutches of the Treecreeper in relation to laying date in southern Finland. The ten-day periods are as follows: 1 = 13.–22.4., 2 = 23.4.–2.5., 3 = 3.–12.5., 4 = 13.–22.5., 5 = 23.5.–1.6., 6 = 2.–11.6., 7 = 12.–21.6., 8 = 22.6.–1.7. and 9 = 2.–11.7.

breeding is finished with rotten wood or the bast fiber of juniper. Others are often used for the second clutches. A finished nest was regarded as a breeding attempt. According to this definition, the breeding attempts also include cases, in which nests have been rejected during the final phases of nest-building, egg-laying or incubation.

The determination of the laying of the first egg is based on the assumption that the Treecreeper lays one egg daily (no exceptions were observed). In some cases the start of laying was calculated indirectly with the aid of information on the length of the incubation period and growth rate of nestlings. Such estimates were used only when data were lumped into periods of 15 days. A clutch was considered to be completed if one of the three criteria of v. Haartman (1969) was met.

Nest card data and other information was obtained from the Finnish nest card collection in Helsinki and the British Trust for Ornithology in Tring. Unpublished data from the Lithuanian S.S.R. was collected by Dr. Aleknonis.

Results

Timing of breeding

The mean date of the laying of the first clutch averaged as 27 April (SD = 5.8, Table 1). The breeding period was relatively long: the earliest laying date observed was 13 April and the latest date the nestlings were found in the nest was 30 July. The mean laying date of the first clutch varied highly significantly between years (Table 1). In 1977 laying was one week and, in 1978, two weeks later than in the normal years (1975, 1976, 1982 and 1983). The first clutches were laid very synchronously each year, 80 % of the population beginning within 8.5 days.

When the first clutch was unsuccessful, 8% of the pairs laid a replacement clutch and 37% a genuine second clutch after a successful first attempt (Fig. 2). The proportion of second clutches varied significantly between years ($\chi^2 = 13.6$, df = 3, $P < 0.004$), showing a negative correlation with population density ($r = -0.85$, df = 4, $P < 0.05$).

On average, the Treecreeper began to lay the second clutch on 10 June but, as in the first clutches, the difference between years was highly significant (Table 1) reflecting the respective variation in the laying times of the first clutches. The mean interval between the clutches was 44 days (Table 1).

Only once was a second clutch laid after a successful replacement attempt. This case was one of the

Table 2. The variation of the clutch size in the Treecreeper during 15-day periods in southern Finland. The timeperiods are as follows: 1 = 12.4.–26.4., 2 = 27.4.–11.5., 3 = 12.5.–26.5., 4 = 27.5.–10.6. and 5 = 11.6.–25.6. The numbers in parenthesis are excluded in ANOVAs.

	15-day periods											
	1			2			3			4		
Years	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
1975	5.16	0.51	32	5.47	0.64	15	(7.00	0.00	1)	6.17	0.75	6
1976	5.11	0.61	38	5.40	0.64	15	(6.50	0.71	2)	5.79	0.58	14
1977	5.60	0.55	5	5.59	0.64	37	(7.00	0.00	2)	5.60	0.55	5
1978	–	–	0	5.53	0.52	15	(6.00	0.00	1)	(6.00	0.00	1)
1982	4.92	0.28	13	(5.67	0.58	3)	–	–	0	–	–	0
1983	5.27	0.53	26	(6.00	0.00	3)	(7.00	0.00	1)	6.14	0.69	7
Mean	5.16	0.54	114	5.54	0.60	88	6.71	0.49	7	5.91	0.63	33
F	1.9			0.4			–			1.2		
P <	0.12			0.75			–			0.32		

	5			All periods			F	P
Years	Mean	SD	n	Mean	SD	n		
1975	–	–	0	5.39	0.68	54	8.1	0.001
1976	(5.33	–	3)	5.35	0.67	72	4.4	0.01
1977	4.78	1.09	9	5.52	0.80	58	3.3	0.03
1978	5.36	1.03	11	5.50	0.75	28	0.3	0.58
1982	(5.00	0.00	1)	5.06	0.43	17	–	–
1983	–	–	0	5.54	0.69	37	13.1	0.001
Mean	5.13	0.99	24	5.42	0.71	266	19.8	0.001
F	1.5			1.2				
P <	0.23			0.29				

latest breedings (the nestlings were ringed on 31 July at the age of about 11 days). This female laid two or three eggs when the nestlings were still in the former nest, which is unusual.

Otherwise, second clutches were laid immediately after the nestlings of the first clutch had fledged. The main part of the second clutch nest bottom was usually built already in March into a nestbox near the place of first breeding and it usually took only some days to finish the nest. An overlap between the first and second clutch was observed once, in addition to the above mentioned case.

The possible factors often found to affect the timing of breeding include size and age of the parents. The wing length and the weight (weight transformed subtracting or adding the difference between the average values to correspond to the weight at noon) were used to indicate the size of parents. These two size variables were slightly correlated in females ($r = 0.25$, $P < 0.001$, df = 207), but not in males ($r = 0.14$, $P < 0.25$, df = 69).

In my material there was no significant relationship between age, weight or wing length and the laying date of the first clutch.

Clutch size

The clutch size of the Treecreeper varied between three and seven eggs:

Clutch size	3	4	5	6	7	n	Mean	SD	SE
n	2	15	152	112	18	299	5.43	0.71	0.04

The variation was strongly related to the laying date (Table 2). Clutch size increased from the beginning of the breeding season, reached a maximum around 20 May and then decreased to the end of the season (Fig. 3B). The linear regression between clutch size (y) and laying time (x = 1 on 1 March) in the beginning (10 April–20 May) of the breeding season, combining the years, was: $y = 0.035x +$

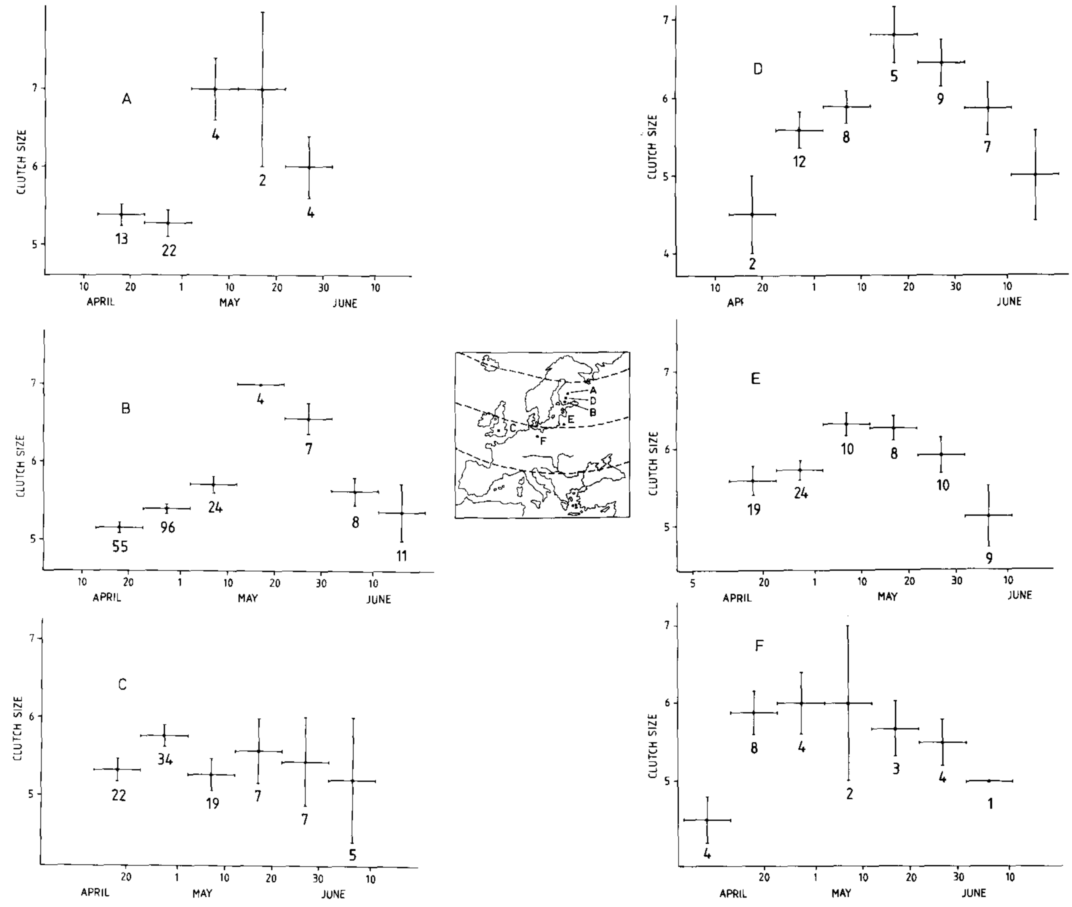

Fig. 3. Clutch size in relation to the laying date in Central Finland (A, Kuitunen & Suhonen, unpubl.), in southern Finland (B, this study), in the British Isles (C, British nest-card material), in the whole of Finland (D, Finnish nest-card material), in Lithuania (E, Aleknonis, unpubl.) and in DDR (F, Schönfeld 1983). The horizontal line indicates the ten days period for which average value has been calculated and the vertical line is the standard error. The geographical position of the study areas is shown in the middle.

3.334, ($r = 0.36$, $P < 0.001$, df = 175), and after 20 May $y = -0.057x + 11.584$ ($r = -0.56$, $P < 0.002$, df = 27).

In my material there was no significant relationship between age, weight or wing and clutch size. Between first (5.35, SD = 0.62, n = 157), replacement (6.25, SD = 0.71, n = 8) and second clutches (5.53, SD = 0.89, n = 57) a significant difference was observed (ANOVA, $F = 7.0$, $P < 0.001$), which was based on the differences in laying date.

Since the laying date was so dominant it was important to test whether clutch size correlated with the calendar date. I tested the "calendar effect" as follows. If the calendar effect is important, then the yearly means in clutch size with respect to the laying date should behave like clutch sizes in single years: for the early part of the season there should be an increase, and for the latter part there should be a decrease. This prediction is upheld, for the regressions were fairly significant between average clutch sizes and the mean laying dates in the different study years ($y = 0.03x + 4.62$, $r = 0.75$, $P < 0.02$, df = 7 for the early part of the season and $y = -0.04x + 9.59$, $r = 0.91$, $P < 0.02$, df = 4 for the latter part, Fig. 4).

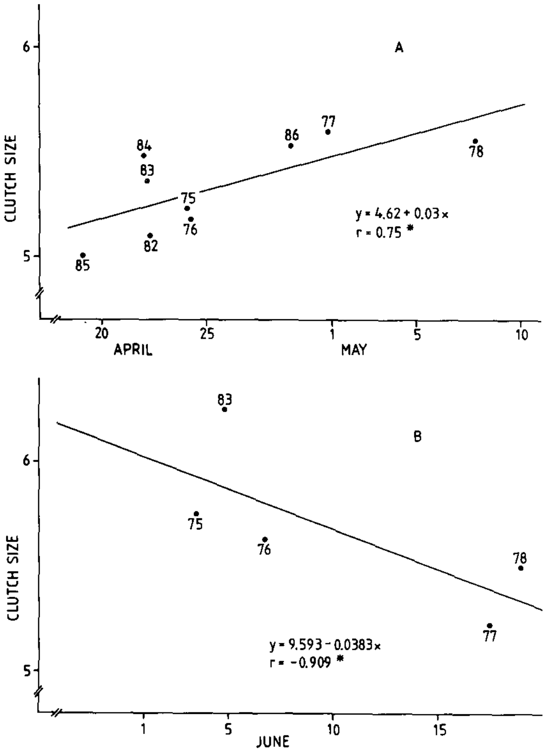

Fig. 4. Annual variation in mean clutch size in relation to the laying date in southern Finland. A = first clutches, B = second clutches.

Table 3. The geographical variation in clutch size of the Common Treecreeper in different studies.

Mean	SD	n	Location	Reference
5.68	1.04	34	Finland	v. Haartman 1969
5.16	1.00	100	British Isles	Flegg 1973
5.55	0.93	11	Michigan, USA	Davis 1978
5.40	0.96	55	Schwarzwald, BRD	Löhrl 1979
6.00	0.56	14	Southern Sweden	Enemar 1981
5.58	0.86	26	DDR	Schönfeld 1983
5.70	0.90	14	Hungary	Kuitunen 1985b
5.82	0.66	56	Lithuania	Aleknonis 1984
5.65	0.91	51	Central Finland	Kuitunen & Suhonen (unpubl.)
5.43	0.71	299	South Finland	This study

These regression equations are quite similar to those calculated from single clutches in different years (above).

Still unexplained variation remained between the years within calender periods. The differences were not significant, however (ANOVA, Table 2).

According to the nest card material, British Treecreepers also show a peak-formed clutch size trend (see also Flegg 1973). This curve is lower and the peak is located about two weeks earlier than for southern Finland (Fig. 3C). The material collected from Lithuania (natural nest-sites, Aleknonis 1976, 1984 and unpubl.) also gives a corresponding trend (Fig. 3E). Both form and peak fall between those observed in this study and results from Britain. The nest card material from Finland gives a trend very similar to that from the restricted study area of this study (Fig. 3D) and unpublished data from Central Finland (Fig. 3A). These results show a geographical clutch size gradient from north or northeast to south or southwest in Europe, with a higher and slightly later seasonal peak in the north and northeast. The average clutch size varied little and there were no clear trends (Table 3).

Breeding success in relation to laying date

The number of fledglings per breeding attempt was positively correlated to clutch size (ANOVA, $F = 6.4$, $P < 0.001$, $df_1 = 3$, $df_2 = 229$, Table 4). In Finland the peak in clutch size is achieved during the period when only replacement clutches usually are laid, and hence few clutches are laid then (compare Fig. 2 and Fig. 3B). Why do the Treecreepers not lay later, although it is likely that they could produce more fledglings per breeding attempt by doing so?

When comparing the productivity of the different phases of the breeding season, the whole season was divided into five 15-day intervals. First, I considered the productivity variation of the same clutch size over different intervals, but no great differences existed between the intervals (Table 4).

There was a seasonal trend in the number of fledglings per breeding attempt similar to that found in the brood size and clutch size. This trend is especially clear, if only the successful or partly successful breedings are taken into account and if losses due to unpredictable factors are excluded (Table 5). It is reasonable to exclude the breedings that have been destroyed by relatively unpredictable factors (predation, competition for nest sites, a sudden death of an adult bird etc.), because they are probably unrelated to clutch size. If the ultimate causes of seasonal trends in clutch size are under study only, predictable factors are of interest.

The most relevant measure of fitness is the number of the recruited offspring. A total of 33 breeding

Table 4. The number of fledglings in different clutch size classes of the Treecreeper in southern Finland in 15-day periods.

	Clutch size								
	3			4			5		
Laying period	Fledglings/ breeding attempt	SD	(n)	Fledglings/ breeding attempt	SD	(n)	Fledglings/ breeding attempt	SD	(n)
12.4. - 26.4.	3.00	0.00	(1)	2.67	1.34	(6)	4.06	1.63	(70)
27.4. - 11.5.	–		(0)	4.00	0.00	(1)	4.23	1.44	(35)
12.5. - 26.5.	–		(0)	–		(0)	–		(0)
27.5 - 10.6.	–		(0)	–		(0)	4.43	0.98	(7)
11.6. - 25.6.	–		(0)	3.67	0.58	(3)	3.64	1.96	(11)
All periods	3.00	0.00	(1)	3.10	1.20	(10)	4.23	1.40	(125)

	Clutch size								
	6			7			All breeding attempts		
Laying period	Fledglings/ breeding attempt	SD	(n)	Fledglings/ breeding attempt	SD	(n)	Fledglings/ breeding attempt	SD	(n)
12.4. - 26.4.	4.52	2.21	(21)	–		(0)	4.06	1.78	(98)
27.4. - 11.5.	4.83	1.86	(41)	4.00	0.00	(1)	4.54	1.67	(78)
12.5. - 26.5.	6.00	0.00	(2)	4.33	3.79	(3)	5.00	2.83	(5)
27.5. - 10.6.	5.18	1.59	(17)	6.25	0.50	(4)	5.14	1.43	(28)
11.6. - 25.6.	–		(0)	0.00	0.00	(1)	3.40	1.92	(15)
All periods	4.94	1.75	(87)	5.09	2.66	(11)	4.49	1.66	(233)

Table 5. Clutch size, number of hatchlings, number of fledglings and next-generation breeders in relation to the time of laying in southern Finland in 1975–1978 and 1981–1983.

	Clutch size			Hatchlings			Fledglings			Breeding adults	
Laying period	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	n
12.4. - 26.4.	5.16	0.54	104	4.63	1.09	114	4.48	1.28	97	0.21	18
27.4. - 11.5.	5.55	0.61	83	5.13	0.85	92	4.85	1.19	78	0.06	4
12.5. - 26.5.	6.67	0.52	6	6.17	0.75	6	6.25	0.50	4	0.25	2
27.5. - 10.6.	5.91	0.64	32	5.40	1.01	35	5.26	1.00	31	0.09	2
11.6. - 25.6.	5.13	0.99	24	4.76	1.09	25	3.39	2.00	18	0.00	0
All periods	5.42	0.71	249	4.94	0.99	272	4.66	1.36	228		
F	17.10			7.90			8.6				
P <	0.001			0.001			0.001				

attempts produced at least one local recruit (breeding young) in the F_1 generation in the study area.

When during the season do breeding attempts most likely produce recruits? In fact the early breeding attempts produced more young to the next generation than expected assuming that offspring dispersal is independent of laying date (laying time of nests with recruits (n = 26) compared with nests without recruits (n = 223), Mann-Whitney U-test, z = 2.54, df = 247, P = 0.01, Table 5).

The clutches laid during the earliest time interval produced next-generation birds from 4.1% of the eggs, which means 0.21 offspring per breeding attempt survived until breeding. Because, on average,

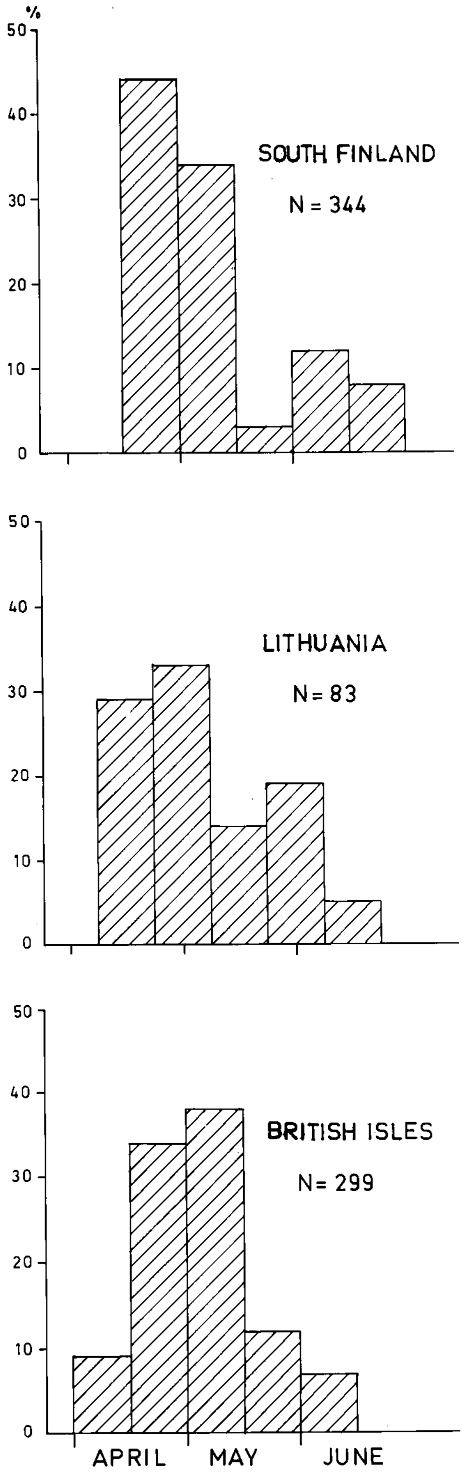

Fig. 5. Start of laying in 15-day periods (%) in the Treecreeper in southern Finland, Lithuania and the British Isles.

36.7% of the pairs also laid a second clutch, this "combined breeding strategy" allowed the parents to produce more offspring to the following year's breeding population than did those breeding only once in the middle of the season. Early breeders sometimes had to lay a replacement clutch, if the first one was destroyed.

The productivity of the second clutch amounted to 1.5% of the eggs laid, which means 0.09 offspring per breeding attempt survived until breeding, while the productivity of the replacement clutches was 0.25 offspring. This means that the strategy to start breeding early produced next-generation birds as follows: 36% of the birds bred twice, producing 0.30 next-generation birds, 57% bred once, producing 0.25 birds, and 7% laid a replacement clutch and produced 0.25 birds to the next generation. The average production would then be 0.25 next-generation birds. It is impossible with these figures to calculate the absolute production per pair because of the considerable dispersal of young birds.

The alternative strategy to lay one clutch in the time of maximum productivity would also have produced 0.25 next-generation birds per breeding attempt, but that strategy was not used probably for two reasons. First, if a later clutch fails, the replacement clutch will be small, if at all possible. Second, an early clutch has an option of a better production if the pair is able to produce two clutches. In the British Isles the alternative strategy still seems to be a better strategy and in Lithuania both strategies seem equal according to the breeding attempt distribution in relation to laying date (Fig. 5).

Predation by the Great Spotted Woodpecker (*Dendrocopos major* L.) may be locally relatively intensive. Since five nearby nests were destroyed in 1976 during period two (27 April–11 May), this fact could explain why period two produced so few next-generation birds. Still, after removing the influence of this predator, the figures did not change essentially (1.1%, cf. Tables 5 and 6). The Great Spotted Woodpecker has been observed to be the most important nest predator during the nestling stage, but not later, whereas the weasels were not observed to rob Treecreeper nests.

Discussion

The food availability hypothesis

The peak-shaped variation in clutch size of the Treecreeper is typical for many multi-brood species (see

Table 6. The number of Treecreeper fledglings (1) per one breeding in southern Finland in 15-day periods. Years 1975–1978 and 1982–1983 are pooled. The numbers include also those breeding attempts, which were destroyed by unpredictable factors (predation, interspecific competition, death of the adult, comp. text). (2) Number of cases, (3) Number of totally destroyed cases, (4) Number of cases destroyed by the Great Spotted Woodpecker, (5) Fully destroyed nests as percentages of the whole number, (6) Nests destroyed by woodpecker as percentages of the whole number and (7) about the destroyed. The destroyed cases do not include those abandoned because of man.

	1	2	3	4	5	6	7
Laying period	Fledglings/ nest	Number of nests	Fully destroyed nests	Nests destroyed by woodpecker	3/2 %	4/2 %	4/3 %
12.4. – 26.4.	3.98	149	16	3	10.7	2.0	18.8
27.4. – 11.5.	4.11	117	18	8	15.4	6.8	44.4
12.5. – 26.5.	4.17	9	3	2	33.3	22.2	66.7
27.5. – 10.6.	5.00	41	2	1	4.9	2.4	50.0
11.6. – 25.6.	3.71	27	4	2	14.8	7.4	50.0
All periods	4.13	343	43	16	12.5	4.7	37.2

Lack 1966 and Klomp 1970) or species building nests on the ground (Slagsvold 1982). Usually the peak-shaped variation in clutch size is not typical for foliage gleaners. Maybe the food supply for them does not increase as gradually as it does for the species foraging on ground (see Slagsvold 1982) or on treetrunks as does the Treecreeper, but explosively after foliage has come out (see Gibb & Betts 1963). Multibrooding is probably a consequence of gradually increasing food supply and long breeding season.

Can availability of food for nestlings explain the seasonal variation in the Treecreeper clutch size? In the study area Treecreepers fed the nestlings mostly with spiders (77% of the offered biomass, Kuitunen & Törmälä 1983). The timing of the appearance of the Arachnida on the treetrunk surface has still been studied little. On the coniferous forest floor the spiders show two population peaks; the first one in May and then in August. The July minimum is about one-half of the peaks (Huhta 1965, 1971).

The two most abundant spider species on the spruce bark belong to the family Thomisidae, the most important spider group used as food by the Treecreeper nestlings. They show a density maximum in July (*Philodromus aureolus*) and in August (*Drapetisca socialis*) (Palmgren 1950, 1975).

The early and the long breeding season of the Treecreeper is advancing the peak-shaped pattern. This may be due to the warm conditions of the trunk surface, the microhabitat used by the Treecreeper. If the microclimatical conditions on bark are compared with the conditions on the ground during the same time, the difference is great. In Finland ground is often covered by snow when Treecreepers start breeding. The conditions in the tree canopy are hardly better at that time. The dark trunk surface of the Norwegian spruce (*Picea abies*, the dominant tree species in the study area) absorbs solar radiation quite well. Jackson (1979) has found temperature differences up to 12°C between opposite sides of the treetrunk. When the sun is shining under 45° above the horizon, it is warming vertical treetrunks more than other forest structures. This causes the early and quick melting of snow or ice cover and early recovery of invertebrates, which probably offer food supply earlier for the Treecreeper than for many other species in the forest bird assemblage. It is probable, therefore, that the variation in the food supply can explain much of the seasonal variation in the clutch size.

The reproductive effort hypothesis

This hypothesis predicts that Treecreepers would increase their reproductive effort for midsummer, even if the conditions for feeding the nestlings would not be the best at that time. This is unlikely for several reasons. The value of offspring is highest for early nests, as indicated by the higher number of recruits at that time. Hence, the early born offspring are most valuable, and if effort in terms of the costs for adults varies, adults should presumably reduce monotonically that effort over the summer. Neither does the risk of predation mirror the variation in clutch size, since predation by the Great Spotted Woodpecker was most intense when the clutch size was still increasing (cf. Slagsvold 1982). Finally, it is possible that the costs of breeding are higher at the end of summer for adults because of the needs for molting, which may be related to the reduction of clutch size at the end of summer, but it cannot explain the initial increase of clutch size before midsummer.

The day-length hypothesis

If the seasonal and geographical variation of day length correlates with clutch size variation as it seems to do in Treecreepers, it means that the length of daylight could be a limiting resource in addition to food.

If it were a minimum factor, it would mean that food is limiting and in consequence it is necessary for the Treecreeper also to use the extra time when available. It is probable that food is limiting and the foraging time may be important because of the microhabitat the Treecreeper uses. The species forages about 95% of its time on trunks (Alatalo 1982), but large trunks occur patchily and the open area between the trunks is quite useless for the Treecreepers. Therefore the Treecreeper has a relatively large home range (about 10 ha, Schnebel 1972, Kuitunen unpubl.). Spruce forests are also shadowed and may be too dark in the twilight hours for a visual forager such as the Treecreeper.

Gibb (1954) reported on the activity of *Parus* spp., the Goldcrest, *Regulus regulus*, and the Treecreeper. The Treecreeper was most often seen to forage when first observed (92.4% of the cases; the corresponding percentage was only 69.5% for the Great Tit, *Parus major*).

Murphy (1978) tested the importance of the length of daylight for the House Sparrow, *Passer domesticus*, but he did not find any clear correlation. Yom-Tov & Hilborn (1981) estimated that the Great Tit adults would be able to raise one fledgling more in England if there were about 35 minutes more daylight. This observation is in good agreement with Lack's (1966) hypothesis on the increase of day-length in explaining the increasing clutch size according to latitude. Still, the meaning of the day-length variation needs more careful analyzing of the "calendar-effect" before final answers can be found.

Calendar-effect

The calendar-effect observed in the Treecreeper means, in this study, that the Treecreeper lays the same clutch size on the same date in different years (see v. Haartman 1971) in a given locality. The reason why clutch size in some species correlates with the calendar date may be due to either (1) the individual benefits of using the calendar to adjust the breeding and clutch size for the same directional phenological (e.g. food supply, Food availability hypothesis) variation (see Ashmole's (1963) hypothesis), or (2) the individual directly benefits from the daylight length variation (foraging time, "Day-length hypothesis").

The calendrical variation of day length is the only environmental factor that is preserved very predictably from year to year. The use of daylength variation as an indicator is probably an easy way to adjust the clutch size to react to variation in environmental resources.

When Lack (1966) suggested that clutch size is related to the daylight period and, as a result, there would exist the calendar-effect, Perrins (1965) objected that the clutch size peak occurred too early. It should coincide with the time when the nestlings need the most food. However, Snow (1955) had already found the necessity of the time lag.

For most species with peak-shaped seasonal variation the maximum average clutch size does not coincide with the time the nestlings are largest in the nest, during the time of summer solstice. However, for the Treecreeper this is the case. The peak of the clutch size occurred on about 21 May, and adding seven days for laying, 15 for incubating and 15 for nestling time gives 27 June. Geographically the peak varies slightly with a one or two week earlier peak in the south, which indicates that either food is more important or the nestlings develop more slowly in the south. The difference cannot be so great although there exists a similar directional trend: the nestlings grow more slowly in Hungary than in two study areas in Finland (ANOVA, $F = 15.7$, $df_1 = 2$, $df_2 = 23$, $P < 0.001$, unpubl. results, see Kuitunen 1987). The difference between southern and central Finland was not significant but there clearly existed the same directional trend.

The calendar-effect has been observed earlier in species with clutch size monotonically decreasing: the Pied Flycather, *Ficedula hypoleuca* (v. Haartman 1971, 1982, Järvinen & Lindén 1978) and the Magpie, *Pica pica* (Törmälä pers. comm.), but once also in a species with an increasing trend in clutch size, namely in the Starling, *Sturnus vulgaris* (Feare 1984).

The clutch size of the Treecreeper seems, according to these results, to be adjusted to come up to the expected variation in the food supply and its foraging possibilities (daylight variation). The laying date depends on the best alternative which will enable them to produce maximally within the limits that clutch size trend forms. The essential feature for the typical breeding pattern realized by the Treecreeper is to produce two broods during a single breeding period, because this is a more productive alternative than to breed only once.

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Selostus: **Puukiipijän *Certhia familiaris* pesyekoon vuodenaikainen ja maantieteellinen muuntelu**

Puukiipijän pesyekoon määräytymistä suhteessa munintaaikaan tarkasteltiin kolmen hypoteesin perusteella: 1) Ravinnonsaatavuushypoteesin mukaan pesyekoko määräytyisi pesäpoikasille tarjolla olevan ravinnon perusteella vaihdellen vuodenajan ja maantieteellisen sijainnin perusteella. 2) Lisääntymispanoshypoteesi tarkastelee mahdollisuutta, etteivät puukiipijät käyttäisi maksimaalisesti saatavilla olevia resursseja (ravinto, aika), vaan lisäisivät kelpoisuuttaan turvaamalla joko oman säilymisensä seuraavaan lisääntymiskauteen tai tuottamalla laadullisesti parempia jälkeläisiä tuottamalla niitä määrällisesti vähemmän kuin resurssien avulla olisi mahdollista. 3) Päivänpituushypoteesi tarkastelee mahdollisuutta, että puukiipijä käyttäisi vuodenaikaisesti ja maantieteellisesti vaihtelevaa valoisan ajan pituutta hyväkseen lisäämällä saalistusaikaa ja ruokittavien poikasten määrää vastaavasti.

Tutkimus toteutettiin Etelä-Suomessa 5870 ha:n kokoisella kuusivaltaisella tutkimusalueella vuosina 1974–1979 ja 1981–1987. Lisäksi käytettiin julkaisematonta aineistoa sekä Keski-Suomesta että Liettuasta ja pesäkorttituloksia sekä Suomesta että Brittein saarilta.

Puukiipijä aloitti munintansa tutkimusalueella keskimäärin 27.4. (n = 236) ja muni 5.43 (n = 299) munaa pesyettä kohden. Pareista 7.6% teki uusintapesyeen ensimmäisen yrityksen epäonnistuttua ja 36.9% muni toisen pesyeen. Pesimäikäisiksi selviäviä poikasia puukiipijäemot tuottivat sitä paremmin mitä aikaisemmin ne pesivät. Käpytikan pesärosvoilulla ei todettu olevan suurta merkitystä poikastuottoon.

Tutkituista tekijöistä ainoastaan muninta-aika vaikutti pesyekokoon. Pesyekoko kasvoi pesimäkauden alusta saavuttaen huippunsa n. 20.5., jonka jälkeen pesyeet pienenivät. Pesyekoko vaihteli eri vuosina samalla tavoin suhteessa kalenteripäivämäärään.

Varpuslinnuilla tavataan kahta vaihtoehtoista vaihtelumallia pesyekoossa muninta-ajan suhteen. Tavallisin on tasainen lasku pesimäkauden aikana. Puukiipijä edustaa toista vaihtoehtoa, jossa pesyekoko ensin kasvaa ja myöhemmin pienenee. Vaihtelua selitti parhaiten ravinnonsaatavuus- ja päivänpituushypoteesien synteesi. Ravinnon saatavuus luo resurssipohjan, joka määrällisesti ei ilmeisesti vaihtele kovinkaan jyrkästi, koska puukiipijä syö etenkin hämähäkkejä toisin kuin tiaiset, jotka käyttävät hyönteisten toukkahuippua. Koska ympäristö on suhteellisen ennustettava ja ravinnon tarjonta varsin tasaista, saalistettavissa olevan ravinnon määrä vaihtelee päivänpituuden mukaan siten, että valoisimpana aikana puukiipijällä on runsaimmin aikaa löytää saalista. Tätä käsitystä tukivat tulokset pesyekoon kalenterisidonnaisuudesta ja päivänpituuden vaihtelua vastaavasta pesyekoon maantieteellisestä muuntelusta. "Lisääntymispanoshypoteesia" tulokset eivät tukeneet kovin voimakkaasti, vaan puukiipijät näyttävät käyttävän mahdollisimman tarkasti tarjolla olevat resurssit hyväkseen.

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