Nestling growth in three *Phylloscopus* warblers in Finland

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The increase of wing length and body weight was studied in nestlings of *Phylloscopus trochilus, Ph. sibilatrix,* and *Ph. collybita* in S Finland in 1972—76. Wing length was used to determine age if the date of hatching was not known. The weight of nestling *trochilus* and *sibilatrix* increased at the expected rate, but greatly reduced rate was found in *collybita.* The nestlings of all three warblers attained their final weights at the age of about 9 days, but they stayed in their nest until the age of 12—14 days, when their wing length was 67—72 % of the adult wing length.

The intraspecific variation in the growth of the wing length of nestling *trochilus* is not very wide, but the weight increase varies greatly, presumably depending on the food supplied to the nestlings. Young in large broods grew faster, but remained lighter than young in small broods. Probably, parent birds with large broods overcompensated the increased stimulus for feeding, but their maximum feeding capacity was attained earlier than with small broods. Young in late broods also remained light, which may be due to the increased energy demand of the parents at the beginning of the moult or the decrease in the food available. No real between-year differences in the growth pattern could be shown. The growth patterns at Lammi were not found to differ from those of *trochilus* in N Sweden or *sibilatrix* in SW Germany. The aging of nestlings is discussed.

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Introduction

The growth pattern of nestlings have been studied in a great number of bird species (for reviews, see RICKLEFS 1968, 1973), and always show some intraspecific variation. Since the papers of LACK & SILVA (1949) and LEES (1949), many field studies have been made of the effect on growth of the quantity of nutrition. In passerine birds the final weights of the young tend to decrease with increasing broodsize, but this depends on the food conditions in the particular year, season, and habitat (HOLCOMB 1970, ASKENMO 1973, VAN BALEN 1973, and DYRCZ 1974; see also LACK 1966, RICKLEFS 1968, and KLOMP 1970). The effect of the food supply on the nestlings also depends on egg size (SCHIFFERLI 1973, O'CONNOR 1975a), and hatching order (e.g. GIBB 1950, LACK 1966). In laboratory experiments, BERTHOLD (1976) showed that the growth rate is also affected by the quality of the food. RICKLEFS (1968) raised several further questions about the nature and causes of intraspecific varia-

TABLE 1. Adult wing lengths (mm) and weights (g) of three *Phylloscopus* warblers measured in the study area during the breeding seasons 1972—76 (from own unpublished data).

	Wing length $\bar{x}$ ±S.D.	n	Weight $\bar{x}$ ±S.D.	n
trochilus	68.99±3.29	159	9.38±0.82	169
sibilatrix	77.32±2.44	31	10.05±0.81	31
collybita	63.88±3.44	8	7.81±0.54	11

tion in growth patterns. These include the extent to which the observed variation is inherited; the nature of the selective forces acting on the growth pattern; how changes in the course of growth influence the ultimate fitness; and the causes of seasonal variation in the growth pattern within a local population. LACK also discusses the adaptive significance of growth rates (e.g. 1968).

This study deals with nestling growth in three *Phylloscopus* warblers common in Finland. The data are most extensive for the Willow Warbler *Ph. trochilus*, in which intraspecific variation was studied. The growth patterns of the Wood Warbler *Ph. sibilatrix* and Chiffchaff *Ph. collybita* are used for interspecific comparison. The three species studied are closely related and similar in appearance. The Wood Warbler is the largest and the Chiffchaff the smallest (Table 1). The Willow and Wood Warblers live sympatrically in the mixed forest habitats of my study area, whereas the Chiffchaff, preferring spruce forest, is segregated from the others by its habitat.

Material and methods

The work was performed at Lammi Biological Station (61.03 N, 25.03 E), S Finland, in 1972—77. The data consist of about 1970 records of the wing length and weight of 451 Willow Warbler nestlings from 76 broods (the period 1972—76 only), 328 records for 101 Wood Warbler nestlings from 17 broods, and 187 records for 30 Chiffchaff nestlings from six broods.

The wing lengths were measured to the nearest 0.5 mm with a ruler. The wing was flattened on the ruler and straightened sideways as in the maximum method by SVENSSON (1970). Small nestlings were weighed with a 10-g Pesola string balance (accuracy 0.05 g), and large nestlings with a 30-g balance (accuracy 0.1 g). The records were usually made daily from the discovery of the nest to the day of fledging, if the young were not taken earlier by predators. In the first two years the young were seldom handled after day 8—10, for fear of their leaving the nest too early. The nests were visited only in the late afternoon or in the evening, except in 1976, when the Willow Warbler nests were also visited in the morning.

In 1976, one Willow Warbler nest containing six young was visited four times a day, to examine the daily growth rhythm. The observations within each day were fitted by the least squares method, and the equations obtained were used to refer all the measurements to 18.00 hr.

Only 18 Willow Warbler nests were found early enough to record the exact time of hatching. Preliminary wing growth curves were constructed from these records for aging the broods with unknown hatching dates. The final curves were constructed from the total material. Brood averages were used for ageing. If one nestling was a day younger than its siblings (see below), it was excluded from the calculation of the average. The Wood Warbler and Chiffchaff broods were aged in a similar way. In addition, their brood averages and daily increase of wing length were compared with the growth curve of the Willow Warbler to check the reliability of the result. The distribution

TABLE 2. Distribution of broods by age (in days) when found (≦0 = found with eggs, hatching recorded).

	≦0	0.5	1	2	3	4	5	6	7	8	9	10	11	12	13	14
trochilus	6	11	8	4	4	7	5	8	4	5	4	3	3	1	—	1
sibilatrix	1	4	2	1	1	—	—	1	1	1	2	2	—	1	—	—
collybita	2	—	—	2	—	—	—	—	—	—	—	—	1	1	—	—

of the broods by age on the day of finding is presented in Table 2.

The age of a nestling was recorded as 0 if it was seen hatching or with the down still wet, and could accordingly not yet have been fed by its parents. The age of all other young found on the hatching day was recorded as 0.5, the age on the following day as 1, etc.

The weight data were used to construct growth curves. The logistic equation

$$\frac{dB(t)}{dt} = rB(t) \left(\frac{B_{max} - B(t)}{B_{max}}\right), \quad (1)$$

(where $B(t)$ is the average weight on day t, B_{max} the weight approached asymptotically, and r the constant which gives the growth rate) was chosen since Ricklefs (1968) found that it described passerine growth better than the equations of Gompertz or von Bertalanffy.

The curves were fitted using Marquardt's iterative algorithm (Conway et al. 1970) and the integrated form of eq. (1):

$$B(t) = \frac{B_{max}}{1 + \exp(c + rt)}, \quad (2)$$

where c is an integration constant. Growth was examined in terms of the means of the field material, and parameters from the fitted equations i.e. the asymptote B_{max} and growth rate r. For the study of the intraspecific variation in the growth patterns of the Willow Warbler, the data were grouped according to the brood size, time of season, and year. For the study of the seasonal variation, the first group (early) was formed from broods hatched before 18 June (1972, 1973, 1975, 1976) or before 25 June (1974). The second group (middle) was formed from broods hatched in the period 19—25 June or 26 June — 2 July, and the third group (late) from broods hatched after 26 June or 3 July (see Table 3). For fitting equation (2), the averages of the total material of the Willow Warbler were used for ages 0 and 0.5 in all the groups.

The growth of the wing length was studied only in terms of means. The wing data for the Willow Warbler were grouped in the same way as the weights.

Table 3. Date of hatching of the Willow Warbler population at Lammi Biological Station in 1972—76.

	$\bar{x}$	Range
1972	21 June	15 June — 5 July
1973	21 June	15 June — 28 June
1974	29 June	22 June — 15 July
1975	23 June	7 June — 2 July
1976	20 June	12 June — 25 June

Growth patterns

The young always hatched asynchronously. In Willow Warbler nests, the first chicks usually hatched in the morning, and the others later in the day. Of the 18 nests where the hatching times of the young were exactly recorded, all the young hatched on the same day in eight nests, while the last one hatched on the following day in 10 nests. Once the first two chicks were observed to hatch in the evening. The younger nestlings could easily be recognized by their shorter wing lengths and lower weights until the age of about 8—10 days, as the difference from the average of the larger siblings roughly equalled the daily increment, and the difference from the second smallest siblings was about half the daily increment. When this difference was used to identify younger nestlings in other broods, it appeared that one nestling was one day younger than the others in 46 broods, and two nestlings in two broods (total material 74 broods), but 15 of these determinations were made on day 8 or later, and probably include mistakes. It can be concluded that the last young hatches on the following day in every second Willow Warbler nest.

The reliability of the ageing criteria was tested by determining the age of all broods whose hatching date was known from the wing lengths and weights given for each day in Appendix 1 (Table 4). The probability of incorrect determinations is quite high. It presumably depends on the mean time of the day at which the young hatched, because most of the incorrect determi-

TABLE 4. Accuracy of age determinations in Willow Warbler broods where the real age was known: numbers of underestimates (—), correct estimates (*c*), and overestimates (+). Seven broods are from 1977; 5.3 determinations per brood could be made.

Age (days)	—	c	+
1	4	15	—
2	1	13	1
3	3	10	—
4	4	9	—
5	2	7	1
6	3	8	—
7	5	7	1
8	2	6	3
9	3	5	2
10	1	2	1
11	2	—	—
12	2	—	—
13	2	—	—
14	1	1	—
total	35	83	9

nations came from the same broods throughout the nestling period, and the brood averages were usually very near the middle of two age-group averages in these cases. The effect of this on the calculation of the growth patterns will be considered later.

Differences in wing lengths and weights were also used to identify younger and older chicks in the Wood Warbler and Chiffchaff broods. In the Wood Warbler broods, one nestling was 1 day younger than its siblings in eight broods, and two nestlings in one brood (total material 16 broods). In the Chiffchaff broods, one nestling was one day younger in one brood, and one nestling was one day older in one. The younger nestlings in all the warbler broods were always treated within their own age groups before further analysis.

At the time of hatching, the wing length of the Willow Warbler is 5.5—5.8 mm (see Appendix 1), and it increases evenly without any observable daily variation (Fig. 1). At the beginning of growth, before the fast phase, most of the variation between nestlings is due to the insufficient accuracy of the measurements, as the wing length is very small. Later, the variation is caused by inherent and external factors. Towards the end of the nestling period, the curves can be divided into two groups (1, 2, 5, 6 and 3, 4 in Fig. 1). A similar more or less clear division into two groups could also be seen regularly in many other broods. This is apparently due to the marked sexual size differences in *Phylloscopus* warblers (unpublished material), which seem to become evident fairly early, at the age of 5—6 days. This could be tested with eight birds from various broods, six males and two females, which were recaptured and sexed when the growth period was over. All of them could have been sexed correctly in the nest, according to the wing length, except two males, for which the determination

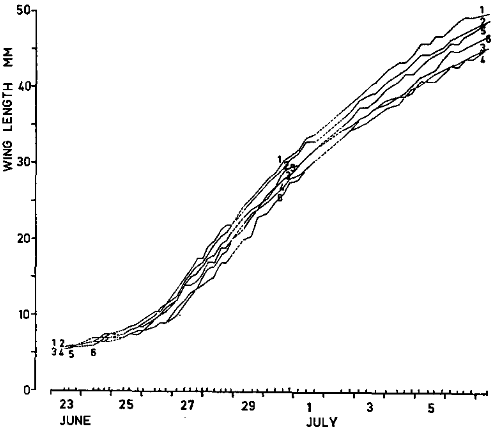

FIG. 1. Growth of wing length in a 6-nestling brood of the Willow Warbler. Measurements were made four times a day, except in the areas of the broken lines. The marks under the *x*-axis indicate midnight (24.00 hr), and those over it the times of the observations. Note that nestlings no. 6 is one day younger than its siblings.

would have been unsure. Sexing from the weights would also have succeeded in most cases. This would have been impossible for one female, but this brood was weighed only once, and unsure for two males.

The hatching weight of the Willow Warbler young is usually 0.80—0.90 g, exceptionally only 0.70 g (see App. 1). The weight increase has a marked daily cycle (Fig. 2), which becomes evident in the fast phase of growth, and is very pronounced near and at the time of the final weights. The faeces in the cloaca were subtracted from the weights used in Fig. 2, to make all the daytime weighings comparable; the intestine processes food continuously, but the dropping of faeces is discrete. No feeding takes place in the night, and the nocturnal weight decline is due partly to the emptying of the gut, and partly to the metabolization of energy reserves in postabsorptive condition. As no figures were available for the nocturnal defaecation rate, the number of droppings had to be estimated from the changes in the indices of faeces in the cloaca. Evidently, one or sometimes possibly two droppings are voided per night, probably very early in the morning. Faeces were responsible for about half of the nocturnal weight decrease.

Figs. 3 and 4 show the overall increase of wing length and weight in all the three *Phylloscopus* species studied. In all of them the weight increase is more rapid than growth of the wing. The rate of weight increase is highest in the Willow Warbler and lowest in the Chiffchaff (Table 5), the difference between these two species being nearly significant (*t*-test, $P < 0.10$). The maximum weights, which are the same as the adult weights (see Table 1), are attained at about 9 days. The logistic equation (2) fitted for the young Willow Warblers whose age was known exactly is given separately, to check the effect of the incorrect age determinations in other broods. The difference is small and not significant ($P > 0.50$). The wing length is still increasing when the young fledge. At the age of 14 days the wing has attained 70—72 % of the adult length, but the young can fly poorly at least at 13 days.

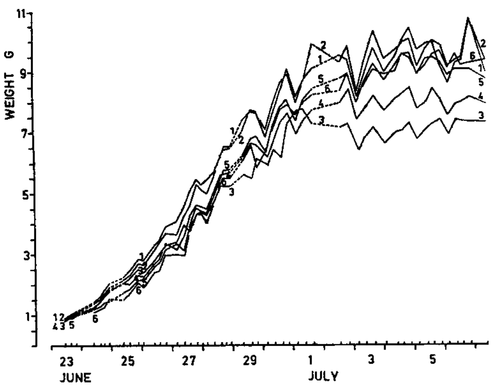

FIG. 2. Weight curve for the 6-nestling brood of the Willow Warbler. Explanations as in Fig. 1.

The curves for wing length in the Willow Warbler presented in Fig. 5 illustrate the variation between brood sizes and seasonal groups. The variation is not great, but the sequence of the curves for the various brood sizes is remarkable (see below). No diagram is given for the different years, because no between-year differences were found in the growth patterns.

Fig. 6 shows the weight curves for Willow Warbler broods of different sizes. During the rapid phase of growth, the young in larger broods seem to be heavier than the young in smaller broods. At the age of 7—9 days, the young in broods of 4—6 become heavier than the young in broods of 7; by that time the young of the latter broods have attained their final

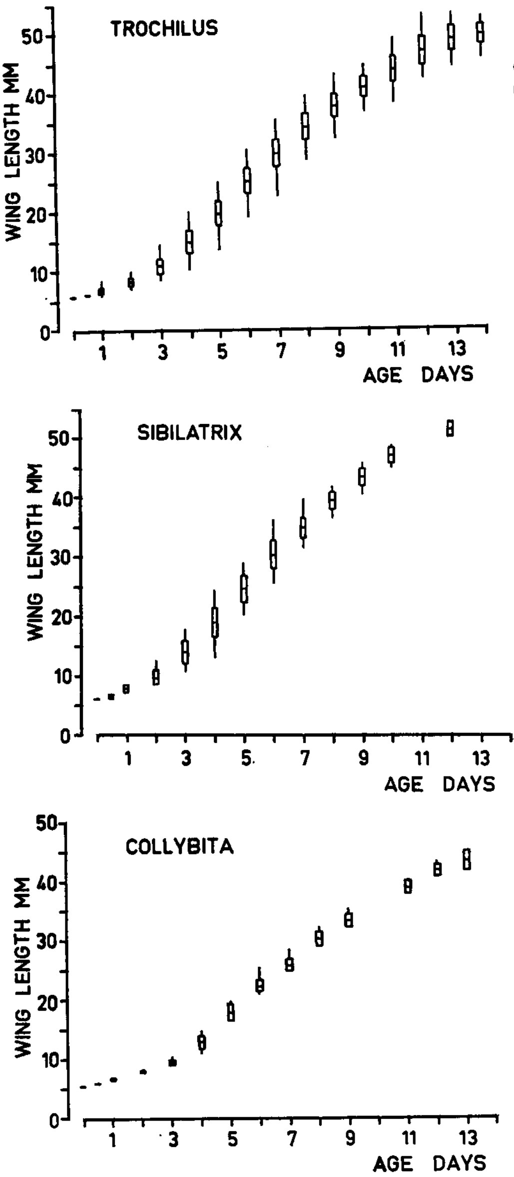

Fig. 3. Growth of wing length in nestling Willow Warblers, Wood Warblers, and Chiffchaffs. Mean, standard deviation, and range of variation shown (see App. 1). In the Wood Warbler the weight of nestlings aged 12 days are given separately.

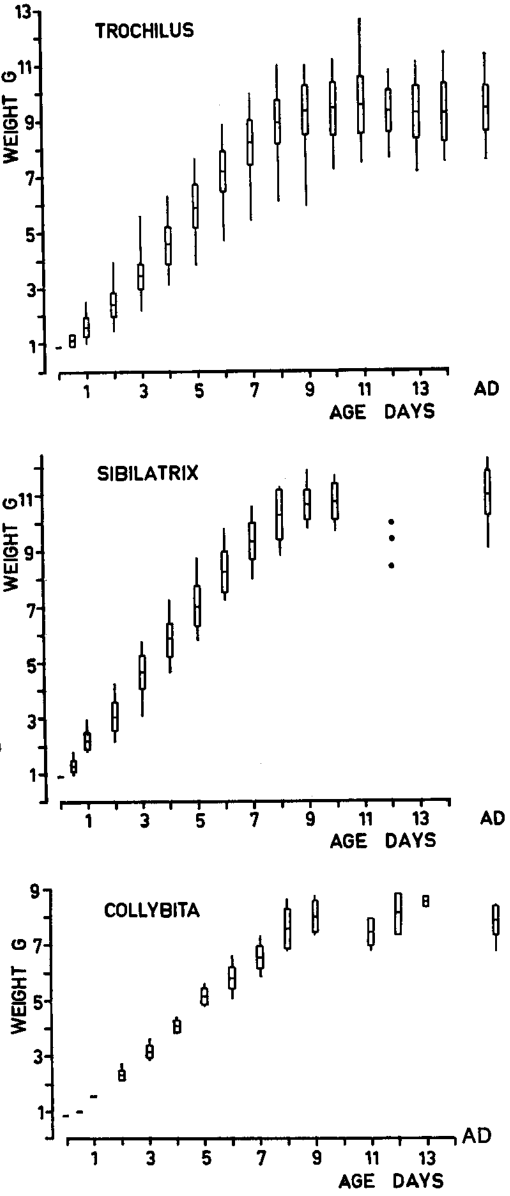

Fig. 4. Weight increase in nestling Willow Warblers, Wood Warblers, and Chiffchaffs. For explanations, see text for Fig. 3.

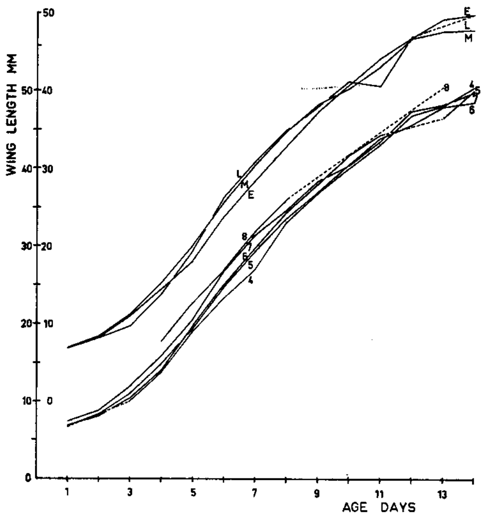

FIG. 5. Wing length curves for Willow Warbler nestlings hatched at different times of the season (*E* early, *M* middle, *L* late; scale on the right side of *y*-axis) and in broods of different sizes (4—8; scale on the left side of *y*-axis). Sizes of samples given in App. 2.

weights, while the young in smaller broods are still gaining weight. The young in broods of 6 lose little weight during the last few days of their nestling time, while the young in broods of 4—5 still gain considerably. Only two broods with 8 young were found. The first, which could be examined on days 4—8, fits the above trends well, but in the second one, which could be examined on days 10 and 13, the young were very heavy. However, all the groups have some broods that deviate strongly from the others. As the weight increase in brood-size classes of 4—6 does not fit the logistic model during the last few days, equation (2) was fitted for both the whole nestling period and the days 0—10 in all the brood-size classes (Table 5). For the whole nestling period, the sequence of the parameters accords with brood size, the asymptote being highest and the growth rate slowest in brood size 4. For the period 0—10 days, the asymptotes and growth rates differ little between the broods with 4—6 young, but the young in broods of 7 have the lowest asymptote and the fastest growth rate. The inverse correlation between the two parameters is high, so the differences in the asymptote partly explain the differences in the growth rate. The levels of significance of the differences are given in Table 6. To conclude, young in small broods become heaviest but grow slowest, and young in large broods stay lightest but grow fastest.

Fig. 7 shows the weight curves of nestlings hatched in the early, middle, and late part of the season. The asymptotes of the fitted equations (Table 5) decline during the season, but the growth rates increase. The differences are not significant ($P > 0.10$), but the trend is clear. The differences become still more obvious if the seasonal decline in brood size is also taken into account (see Table 7).

Fig. 8 shows the weight curves of Willow Warbler nestlings in different years. The maximum weights in 1973

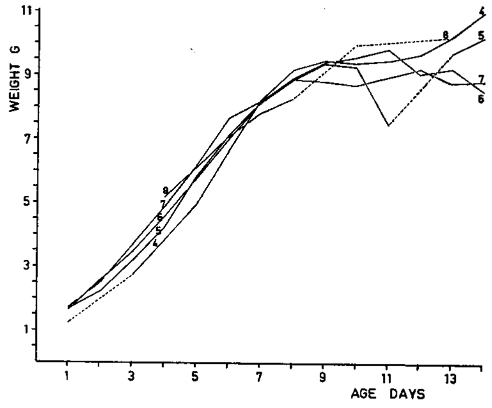

FIG. 6. Weight curves of Willow Warbler nestlings in broods of different sizes (4—8). Sizes of samples given in App. 2.

TABLE 5. Logistic equations describing nestling growth in *Phylloscopus* warblers. For *trochilus* the equations fitted to the total material and those for the broods where the exact date of hatching was known are given separately. Two equations are given for the different brood sizes, the first for the whole nestling period (14 days, n = 15 or 16) and the second for days 0—10 (n = 11 or 12). In the second equation for 1976 *(corrected)* the weights of faeces in the cloaca were subtracted from the body weights. The groups *early, middle,* and *late* denote the time of season at hatching. n gives the number of means which were available or used in fitting. The correlation (R) between the asymptote (*Bmax*) and the growth rate (r) is also given.

	Bmax ± S.E.	c ± S.E.	r ± S.E.	n	R
trochilus	9.568 ± 0.098	2.309 ± 0.086	0.574 ± 0.024	16	0.561
exact	9.536 ± 0.114	2.336 ± 0.106	0.576 ± 0.028	16	0.561
brood size 4	10.446 ± 0.222	2.629 ± 0.197	0.537 ± 0.043	15	0.618
	10.540 ± 0.406	2.664 ± 0.166	0.540 ± 0.045	11	0.789
brood size 5	9.592 ± 0.337	2.343 ± 0.277	0.566 ± 0.073	15	0.568
	10.085 ± 0.193	2.344 ± 0.075	0.536 ± 0.023	12	0.770
brood size 6	9.541 ± 0.191	2.278 ± 0.174	0.573 ± 0.046	16	0.561
	10.384 ± 0.161	2.204 ± 0.050	0.498 ± 0.016	12	0.796
brood size 7	9.135 ± 0.091	2.254 ± 0.097	0.625 ± 0.028	16	0.516
	9.276 ± 0.165	2.233 ± 0.094	0.608 ± 0.031	12	0.700
1972	9.473 ± 0.134	2.235 ± 0.090	0.552 ± 0.025	14	0.658
1973	10.093 ± 0.213	2.274 ± 0.136	0.542 ± 0.037	14	0.632
1974	10.166 ± 0.164	2.266 ± 0.131	0.546 ± 0.034	16	0.586
1975	9.257 ± 0.179	2.379 ± 0.192	0.622 ± 0.052	16	0.542
1976	9.301 ± 0.147	2.360 ± 0.142	0.582 ± 0.037	16	0.557
1976 corrected	9.361 ± 0.200	2.367 ± 0.180	0.552 ± 0.045	16	0.584
early	9.618 ± 0.155	2.328 ± 0.141	0.572 ± 0.039	16	0.564
middle	9.305 ± 0.132	2.336 ± 0.136	0.610 ± 0.037	16	0.531
late	9.121 ± 0.263	2.419 ± 0.256	0.612 ± 0.069	15	0.563
sibilatrix					
present study	11.281 ± 0.205	2.121 ± 0.070	0.532 ± 0.024	12	0.762
Rheinwald (1971)	11.671 ± 0.236	2.249 ± 0.142	0.500 ± 0.045	11	0.808
collybita	8.175 ± 0.167	2.058 ± 0.120	0.495 ± 0.033	15	0.667

TABLE 6. Levels of significance (t-test) of the differences in the parameters of logistic equations for different brood sizes. The first figures are for equations fitted for the whole nestling period, and the second for equations for days 0—10. — indicates $P > 0.10$.

	B_{max} 4	5	6	7
r 4		0.05	0.01	0.001
		—	—	0.01
5	—		—	0.10
	—		—	0.01
6	—	—		0.10
	—	—		0.001
7	0.10	—	—	
	—	0.10	0.10	

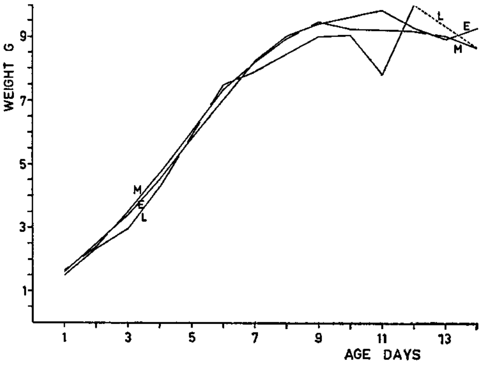

FIG. 7. Weight curves of Willow Warbler nestlings hatched at different times of the season (E early. M middle, L late, see text). Sizes of samples given in App. 2).

TABLE 7. Mean brood size of the Willow Warbler according to the hatching date.

	— 18 June		19—25 June		26 June — 2 July		3 July —	
	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n
1972	6.00	5	6.00	11	6	1	5	1
1973	6.33	3	5.67	7	5	1	—	—
1974	—	—	5.75	4	6.33	13	4.00	3
1975	5.80	3	5.83	7	5.80	5	—	—
1976	6.67	3	5.70	10	—	—	—	—

and 1974 seem to be higher than in other years. However, the data of 1973 for days 10 and 13 were obtained from only one brood, the one with 8 nestlings shown in Fig. 6. The data from the other years are not so scanty. The asymptote for 1974 is higher than in the other years ($P<0.01$), but the difference may be at least partly due to the smaller mean size of the broods examined (Table 8) and is not certain. The fitted equations show no significant differences in the growth rates. The effect of the faeces in the cloaca on the logistic equation was examined with the data from 1976, but no significant differences could be found (Table 5).

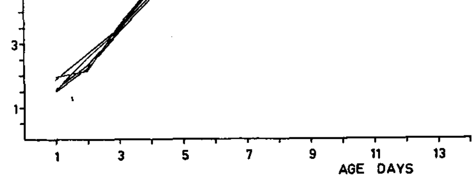

FIG. 8. Weight curves of Willow Warbler nestlings in different years. Sizes of samples given in App. 2.

TABLE 8. Numbers of Willow Warbler broods examined in various size classes.

Brood size	4	5	6	7	8	$\bar{x}$
1972	0	5	9	4	0	5.95
1973	1	3	6	1	1	5.83
1974	3	3	4	2	1	5.62
1975	2	4	5	5	0	5.81
1976	2	0	8	3	0	5.92

Discussion

In altricial birds the length of the nestling period seems to be related to the safety of the nest site (LACK 1968). On the other hand RICKLEFS (1973) stated that "in most species, nestling mortality is such a selective force that growth rate of weight is driven to a physiological maximum rather than adjusted to some ecological optimum" (see also RICKLEFS 1968, 1969). This implies that the time spent in the nest after attaining maximum weight may vary with the safety of the nest.

The chicks of open-nesting altricial birds, which have the shortest nestling periods (LACK 1968), normally fledge as soon as they have attained their maximum weights. The young of species which have their nests in safe places and show longer nestling periods often stay for several days in the nest after having attained their maximum weights. However, as is commonly known among ringers, they are very apt to leave the nest a few days before

TABLE 9. Fledging wing lengths (% of adult length) and nestling period in some species with different types of nest site. Figures taken or calculated from the literature.

	Wing length (%)	Length of nestling period (days)	Source
Open nests			
Sylvia borin	45—55	9—10	SOLONEN 1977
Luscinia luscinia	47—53	9—10	PRYL 1977
Turdus migratorius	60—65	12—15	PINKOWSKI 1975
Euphagus cyanocephalus	63	13	BALPH 1975
Gymnorhinus cyanocephalus	62	21—22	BATEMAN & BALDA 1973
Agelaius phoeniceus	55	12	HOLCOMB & TWIEST 1968
Roofed nests			
Ph. trochilus	70—72	13—14	Present study v. HAARTMAN 1969
Ph. sibilatrix	67	12(?)	Present study
Ph. collybita	67	13	Present study
Campylorynchus brunneicapillus	65	c. 21	RICKLEFS 1975
Delichon urbica	91	29	O'CONNOR 1975b
Nests in holes or cavities			
Parus caeruleus	75	19	O'CONNOR 1975b
Passer domesticus	73	14	O'CONNOR 1975b
Sialia sialis	70—75	16—22	PINKOWSKI 1975

their normal fledging time once their maximum weights have been attained. I have observed Willow Warbler nestlings leaving their nest successfully at the age of only 10 days when the nest was attacked by a Jay *Garrulus glandarius*. The relationship between the ontogenic development of the young at the time of fledging and the safety of the nest site is examined for various species in Table 9. In species whose nests are open, the wing length at fledging time is usually only 50—65 % of the adult wing length, the young being quite unable to fly. In species which stay long in the nest in relation to their weight development, the wing length at fledging time is usually more than 70 % of the adult wing length, and the young can fly at least poorly. The survival of the young of open-nesters will probably improve if the young are able to disperse as early as possible, whereas it is disadvantageous for the young to leave a safe, well-hidden nest in a hole or on the ground, before they can fly.

In his comparative study, RICKLEFS (1968) derived an exponential relationship $r = 1.11B_{\text{max}}{—}0.278$ from equations fitted to the weights of more than one hundred altricial species. This relationship gives the following estimates for r for *Phylloscopus* warblers studied in this paper:

trochilus	0.592
sibilatrix	0.565
collybita	0.611.

The predictions for the Willow Warbler and Wood Warbler agree fairly well with the growth rates in Table 5, but those for the Chiffchaff do not. The slow growth rate for the Chiffchaff may be due to the poor productivity of the spruce forest habitats preferred by it.

If the data are extensive and representative, intraspecific variation in growth patterns can conveniently be studied in terms of means and standard deviations. RICKLEFS (1968) suggested the use of a standardized curve-fitting technique; in comparison with simpler methods, the amount of additional information from calculation of growth equations depends on the degree of dependence between the asymptotic weight and the growth rate (RICKLEFS 1968). If the increase of the weights no longer fits the logistic model after the curves have levelled off, the final non-logistic part ought to be studied in some other way. However, exclusion of the final part makes it difficult to determine the asymptote exactly enough. Whenever the asymptote of the growth curve is overestimated by a certain amount, the growth rate of the logistic equation is underestimated by a proportionate amount (R. E. Ricklefs, pers. comm.). This can be seen in the higher correlations between these parameters in the equations for different brood sizes for age 0—10 days in Table 5.

The intraspecific variation in the growth patterns of *Phylloscopus* warblers is fairly wide. The within-brood part of the variation may be caused by inherent size differences, both sex-dependent and sex-independent, or by sibling competition for food, but this was not studied in the present paper. Between-brood variation might also be expected from differences in the breeding experience (PERRINS 1965, LACK 1966) or the genotype of the parents. The variation found between groups formed according to some natural factor is probably caused by differences in the quantity or quality of the nutrition (see Introduction).

In the Willow Warbler, the dependence between the pattern of weight increase and brood size might be interpreted as follows. Parents of large broods overcompensate the increased stimulus for feeding, which leads to a faster growth rate. The maximum feeding capacity of birds with large broods is attained fairly early, whereas in the case of small broods it is not attained at all. Broods with 6 young are intermediate; here the parents' full feeding capacity is not reached until the young become more active on the last one or two days of the nestling period. The energy cost of thermoregulation cannot play a significant role. When the young are small and incapable of thermoregulation, the female keeps them warm by incubating. Later, the amount of energy needed for thermoregulation is less in larger than in smaller broods (O'CONNOR 1975b, MERTENS 1977).

The reason for the seasonal decline in the maximum weights may lie in the food supplied to the young. The simultaneous increase in the growth rate is difficult to explain, except by the correlation of these two variables. In southern Finland, adult Willow Warblers begin their postnuptial moult in early July (HAUKIOJA & KALINAINEN 1968, 1972), the females one week later than the males (P. Niemelä, pers. comm.). The timing of the moult is internally determined, the photoperiod being an additional *Zeitgeber* (GWINNER 1969, GWINNER et al. 1971), and so is not likely to be affected by the phase of the breeding cycle. When the moult starts, the adult birds allocate an increasing amount of energy to their own feather production, but at the very beginning the energency cost is probably small. Some feeding parents were found in active moult, but if the moult had just begun, no effect on the growth of the young could be noted. If the breeding season extended until very late, as in 1974, the moult of the parents tending the latest nests had proceeded rather far, and the growth of the young was reduced. Besides the increase in the energy need of the parent birds, another factor that may decrease the amount of food supplied to the young is the effect of the moult on the flying ability of the parents. This is reduced when the raggedness of the wing and tail is great (HAUKIOJA 1971), and must also reduce their food harvesting efficiency.

RICKLEFS (1968) demonstrated geographical variation in the growth patterns of some species. By comparing published data, he found fairly large variation in the Yellow-headed Blackbird *Xantocephalus xantocephalus*, small variation in the Starling *Sturnus vulgaris*, possible variation in the Robin *Erithacus rubecula*, and little or no variation in the Chipping Sparrow *Spizella passerina*. Little has been published earlier on the growth of *Phylloscopus* warblers. LENNERSTEDT (1964) gives the weight increase of Willow Warbler young up to about 9 days from a few nests from Ammarnäs, N Sweden (65.58 N, 16.13 E). The weight on day 9 is about 0.20 g, or 2.2 %, higher in my than his data, but the difference may not be significant. Data on the growth pattern of the Wood Warbler are available from SW Germany (RHEINWALD 1971). No significant differences in the parameters of fitted equations (Table 5) could be found between the two localities ($P > 0.10$). The small differences observed in both cases may be due to the factors studied above or the different habitats (VAN BALEN 1973).

The development of the feathers is affected much less by the quantity of food than the weight increase (LACK & SILVA 1949), although the growth rate of feathers may be changed by the quality of the nutrition (BERTHOLD 1976). Accordingly, some authors have used the wing lensth for ageing the young (e.g. HOLCOMB & TWIEST 1971, KARHU 1973, HAMEL 1974, RICKLEFS 1975, RICKLEFS & WHITE 1975). The wing length is in fact preferable to the weight, because its age specific variation is much smaller; it grows continuously without any daily cycle, and the rate of growth remains fairly high to the end of the nestling period. However, the wing length is subject to fairly wide intrabrood variation and for accurate determinations only brood averages should be used. Wing lengths for ageing the three *Phylloscopus* warblers studied are given in App. 1.

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Selostus: **Siiven pituuden ja painon kehitys uunilintujen pesäpoikasilla**

Pajulinnun, sirittäjän ja tiltaltin pesäpoikasten kasvua tutkittiin Lammin biologisella asemalla vuosina 1972—77. Poikasista mitattiin päivittäin siiven pituus ja paino.

Uunilintujen poikaset kuoriutuvat aina eriaikaisesti. Joka toisessa pesässä kaikki poikaset kuoriutuivat saman päivän kuluessa, lopuissa viimeinen kuoriutui vasta seuraavana päivänä. Poikasten kasvukäyrät on esitetty lajeittain kuvissa 3 (siiven pituus) ja 4 (paino) sekä liitteessä 1. Siiven pituuksien päivittäiset keskiarvot ovat käyttökelpoisia iänmääritysperusteina (luotettavuutta testattu taulukossa 4). Kasvun vuorokausirytmiikkaa tutkittiin yhdestä pajulintupesyeestä (kuvat 1 ja 2). Siiven pituus kasvaa hyvin tasaisesti, mutta painon kasvussa on selvä rytmi, joka johtuu puoliksi ulostamisesta ja puoliksi varastoidun energian kulutuksesta yöllä. Kuvissa 1 ja 2 esiintyvät kaksi poikasryhmää on tulkittu kuuluviksi eri sukupuoliin.

Taulukossa 4 esitetään painon kasvun logistiset kuvaajat. Lajien väliset erot eivät ole tilastollisesti merkitseviä. Pajulinnun ja sirittäjän poikasten kasvunopeudet eivät eroa ennusteesta, joka saadaan yli sadan pesäviipyisen lintulajin kasvumalleista lasketusta lopullisen koon ja kasvunopeuden välisestä riippuvuudesta. Tiltaltin poikaset sen sijaan kasvavat huomattavasti odotettua hitaammin, mikä saattaa merkitä sopeutuneisuutta niukkatuottoisiin kuusimetsiin.

Uunilintujen poikaset saavuttavat n. 9 päivän ikäisinä lopullisen painonsa, joka vastaa suunnilleen aikuisten painoa (vrt. taulukko 1). Siiven pituus ei vielä poikasten lähtiessä pesästä ole kuin 70—72 % aikuisten siiven pituudesta; poikaset osaavat kuitenkin tällöin jo lentää. Yleensäkin koloissa tai katollisissa pesissä pesivien lajien poikaset lähtevät pesästä varsin myöhään, kun taas avopesijöiden poikaset lähtevät pian lopullisen painonsa saavutettuaan, mutta lyhytsiipisinä ja huonosti lentävinä (taulukko 9). Edellisten on ilmeisesti hyödyllistä viipyä suojaisassa pesässä mahdollisimman kauan, kun taas jälkimmäisille on edullista hajaantua kasvillisuuteen mahdollisimman varhain.

Pajulinnun lajinsisäinen kasvun vaihtelu esitetään kuvissa 3—8 ja taulukossa 5. Siiven pituuden kasvun vaihtelu on mitätöntä (kuva 5). Pienissä (kuva 6) ja varhaisissa pesyeissä (kuva 7) poikaset tulevat painavammiksi, mutta kasvavat hitaammin kuin suurissa ja myöhäisissä pesyeissä. Pesyekoosta riippuva vaihtelu saattaa aiheutua siitä, että emot ylikompensoivat saamansa lisääntyneen ruokintaärsykkeen, mutta niiden maksimaalinen ruokintakapasiteetti saavutetaan sitä varhemmin kuta suurempi poikue niillä on huollettavanaan. Poikasten lopullisten painojen alenemista pesimäkauden kuluessa korostaa samanaikainen pesyekoon pieneneminen (taulukko 7). Muutos saattaa johtua siitä, että emot alkavat sulkimisensa hyvin säännöllisesti pesinnän vaiheesta riippumatta. Etenkin vuosina, jolloin pesintä on myöhäistä (ks. taulukko 3), emot joutuvat käyttämään yhä enemmän energiaa omaan sulkimiseensa eivätkä ne pysty ruokkimaan poikasiaan entisellä teholla. Vuosien välillä ei ole merkitseviä eroja. 1973 aineisto oli pieni ja 1974 pesyekoko oli alhaisempi kuin muina vuosina (taulukko 8). Mahdollista maantieteellistä vaihtelua kasvussa tutkittiin vertaamalla pajulinnun kasvua pohjoisruotsalaisten poikasten kasvuun ja sirittäjän lounaissaksalaisten poikasten kasvuun, mutta merkittäviä eroja ei havaittu.

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APPENDIX 2. Sizes of samples (no. of nestlings) in the study of the intraspecific variation of the weight increase of Willow Warblers (see Figs. 5—8). The sizes of some of the wing length samples were slightly different.

Age	Brood size				Season			Year				
(days)	4	5	6	7	E	M	L	1972	1973	1974	1975	1976
1	6	35	36	21	24	71	11	22	16	14	33	37
2	—	25	45	21	20	20	6	35	1	17	25	30
3	1	31	73	21	31	73	17	59	7	19	29	25
4	4	34	87	28	31	90	19	59	16	33	35	30
5	6	31	109	34	48	93	22	70	7	41	40	36
6	11	35	114	33	48	107	7	61	22	59	37	37
7	8	29	97	30	47	91	13	61	23	49	29	97
8	11	28	77	45	51	90	13	65	13	46	27	36
9	4	38	57	32	60	46	20	35	9	35	23	36
10	5	13	47	16	46	25	10	16	7	24	24	24
11	8	2	29	19	33	20	3	8	—	16	11	28
12	6	—	13	16	9	22	3	9	2	6	3	22
13	1	1	10	12	15	15	—	—	7	9	1	21
14	3	4	9	12	14	5	6	—	—	9	14	5

APPENDIX 1. Wing lengths and weights of nestling ***Phylloscopus*** warblers calculated from the total material. The records for the Willow Warbler were transformed to 18.00 hr. The measurements of the Wood Warbler and Chiffchaff were always made in the evening.

Wing length

Age (days)	*trochilus* $\bar{x}$ ±S.D.	n	*sibilatrix* $\bar{x}$ ±S.D.	n	*collybita* $\bar{x}$ ±S.D.	n
0	5.74±0.11	25	6.00±0.00	2	5.4	1
0.5	6.13±0.27	69	6.49±0.40	25	5.86±0.13	5
1	6.87±0.57	111	7.47±0.49	24	6.56±0.30	9
2	8.31±0.67	108	9.57±1.09	27	7.93±0.42	15
3	10.94±1.28	127	13.67±1.98	27	9.48±0.64	20
4	14.92±2.09	168	18.63±2.49	39	12.70±1.36	20
5	19.66±2.12	188	24.23±2.38	32	17.28±1.46	20
6	25.08±2.18	216	30.44±2.55	32	21.33±1.76	20
7	29.75±2.40	192	35.05±1.71	47	25.58±1.84	19
8	34.08±2.22	188	39.66±1.54	29	30.50±2.74	14
9	37.61±2.03	132	43.61±1.54	27	34.00±2.92	13
10	40.70±1.79	94	47.27±1.37	11	37.79±3.59	7
11	43.61±2.18	64			38.63±1.60	8
12	46.68±2.52	42	51.67±1.26	3	42.82±2.68	11
13	48.76±2.15	38			42.90±1.95	5
14	49.51±1.69	28				

Weight

Age (days)	*trochilus* $\bar{x}$ ±S.D.	n	*sibilatrix* $\bar{x}$ ±S.D.	n	*collybita* $\bar{x}$ ±S.D.	n
0	0.89±0.06	19	0.91±0.00	2	0.81	1
0.5	1.15±0.19	66	1.29±0.21	24	0.95±0.03	5
1	1.61±0.34	122	2.05±0.46	19	1.51±0.16	7
2	2.42±0.42	108	3.05±0.52	29	2.26±0.18	13
3	3.42±0.46	139	4.40±0.64	27	3.03±0.26	18
4	4.58±0.61	173	5.76±0.69	39	3.93±0.28	18
5	5.86±0.67	194	6.91±0.77	32	4.85±0.44	18
6	7.18±0.73	216	8.26±0.74	32	5.69±0.36	18
7	8.20±0.81	191	9.33±0.64	47	6.50±0.37	17
8	8.93±0.79	187	10.28±0.89	29	7.36±0.54	12
9	9.36±0.89	138	10.58±0.54	27	7.81±0.55	11
10	9.45±0.90	95	10.74±0.64	11	7.66±0.36	5
11	9.54±1.00	63	9.27±0.81	3	7.33±0.45	5
12	9.32±0.76	42			7.89±0.52	9
13	9.26±0.94	38			8.50±0.18	3
14	9.24±1.04	28				

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