

Nestling growth in the Great Tit *Parus major* and the Willow Tit *P. montanus*

Markku Orell

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The increase of body weight, and of wing, tail and tarsus length was studied in nestlings of the Great and Willow Tit, in the Oulu area of northern Finland in 1969 and 1977—1981. In both species the nestlings had attained their maximum weight by about the age of 13—14 days, though undernourished young continued to put on weight. The Willow Tit tended to grow slightly more slowly than the Great Tit, but the difference was not significant. Both species grew more slowly than expected. In the Great Tit the intra-brood weight variation was larger when food was scarce than when it was plentiful. In poor years nestling mortality was pronounced and was concentrated among the late hatchlings. In the most favourable year (1980) the late hatchlings survived. The Willow Tit fledglings were as heavy as the adults of the species, but the Great Tit fledglings were much lighter, except in 1980. The wings and tail were slightly more developed in the Willow Tit fledglings than in the Great Tit. In both species the tarsus length was the same in the fledglings and adult birds. Growth strategies and the importance of size at fledging for future survival are discussed.

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Introduction

A large amount of information concerning the growth patterns of birds has been collected by Ricklefs (1968, 1973, 1976). These data show that each species has a typical growth rate, which varies within a certain range. The intraspecific variation in the weight of nestlings, the criterion generally used as the measure of body size, is considered to depend on brood size, season and habitat.

Losses due to starvation, referred to as "brood reduction" (Ricklefs 1965), have been shown to occur in many species whose food resources fluctuate unpredictably (e.g. Lack 1954, 1966, 1968, Hussell 1972, Bryant 1978b, O'Connor 1978b). These deaths due to food shortages are concentrated among the younger chicks in the brood (Gibb 1950, Lack 1954, 1966, 1968, Löhrl 1968, Seel 1970, Dyrz 1974, Bryant 1978b, O'Connor 1978a, Neub 1979), the age hierarchy being the result of hatching asynchrony.

In the Oulu area there are marked differences in overall nesting success between the Great and the Willow Tit, with nestlings of the latter species showing a much lower mortality rate in broods not destroyed by predators. Nestling mortality increases with brood size in the Great Tit, but not in the Willow Tit (Orell & Ojanen 1983b, c).

The aim of the present study was to investigate how the differences in nesting success between these species are reflected in nestling growth. Special attention is paid to the effect of the size hierarchy caused by asynchronous hatching.

Material and methods

The work was performed in two study sites at Oulu (65°N, 25°30'E), Taskila and Kuivasjärvi. These are described in detail in Orell & Ojanen (1983a). The material consists of 404 Great Tit and 36 Willow Tit nestlings. The growth of the Great Tit was studied in 1969, 1977, 1978 and 1980, and that of the Willow Tit in 1977—1981. The records for the Great Tit were made daily or at longer intervals in 37 first broods, 11 repeat broods and 3 second broods, and those for the Willow Tit in 4 first broods and 1 repeat brood.

All the Great Tit broods were located in wooden nest boxes, and three of the five Willow Tit broods were in special Willow Tit boxes filled with decaying wood, the other two being in decaying stumps bound to tree trunks with wire. The last two nests were checked with the aid of a small mirror and a torch. In one of them the chicks were taken out through the roof by removing the wood above the nest cavity, this hole being filled with moss afterwards. In the other nest a hole was cut at the level of the nest and the entrance then covered with birch bark.

The age of the chick was recorded as 0 on the day of hatching, 1 on the following day, etc. Most of the broods were visited for the first time on the day(s) of hatching or when the young were no older than 3 days. Up to that age it is possible, in the author's experience, to determine the age of the bird from its appearance. Only in 9 broods, the nestlings were as much as 4 or 5 days old when visited for the first time. In all cases in which the exact hatching date was not known, the age was verified by reference to a preliminary weight and wing length curve constructed from the records of exact ages (see also Tiainen 1978). The young were usually weighed and measured up to the age of 15 days, but some broods were visited at the age of 21 days. Each visit was made at the same time of the day, mostly at noon or in the afternoon.

About 50 % of the young were marked individually on the leg with non-toxic ink on the first day when

they were weighed. All the young were marked with aluminium rings before fledging.

The small nestlings (age 0–5 days) were weighed with a 10-g Pcsola spring balance (accuracy 0.05 g) and the larger ones with a 30- or 50-g balance (accuracy 0.1 g).

The wing length of the nestlings aged 0–4 days was measured with a ruler to the nearest 0.5 mm; in the older ones the length was taken to the nearest 1 mm. The maximum method as described by Svensson (1970) was used, the wing being flattened on the ruler and straightened sideways. The tail was measured using the "right angle" method of Busse & Kania (1970), to the nearest 0.5 mm in the chicks younger than 9 days and to the nearest 1 mm in the older ones. The tarsus length was measured to an accuracy of 0.05 mm, using the standard method described by Svensson (1970).

Wing and tail lengths of adult birds were measured in 1969–1975 to the nearest 0.1 mm with sliding calipers. The wing was measured from the metacarpal joint to the tip of the longest primary (van Balen 1967), being kept in its natural position during measurement and retaining its natural curvature (Svensson's (1970) minimum method). The tail was measured from the base of the middle feathers to the tip of longest feathers. After 1975 the wing and tail were measured with a ruler as described above. Tarsus length was measured in 1975–1981 by the same method as for the nestlings. The measurements taken with sliding calipers were standardized to those obtained with a ruler by adding 2.90 mm and 2.33 mm to wing and tail lengths, respectively, for the Great Tit and 2.19 mm and 1.21 mm for the Willow Tit. These corrections were obtained by using the two methods in parallel in 46 wing and 43 tail measurements on Great Tits and 15 and 14 measurements on Willow Tits, and averaging the differences.

The wing and tail lengths quoted for adult birds are derived from measurements made in September–April. In late spring and summer, before the postnuptial moult, the feathers are somewhat worn, resulting in shorter wing and tail lengths than those measured in autumn and winter (van Balen 1967, Laaksonen et al. 1974, author's own observations). Individuals which were still in moult when captured in September were ignored, because the wing and tail had not attained their final length.

The weights of the adult birds apply to the end of the nestling period. There is a pronounced seasonal weight variation in both species (van Balen 1967, Garnett 1976, Haftorn 1976, Orell 1976), the weight being lowest at the end of nesting (Orell 1976).

According to Ricklefs (1976), the growth curves of passerines fit the logistic equation better than the Gompertz or von Bertalanffy equations. In the logistic equation

$$1) W(t) = A/(1+e^{-K(t-t_i)}),$$

$W(t)$ is the weight at age t , A is the final weight or asymptote, K is a constant equivalent to the overall growth rate (days^{-1}) and t_i is the inflection point of the growth curve (days), where $W(t_i) = A/2$.

The graphic method for fitting growth data developed by Ricklefs (1967) can be used for all three of the above equations. Here the accuracy of the parameters depends on the subjective estimate for the asymptotic weight. Crossner (1977) described a method by which K and A in the logistic equation can be calculated simultaneously by regression analysis. This method was used here. It includes two conversions of the weight data:

$$2) W(t)^* = (W(t) + W(t+1))/2$$

$$3) dW(t)/dW(t)^* = (W(t+1) - W(t))/W(t)^*.$$

The linear regression equation is calculated using weights of 2 on the abscissa and weights of 3 on the ordinate. The intercept x in the equation represents the A of the logistic equation and the intercept y represents K . The

constant t_i can be calculated from equation 1 using the values for A and K and the observed weights. Crossner's method requires that the weighing has been carried out every day, or that throughout the nestling time there are periods when the chicks have been weighed daily. If the nestlings were weighed only every second day, or only at the end of the nestling period, for example, the material cannot be used.

The wing, tail and tarsus lengths were studied only in terms of mean values.

The sex and age (yearlings versus older birds) of the Great Tits were determined from the plumage characteristics as described by Drost (1937) and Svensson (1970). The incubation patch can also be used in sexing during nesting time (Svensson 1970).

The Willow Tit can be sexed during breeding, with the aid of the incubation patch, but not at other times of the year (Svensson 1970).

The age of one year means that the bird was born in the previous breeding season. The older individuals have bred at least once.

The hatching period, i.e. the time elapsing from the hatching of the first egg to the hatching of the last one, was determined in the following way. The nests were checked daily from the time that the incubation had lasted about 13 days. If there were, say, 3 chicks and 4 eggs in a clutch on one day and 7 chicks on the following day, the hatching period was estimated as 2 days. If the last egg hatched 2 days after the first day on which there were young present in the nest, the estimate was 3 days. If all eggs had hatched between consecutive visits the period was estimated to be 1 day. If all the chicks in a brood clearly appeared to be newly hatched, the estimate was also 1 day, even though the nest had not been visited the day before. The method is a crude one, but gives an idea of the length of the hatching period (e.g. Bryant 1978a). Material for this analysis was available for 6 years in the case of the Great Tit and 5 years in that of the Willow Tit.

Results

Growth patterns

Weight. The Great Tit chicks weighed about 1.1–1.7 g at hatching, and those of the Willow Tit 0.9–1.4 g. During the first day of life the weight increased by 0.3–0.8 g. The overall weight increase in successful young of the two species during the nestling period can be seen in Fig. 1 and Appendix 1. If the nestlings were not individually marked and some chicks died before fledging, the lightest of the previous weight records were assumed to be theirs and were excluded. The same was done with the wing, tail and tarsus lengths.

In the Great Tit, the absolute growth rate (g/day) increased during the first days of life and was highest at 3–7 days. The largest daily weight increase was 1.71 g, at the age of 3 days (Fig. 2). After the age of 7 days, the daily weight increase became smaller, and some weight recession even occurred on the days just before fledging, which takes place at an average age of 18 days in the Oulu area (Orell & Ojanen 1983a, Fig. 2). The irregular fluctuation in the daily weight increase at the end of nestling period (Fig. 2) is due to sampling error.

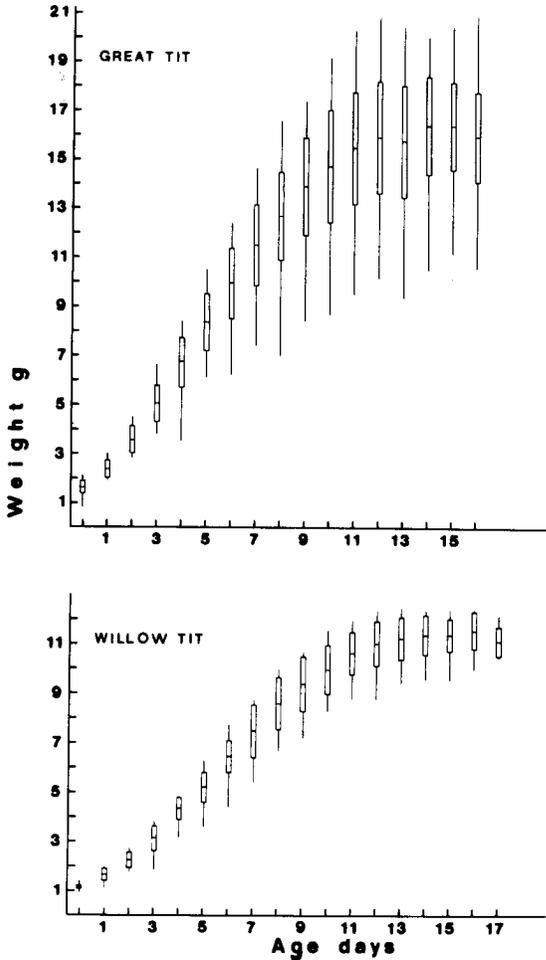


Fig. 1. Weight increase in the Great Tit and Willow Tit nestlings (cf. Appendix 1). The bars indicate the mean \pm one standard deviation and the vertical lines maximum and minimum values.

In the Willow Tit, the daily weight gain increased up to the age of 5 days, when the increase was highest, 1.22 g/day (Fig. 2). Thereafter it gradually became smaller, as in the Great Tit. Again some nestlings lost weight on the days before fledging, although this is not apparent from the total material.

The relative weight increase was highest during the first day of life in both species, when the figure was about 50 % (Fig. 2), and then progressively slowed down. The Great Tit tended to grow faster than the Willow Tit, i.e. the proportional weight increase was higher, from hatching up to the age of about 8 days, after which the difference disappeared.

In broods with light young, the weight increase was still marked during the days before fledging

(Fig. 9A), and there is great weight variation among chicks of 7 days and older, especially in the Great Tit (Fig. 1). In that species the most underweight young weighed only 10–12 g at the age of 15–16 days, while the heaviest were over 20 g. The range of fledgling weights in the Great Tit is thus about 10 g. The variation was not so great in the Willow Tit (Fig. 1). The average coefficient of the variation in weights ($CV = 100 \times SD/mean$) at the age of 14–16 days was about twice as high in the Great Tit (11.8 %) as in the Willow Tit (6.7 %). The weight variation would have been even more pronounced if the chicks that had died before fledging had been included.

The parameters for the fitted growth curves presented in Table 1 were calculated in two ways. Firstly, the weights of all the young fledged in each year and all years together were combined and the average weights fitted to the logistic equation, and secondly, the parameters were computed for each brood separately and then averaged to achieve annual and total means.

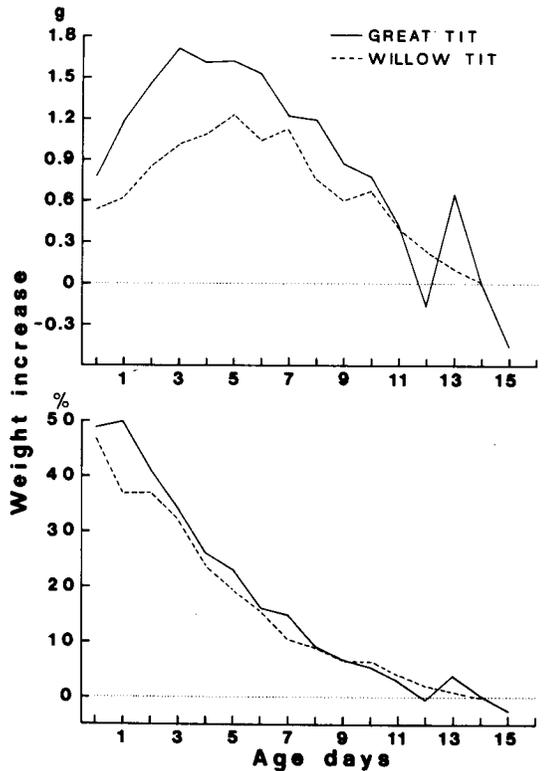


Fig. 2. Mean daily (upper graph) and daily percentage increase (lower graph) of the weight in the Great Tit and Willow Tit nestlings, based on the data in Appendix 1.

Table 1. Parameters of the logistic equations describing the growth of Great Tit and Willow Tit nestlings. Two equations are given for the total material of each species and for individual years in the Great Tit material. The first equation is calculated using all weights as a single group, while the second is the average of equations fitted for each brood separately. N gives the number of broods.

| | A | ±SD | K | ±SD | t _i | ±SD | N |
|------------|-------|-------|-------|-------|----------------|-------|----|
| Great Tit | | | | | | | |
| all data | 16.41 | | 0.449 | | 4.986 | | |
| all broods | 16.73 | 1.938 | 0.436 | 0.054 | 5.072 | 0.645 | 36 |
| 1969 | 16.90 | | 0.403 | | 5.135 | | |
| | 16.52 | 2.567 | 0.453 | 0.060 | 4.930 | 0.892 | 12 |
| 1977 | 15.20 | | 0.436 | | 4.720 | | |
| | 15.85 | 0.801 | 0.407 | 0.045 | 4.544 | 0.544 | 4 |
| 1978 | 16.50 | | 0.424 | | 5.619 | | |
| | 16.43 | 1.574 | 0.420 | 0.056 | 5.340 | 0.397 | 14 |
| 1980 | 18.34 | | 0.468 | | 5.008 | | |
| | 18.47 | 0.598 | 0.459 | 0.020 | 5.079 | 0.314 | 6 |
| Willow Tit | | | | | | | |
| all data | 11.66 | | 0.406 | | 5.541 | | |
| all broods | 11.41 | 0.843 | 0.390 | 0.034 | 5.754 | 0.816 | 5 |

Note. Only fledged nestlings included.

Good fit with the logistic equation was obtained for the combined material for the Great Tit ($\chi^2=0.067$, $df=14$, age groups 1–15 days) and the Great Tit data from 1980 ($\chi^2=0.053$), and for the combined material for the Willow Tit ($\chi^2=0.009$). Great Tit data from 1969 ($\chi^2=0.096$) and 1977 ($\chi^2=0.160$) did not fit as well.

In 1977 the weight increased normally during the first days of life (0–7 days) but thereafter growth was clearly retarded (Fig. 3) and in many broods there were periods of weight recession.

Many of the young died at this time. Irregularly growing broods also occurred in 1969 and 1978, but they were less common than in 1977. Their existence in these years was nevertheless reflected in the failure of the weight data to fit the logistic equation as well as they did in 1980, when all the broods showed normal growth curves.

In the Great Tit the year 1980 deviated markedly from the others, showing the highest asymptotic weight and overall growth rate (Table 1). In 1969 and 1978 the nestlings grew at about the same rates and attained the same asymptotic weights, but in 1977 the final weight was much lower than in other years, although the rate of growth was about the same.

There were significant differences between the asymptotic weights in the years 1980 and 1977 and the years 1980 and 1978 (analysis of variance, $P < 0.05$). In 1969 there was a large standard deviation due to some broods with high (e.g. 20.6 g) and some with low asymptotes (as low as 12.0 g).

The average growth rates in 1969 and 1980 were significantly higher than in 1977 (ANOVA, $P < 0.05$). This difference is not apparent in the constants obtained from the total materials for those years, since the growth rate in 1977 was fairly high.

Comparison of the inter-brood variations in asymptotic weight and the growth constant reveals that the CV of the weight in 1969 (15.5 %) was significantly larger than in the other years, while the value was smaller in 1980 (3.2 %) than in 1978 (F test, $P < 0.05$). The inter-brood variation in the constant K was low in 1980 (CV = 4.4 %), but much more pronounced in the other years (CV = 13.2 % in 1969, 11.1 % in 1977 and 13.3 % in 1978). The material for 1980 was significantly less variable than that for any other year

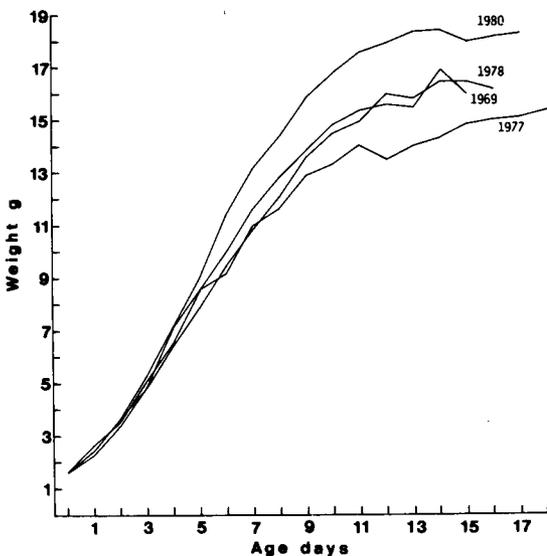


Fig. 3. Mean weight curves for Great Tit nestlings in 1969, 1977, 1978, and 1980.

(F test, $P < 0.05$), although the comparison between the years 1977 and 1980 is not very conclusive because of the scarcity of data for the former year.

In 1969 the growth rate was significantly higher in repeat broods than in first broods (ANOVA, $P < 0.05$, Table 2), but in 1980 there was no significant differences between the first and the second broods. In both years the first broods tended to attain higher asymptotic weights than the late broods, but the differences were not significant (ANOVA).

There were large differences in asymptotic weights between broods of different initial size (Table 2). In three years the larger broods tended to have smaller weights, but only in 1980 was the variation significant (ANOVA, $P < 0.01$). Similar results were obtained when the size at fledging was used in grouping the broods.

In three of the four years the growth constant (K) tended to increase with brood size (Table 2), but this variation was not significant (ANOVA). Only in 1978, when the trend was reversed, did the analysis of variance reveal significant inter-brood variation ($P < 0.05$).

In the Willow Tit broods growth was slowest in 1977 and 1979 ($K = 0.390$ and 0.334 respectively), and the young in these broods had the lowest weight recorded before fledging (Fig. 4). The highest weights were recorded in 1980 and 1981 (Fig. 4). In the Great Tit, too, the fledging weight was low in 1977 and high in 1980. In the Willow Tit the growth rate was highest in 1978 ($K = 0.422$) and somewhat lower in 1980 ($K = 0.398$) and 1981 ($K = 0.410$). Up to the age of 8 days the growth of these three broods was similar (Fig. 4), but beyond that age the growth of the 1978 brood slowed down, causing the value for K to be higher, since the asymptotic weight remained low.

The low fledging weights in 1977 and 1978 were consistent with the fact that the male was lazy in feeding the young, and probably abandoned the brood in 1977. In this repeat brood only one of the 7 hatchlings fledged. Two undernourished chicks died after the largest one had fledged, and the female had evidently stopped feeding them. In the 1979 brood 4 of the 8 chicks died.

Wing length. In both species the weight increase is more rapid than the increase of wing length (cf. Figs. 1 and 5). The average wing lengths for each age are given in Appendix 2. The wing length of the Great Tit at hatching is about 4.5–6.0 mm, and that of the Willow Tit slightly smaller. In the Great Tit the growth rate was low at 0–4 days, increasing from 1.0 to 2.0 mm/day, and became linear at a much higher rate, 4.5–5.0 mm/day at 5–10 days. Towards the end of the nestling period growth slowed down, but the wings

Table 2. Average asymptotic weights (A) and growth constants (K) of the logistic equations fitted for first, repeat and second broods and different initial brood sizes in the Great Tit. N gives the number of broods.

| | A | ±SD | K | ±SD | N |
|---------------|-------|-------|-------|-------|---|
| 1969 | | | | | |
| first broods | 17.03 | 2.055 | 0.402 | 0.073 | 4 |
| repeat broods | 16.26 | 2.885 | 0.479 | 0.033 | 8 |
| 1980 | | | | | |
| first broods | 18.53 | 0.605 | 0.459 | 0.030 | 3 |
| second broods | 18.41 | 0.720 | 0.460 | 0.011 | 3 |
| 1969 | | | | | |
| brood size | | | | | |
| 3–6 | 17.45 | 3.258 | 0.449 | 0.074 | 5 |
| 8 | 16.12 | 2.453 | 0.440 | 0.063 | 4 |
| 9 | 15.50 | 1.395 | 0.478 | 0.038 | 3 |
| 1977 | | | | | |
| 6–7 | 15.54 | 1.152 | 0.396 | 0.073 | 2 |
| 8–9 | 16.15 | 0.481 | 0.418 | 0.016 | 2 |
| 1978 | | | | | |
| 6–8 | 17.30 | 0.980 | 0.455 | 0.021 | 5 |
| 9 | 16.26 | 1.228 | 0.438 | 0.044 | 4 |
| 10–11 | 15.69 | 2.072 | 0.380 | 0.029 | 5 |
| 1980 | | | | | |
| 5–6 | 18.82 | 0.049 | 0.456 | 0.012 | 2 |
| 7 | 18.87 | 0.156 | 0.444 | 0.019 | 2 |
| 8 | 17.71 | 0.184 | 0.478 | 0.015 | 2 |

Note. Only fledged nestlings included.

were still growing during fledging, the rate being about 2.5 mm/day.

Wing growth in the Willow Tit followed the same pattern, but with a smaller daily increase, 3.5–4.0 mm/day, during the most intensive growth period, at 5–10 days. Before fledging, the growth rate decreased to about 2.5 mm/day.

The inter-individual variation in wing length seems to be much higher in the Great Tit than in the Willow Tit (cf. Fig. 5), the coefficient of variation averaging 8.0 % at 14–16 days in the

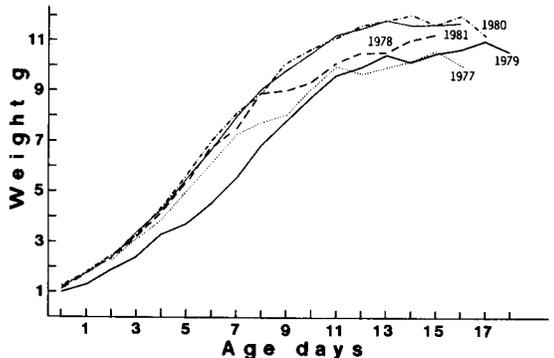


Fig. 4. Mean weight curves for five Willow Tit broods.

Table 3. Distribution of broods by length of hatching period in the Great Tit and Willow Tit in the Oulu area. A = first broods; B = second broods.

| | Days | | | | | N | Mean |
|-------------------|------|----|----|---|---|----|------|
| | 1 | 2 | 3 | 4 | 5 | | |
| Great Tit | | | | | | | |
| 1969 | — | 3 | 1 | 1 | — | 5 | 2.6 |
| 1971 | — | 6 | — | 1 | — | 7 | 2.3 |
| 1977 | 8 | 8 | 2 | 2 | — | 20 | 1.9 |
| 1978 | 5 | 14 | 1 | — | — | 20 | 1.8 |
| 1979 | 3 | 4 | 2 | 1 | — | 10 | 2.7 |
| 1980 A | 6 | 12 | 4 | — | — | 22 | 1.9 |
| 1980 B | — | 3 | 4 | 1 | 1 | 9 | 3.0 |
| Total | 22 | 50 | 14 | 6 | 1 | 93 | 2.1 |
| Willow Tit | | | | | | | |
| 1975 | — | 1 | — | — | — | 1 | 2.0 |
| 1977 | 1 | — | — | — | — | 1 | 1.0 |
| 1978 | 2 | 7 | — | — | — | 9 | 1.8 |
| 1979 | 2 | 1 | — | — | — | 3 | 1.3 |
| 1980 | 1 | 10 | — | — | — | 11 | 1.9 |
| Total | 6 | 19 | — | — | — | 25 | 1.8 |

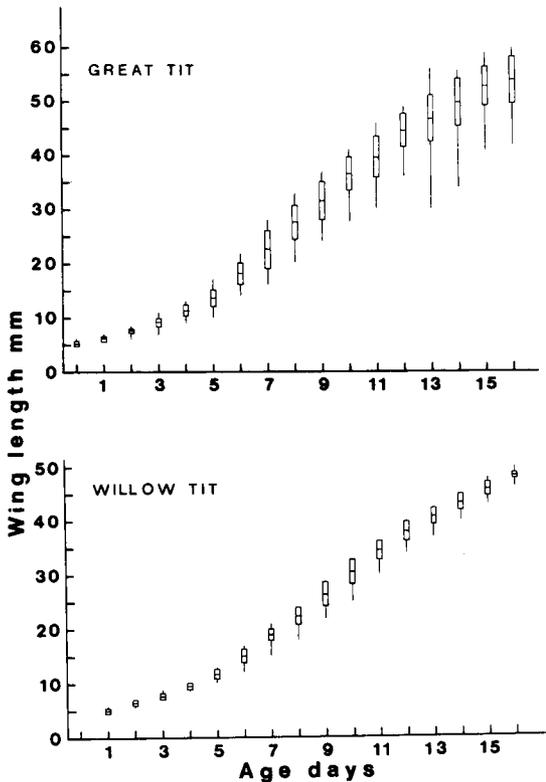


Fig. 5. Increase of wing length in nestling Great Tits (1978 and 1980) and Willow Tits (1978—1981) (cf. Appendix 2). For explanations, see Fig. 1.

Great Tit but only 2.8 % in the Willow Tit. The large variation in the former species is attributable to the records for 1978 (CV=8.4 %; cf. 1980, CV=2.6 %). The annual differences in overall wing length also serve to increase the total variation.

In the Great Tit wing growth was clearly retarded in 1977 and 1978 compared with 1980 (Fig. 6), by about 1.5—2.0 days in 1978 and as much as 4 days in 1977. The delay in growth in 1978 can already be seen at 6—7 days.

In the siblings which succumbed, wing length increased until the day of death, unlike weight, although the wings of these nestlings were clearly shorter at a given age than those of the siblings that fledged.

Tail length. In both species the sheaths of the tail feathers penetrate through the skin at the age of 5—6 days, though tail development may be retarded by up to 3 days in broods with delayed growth. The growth of the tail is slow for the first 3 days, but then increases and seems to be linear for the rest of the nestling period (Fig. 7). During the most intensive period (9—16 days) it grows at a rate 2.7 mm/day in both species. There was considerable variation in the tail length within a given age group (Fig. 7). At 14—16 days the CV averaged 20.3 % and 14.7 % in the Great Tit and Willow Tit, respectively. Hence the tail length just before fledging varied much more than did the wing length.

Tarsus length. The length of the tarsus was not measured until the young were at least 6 days old, the bones of younger nestlings being so soft that measurement could have injured their feet. In both species the tarsus stops growing at the age of 12 days (Fig. 8), and it was even found to shorten in many chicks just before fledging. This is because the ankle joints are not as swollen at that age as in younger chicks (see also Garnett 1976). The fact that the tarsus attains its final length before fledging has been reported earlier

Table 4. Number of nestlings hatching and dying (% died) among the early- and late-hatching chicks in broods of the Great Tit and Willow Tit.

| | Early | | Late | |
|----------------------|---------|---------|---------|-----------|
| | Hatched | Died | Hatched | Died |
| Great Tit | | | | |
| 1969 | 31 | 3 (9.7) | 19 | 14 (73.7) |
| 1978 | 36 | 2 (5.6) | 23 | 10 (43.5) |
| 1980 | 26 | 0 (0.0) | 23 | 1 (4.3) |
| Willow Tit | | | | |
| 1978-81 ¹ | 15 | 0 (0.0) | 15 | 5 (33.3) |

¹) One nestling which died accidentally is not included.

in passerines (Inozemtsev 1962, Garnett 1976, O'Connor 1977, Törmälä & Kovanen 1979).

Effects of asynchronous hatching on the size of nestlings

In about 24 % of the Great and Willow Tit clutches all the eggs hatched within one day (Table 3). In most nests, however, hatching spread over 2 days, and there were some Great Tit clutches in which the hatching period was much longer, as much as 5 days in one second clutch. In 1980 the hatching period was significantly longer in second than in first clutches of the Great Tit (Fisher's exact test, two-tailed, $P=0.028$). No hatching periods longer than 2 days were detected in the Willow Tit, and accordingly the hatching period was shorter than in the Great Tit (χ^2 test, $P<0.05$, $df=2$ after combining days 3–5).

The impact of the hatching hierarchy upon nestling survival was tested by dividing the chicks into two groups, early and late hatchlings. The analysis included only those broods in which the young were individually marked and their weights were known on the day when the last chick hatched (day 0). Chicks lighter than the average weight of the brood on day 0 were classified as "late", and the rest were "early" chicks. This

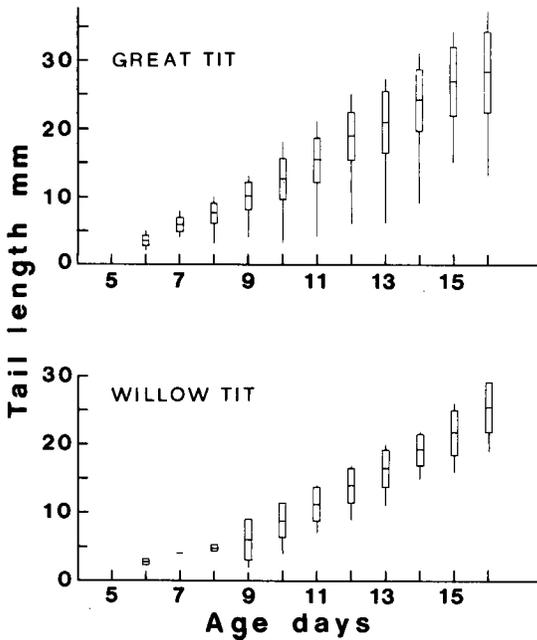


Fig. 7. Increase of tail length in nestling Great Tits (1978 and 1980) and Willow Tits (1978–1981). For explanations, see Fig. 1.

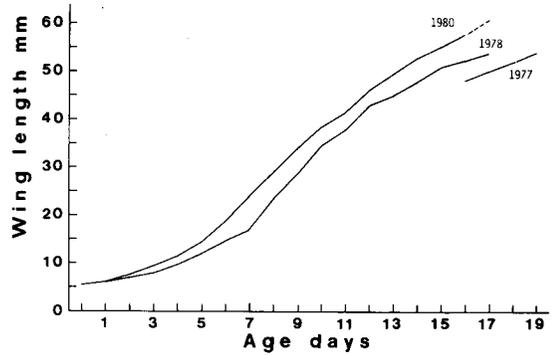


Fig. 6. Mean wing length curves for the Great Tit in 1977, 1978 and 1980.

method assumes a linear decrease in size from the first to the last hatchling. The size of the eggs, related to the hatchling size, need not be considered, since the intraclutch variation in the Great Tit in the Oulu area is small (Ojanen et al. 1981), and the same is assumed to be true of the Willow Tit. In any case, the method always places the first and last chicks in the right class, and only some chicks of medium size (from the middle of

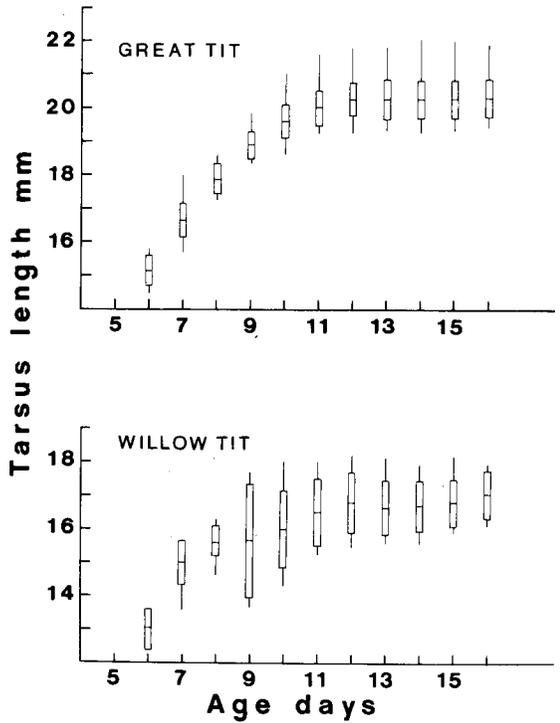


Fig. 8. Increase of tarsus length in nestling Great Tits (1980) and Willow Tits (1978–1981) after the age of 6 days. For explanations, see Fig. 1.

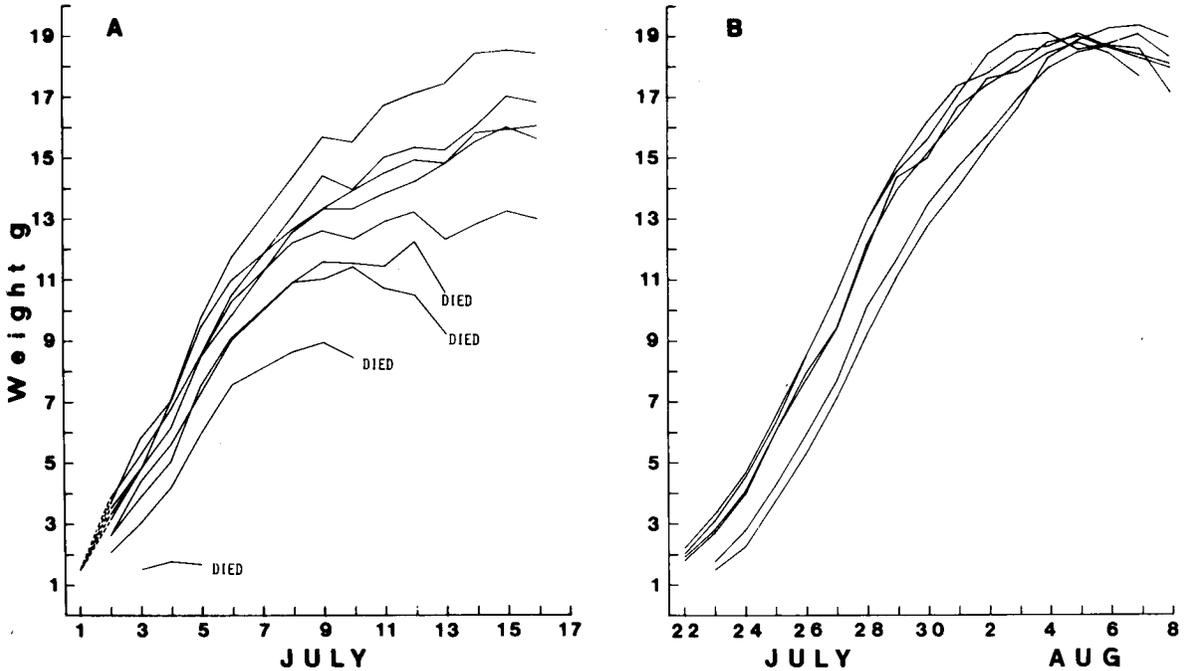


Fig. 9. Weight curves for Great Tit nestlings in a brood with chick deaths (A; repeat brood 56/1969, Taskila) and a brood in which all the young fledged (B; second brood 101/1980, Kuivasjärvi). Note the hatching asynchrony in both broods.

the hatching period) may be placed in the "wrong" class.

No statistical test is needed to demonstrate that mortality is higher among the chicks hatching late than among the early hatchlings (Table 4). In the Great Tit only the year 1980 saw practically no mortality in either of the groups. The hatching asynchrony was similar in 1977, 1978 and 1980 (Table 3) and resulted in great differences in mortality rates among the siblings (Table 4).

Inspection of the intra-brood and inter-brood coefficients of variation for nestling weights (Table 5) revealed that the weight differences within a brood were pronounced in both species on day 0, owing to the fact that some of the chicks had already been fed while others had not. The weight variation declined up to day 10, this trend being most pronounced in 1980 in the Great Tit.

The intra-brood variation declined further from day 10 up to fledging, except in 1980 in the Great Tit, when the variation was already small by day 10. As practically no Great Tit nestlings succumbed in 1980, the decline in intra-brood variation was the result of the late hatchlings attaining the same weight before fledging as their older siblings. A concurrent weight recession was apparent in the older chicks. These patterns are exemplified in Fig. 9B.

The pronounced weight variation on day 10 in the Great Tit in 1969, 1977 and 1978 was attributable to the presence of underweight runts. This is exemplified in Fig. 9A. Some nestlings died between day 10 and fledging. This, together with the fact that the largest nestlings ceased to put on weight and that some smaller ones continued to gain weight on the days before fledging, reduced the intra-brood variation (Fig. 9B). Most of the decline in the intra-brood variation in the Willow Tit (Table 5) was attributable to a repeat brood in 1977, in which the two smallest chicks gained weight more rapidly between days 10 and 16 than their larger sibling.

Although the intra-brood variation declined as the chicks grew older, the Great Tit fledglings in 1980 were not only clearly heavier but, what is more important, more uniform in weight than the young in the other years. In the 5 Willow Tit broods studied the intra-brood weight variation before fledging was the same as in the Great Tit in 1980.

A decline in inter-brood weight variation with age was clear in all the years in the Great Tit, especially in 1980; the fledgling population of that year was the most uniform in size. The increased inter-brood variation in the Willow Tit between days 0 and 10 is attributable to the repeat brood

from 1977, which included material for day 10. This brood was poorly nourished because the male abandoned it.

In order to study the effect of hatching order upon body size, the average weights and the average wing, tail and tarsus lengths were computed separately for the nestlings hatching early and late in a brood (Table 6). The last records for each brood were used, i.e. the figures represent approximately the size of the young at fledging. In the Great Tit the weights of the groups did not differ significantly from each other in any year (ANOVA). Nor did the average tarsus length depend on the hatching order. Only in 1980 were the wing and tail lengths of the early hatching Great Tits significantly longer than those of their younger siblings. The pooled data for the Willow Tit also revealed differences only in the wing and tail lengths.

The results in Table 6 do not tell us the whole truth, however. In 1969 the early-hatching Great Tits weighed more than their siblings in five broods, and in 1978 the early-hatching chicks were heavier than their siblings in four of the seven broods and had greater wing lengths in five. In the material described in Table 6, the average weight, wing length and tail length in the early-hatching young are greatly decreased by the records for two badly undernourished broods.

No weight hierarchy existed in 1980, but there was a hierarchy in wing and tail lengths. In 1978 most of the chicks which hatched latest died and the nestlings alive at the time of fledging were more uniform in age than those observed in 1980.

Table 5. Coefficients of weight variation between siblings and broods on the day of hatching, day 10 and just before fledging. The CV between siblings is the average of the values calculated for each brood.

| | Coefficient of variation | | Number of | |
|-------------------|--------------------------|--------|-----------|--------|
| | Siblings | Broods | Nestlings | Broods |
| Great Tit | | | | |
| day 0 | | | | |
| 1969 | 19.67 | 20.00 | 25 | 3 |
| 1977 | — | — | — | — |
| 1978 | 15.46 | 10.49 | 109 | 12 |
| 1980 | 20.66 | 19.04 | 46 | 6 |
| day 10 | | | | |
| 1969 | 12.67 | 13.73 | 79 | 13 |
| 1977 | 12.05 | 13.47 | 69 | 9 |
| 1978 | 10.98 | 17.69 | 110 | 14 |
| 1980 | 4.85 | 2.82 | 48 | 7 |
| before fledging | | | | |
| 1969 | 9.00 | 13.40 | 74 | 13 |
| 1977 | 7.48 | 6.23 | 83 | 14 |
| 1978 | 6.69 | 6.24 | 112 | 16 |
| 1980 | 4.90 | 3.50 | 59 | 8 |
| Willow Tit | | | | |
| day 0 | 15.61 | 6.07 | 23 | 3 |
| day 10 | 8.18 | 15.39 | 28 | 5 |
| before fledging | 4.81 | 10.63 | 28 | 5 |

Note. Day 0 is the day when the last chick hatched, day 10 is that when it was 10 days old and the day before fledging is the last day of weighing. Nestlings which died later are included.

Table 6. Weights (g) and wing, tail and tarsus lengths (mm) before fledging of early- and late-hatching Great Tit and Willow Tit siblings.

| | Mean | Early ±SD | N | Mean | Late ±SD | N | Significance of difference (ANOVA) |
|-------------------|-------|-----------|----|-------|----------|----|------------------------------------|
| Great Tit | | | | | | | |
| Weight | | | | | | | |
| 1969 | 15.96 | 2.263 | 29 | 14.30 | 3.948 | 6 | NS |
| 1978 | 15.80 | 2.641 | 38 | 15.94 | 1.733 | 15 | NS |
| 1980 | 18.24 | 0.944 | 18 | 18.08 | 0.928 | 16 | NS |
| Wing | | | | | | | |
| 1978 | 52.03 | 6.724 | 38 | 52.27 | 5.934 | 15 | NS |
| 1980 | 57.33 | 1.533 | 18 | 56.06 | 1.806 | 16 | P<0.05 |
| Tail | | | | | | | |
| 1978 | 26.47 | 7.490 | 38 | 26.33 | 6.873 | 15 | NS |
| 1980 | 33.39 | 1.685 | 18 | 31.06 | 3.043 | 16 | P<0.01 |
| Tarsus | | | | | | | |
| 1978 | 19.35 | 0.894 | 38 | 19.52 | 0.796 | 15 | NS |
| 1980 | 20.16 | 0.366 | 18 | 20.11 | 0.508 | 16 | NS |
| Willow Tit | | | | | | | |
| Weight | 11.52 | 0.702 | 15 | 11.60 | 0.655 | 10 | NS |
| Wing | 47.27 | 1.870 | 15 | 45.20 | 2.670 | 10 | P<0.01 |
| Tail | 25.69 | 2.496 | 15 | 23.10 | 3.725 | 10 | P<0.05 |
| Tarsus | 16.63 | 0.785 | 15 | 16.68 | 0.644 | 10 | NS |

Table 7. Weights (g) and tarsus, wing and tail lengths (mm) of adult and nestling Great Tits and Willow Tits. The adult weights were obtained at the end of the nestling period and the tarsus lengths refer to breeding individuals. The values for the nestlings were obtained from the last records before fledging. The adult wing and tail lengths were measured in September–April. In the Great Tit the measurements are given separately for yearlings (first figure) and older individuals (second figure). The nestling wing and tail lengths are estimates for the average fledging age (18 days, see text). % = nestling values as percentages of the adult averages.

| | Weight | | | Tarsus length | | | Wing length | | | Tail length | | |
|------------|--------|-------|-----|---------------|-------|-----|-------------|-------|-----|-------------|-------|-----|
| | Mean | ±SD | N | Mean | ±SD | N | Mean | ±SD | N | Mean | ±SD | N |
| Great Tit | | | | | | | | | | | | |
| females | 17.86 | 0.786 | 402 | 19.52 | 0.585 | 359 | 75.26 | 1.753 | 329 | 64.00 | 2.295 | 183 |
| | | | | | | | 76.46 | 1.431 | 97 | 65.66 | 2.062 | 57 |
| males | 18.63 | 0.782 | 281 | 20.08 | 0.646 | 339 | 78.08 | 1.650 | 334 | 67.81 | 2.153 | 213 |
| | | | | | | | 80.04 | 1.626 | 134 | 70.17 | 2.116 | 82 |
| fledglings | 16.43 | | | 19.83 | 0.705 | 169 | 58.2 | | | 33.8 | | |
| % | 90.5 | | | 100.2 | | | 75.5 | | | 50.9 | | |
| Willow Tit | | | | | | | | | | | | |
| females | 11.03 | 0.537 | 99 | 16.38 | 0.465 | 103 | | | | 59.51 | 1.961 | 64 |
| males | 11.64 | 0.473 | 84 | 16.85 | 0.715 | 86 | 64.68 | 1.937 | 102 | | | |
| fledglings | 11.47 | | | 16.67 | 0.715 | 25 | 50.2 | | | 30.7 | | |
| % | 101.2 | | | 100.3 | | | 77.6 | | | 51.6 | | |

As a result, the averages for the late-hatching nestlings in 1978 were about the same as those for the early hatchlings.

In more than half of the broods in 1969 and 1978 the size hierarchy attributable to hatching order still existed in terms of weight, wing length and tail length at the time of fledging. In most of the remaining broods the late hatchlings had succumbed before the last day of weighing.

Fledgling size in relation to adult size

The adult weights and lengths of the wing, tail and tarsus are given for both species in Table 7. The wing and tail lengths of the Great Tit are calculated separately for both sexes and for yearlings and older birds, since pronounced sexual dimorphism and age-specific differences are known to exist (e.g. van Balen 1967, Laaksonen et al. 1974, Garnett 1976, Haftorn 1976, Winkel 1980). Reliable sexing of the Willow Tit is not possible during wintertime and reliable age data are limited, so that only one average is given for the wing and tail lengths of this species.

The values used as the fledging weights were those obtained on the last day of weighing.

The average fledging ages of the Great Tit young were 17 (1980), 18 (1978) and 20 days (1977), and the wing and tail lengths at these ages were estimated from the growth data, assuming a linear increase after the last reliable mean. The values from the different years were then averaged to obtain the length at fledging. For the Willow Tit a figure of 18 days was used as the fledging age in the calculations.

The estimated wing length at fledging was about 76–77 % of that in the full-grown bird but the tail length only about 50 % (Table 7). Although the data are limited, there is a tendency for Willow Tits to be slightly more developed upon leaving the nest than are Great Tits, the relative lengths of the wing and tail being greater in the former.

Most of the Great Tit yearlings moult their rectrices during the post-juvenile moult in late summer (Svensson 1970), and Willow Tit yearlings may lose some of their middle tail feathers, but this is rare (Laaksonen & Lehtikoinen 1976). In both species the yearling birds keep their primaries and secondaries until the post-nuptial moult of the following summer (Svensson 1970). Therefore the yearlings measured for Table 7 had the wing feathers grown in the nest, but in most of the Great Tits the tail had moulted. Comparison between the fledgling and yearling Great Tits shows that the young attain about 76 % of their final wing length as nestlings.

In both species the tarsus length recorded at the last measurement of the nestlings was the same as that of the parent birds (Table 7).

The Willow Tit fledglings attained the same weight that their parents, but the Great Tits had reached only about 90 % of the adult weight by fledging (Table 7), being equal in weight to their parents only in 1980. In terms of weight as well, the Willow Tits leave the nest at a more advanced stage than the Great Tits.

It is interesting that those parts of the body which are essential for mobility, the wing and tar-

sus, are much more developed at the fledging stage than is the tail, which a bird can manage without for short periods.

Discussion

Brood reduction and clutch adjustment strategies

In altricial birds the investment in reproductive effort is optimal when all the eggs laid can be raised to fledglings. Attempts to rear a large number of young under poor feeding conditions not only decrease the amount of food brought to an individual nestling, resulting in lowered fledgling weights (cf. Gibb 1950, Gibb & Betts 1963, Perrins 1965, van Balen 1973), but may also endanger the whole brood because of the increased risk of predation upon hungry and noisy chicks (e.g. Perrins 1965). The increased stress of the parent birds will decrease their survival, thus reducing the fitness of the genotype (Ricklefs 1969b, Hussell 1972, Bryant 1979, Askenmo 1979, see also Drent & Daan 1980). Hence it is adaptive to adjust the clutch size to correspond to the number of young which the parents can feed. The clutch adjustment strategy is possible when food supplies are stable and predictable during laying (O'Connor 1978b). In unpredictable conditions the brood size is adjusted by brood reduction (e.g. Lack 1954, 1966, 1968, Ricklefs 1965, 1976, Löhrl 1968, van Balen 1973, Howe 1976, 1978, Bryant 1978a, b, O'Connor 1978a, b, Neub 1979, Drent & Daan 1980).

In the Great Tit in the Oulu area pronounced inter-annual differences existed in asymptotic weights and nestling mortalities. When the nestling weight was low, mortality was high (1977), and when the nestling weight was high mortality was low (1980). In both species studied mortality was concentrated among the late-hatching chicks. The hatching asynchrony was the same in years of poor (1977), moderate (1978) and high (1980) nestling survival. This is evidence that the observed asynchrony in hatching is sufficient to achieve a hierarchy among the nestlings that causes selective mortality (e.g. Lack 1954, 1966, 1968, Ricklefs 1965, 1976, Löhrl 1968, Bryant 1978a, b, Neub 1979). If the post-hatching conditions deteriorate, the late-hatching chicks are the first to succumb.

Hussell (1972), Bryant (1978a, b) and Bryant & Gardiner (1979) have suggested an alternative or additional function of hatching asynchrony. By spreading out the peak requirements of the individual nestlings, it reduces the demands on the parents. This is especially advantageous in large broods.

The parents evidently do not use up all their

energy when feeding their young (e.g. Royama 1966), although they may work at a level which is about four times the basal metabolic rate (Drent & Daan 1980), but under poor feeding conditions sibling competition rapidly increases the size hierarchy and the inferior chicks starve until the brood size matches the feeding capacity of the parents.

Hussell (1972) suggested that hatching asynchrony reduces the risk of predation by shortening the breeding period. Clark & Wilson (1981) rejected the brood reduction model and used the nest failure model for explaining hatching asynchrony in birds. Later Richter (1982) criticized the latter model and found brood reduction as an adaptive consequence of asynchronous hatching. In the case of the Great Tit avoidance of predation cannot be the main cause for asynchronous hatching since in second broods, laid late in the season, hatching is even more asynchronous than in early broods (e.g. Gibb 1950, this study), though predation pressure is no heavier than upon the early broods (Dunn 1977, Orell & Ojanen 1983b).

In many birds the egg size is a good predictor of hatchling weight (e.g. Parsons 1970, 1975, Jones 1973, Schifferli 1973, Davis 1975, Howe 1976, Bryant 1978a, Ricklefs et al. 1978, Lundberg & Väisänen 1979), and it has been shown that large chick size leads to accelerated growth (Parsons 1970, Schifferli 1973, O'Connor 1975b).

Howe (1976, 1978) found that egg size increased as laying progressed in the Common Grackle *Quiscalus quiscula*. He suggested that the egg size variation was a means of maximizing the reproductive output in unpredictable conditions; brood reduction was slowed down by the late chicks hatching from large eggs.

The influence of the egg size upon the size and subsequent growth of the chicks has not been studied in the Great Tit or the Willow Tit in the Oulu area. The intra-clutch variation in egg size in the Great Tit has been shown to be nearly negligible and smaller than among three other passerine species studied at Oulu, the Redstart *Phoenicurus phoenicurus*, Pied Flycatcher *Ficedula hypoleuca* and Starling *Sturnus vulgaris* (Ojanen et al. 1981). Therefore, differences in egg size seem to be less important than the hatching asynchrony in achieving a sibling hierarchy in the brood. Hence brood reduction is facilitated by hatching asynchrony when food is scarce in the Oulu area.

In the Blue Tit *Parus caeruleus* and House Sparrow *Passer domesticus* a size hierarchy exists among the siblings after hatching and a large weight on day 0 allows the nestlings to attain their maximum weight early and develop their flight feathers further before fledging (O'Connor 1975c).

Bryant (1978b) found that in the House Martin *Delichon urbica* the chicks that were largest at hatching had the best developed wings at the time of fledging. This was also observed in the Great and Willow Tit at Oulu.

Clutch adjustment evidently occurs among Great Tits and Blue Tits in English broad-leaved woods, as nestling mortality (excluding predation) appears to be negligible (Gibb 1950, Lack 1955, 1958, 1966, Perrins 1965, 1979, O'Connor 1978b). Late broods in the same woods and early broods in coniferous woods show brood reduction (Lack 1955, 1958, 1966, Lack et al. 1957, Gibb & Betts 1963, Perrins 1965, 1979, O'Connor 1978b).

The results obtained in the Oulu area show that nestling mortality is marked in most years in the Great Tit, and consequently it is suggested that a brood reduction strategy exists here in first broods (Ojanen et al. 1981, Orell & Ojanen 1983c). Sometimes, however, there are sufficient cues during egg laying for adjustment of the clutch size to the probable food level during the nestling time, e.g. in 1980. Willow Tits seem to be able to adjust the clutch size to the conditions prevailing during the nestling time in most years, thus showing a clutch adjustment strategy (Orell & Ojanen 1983c). However, the adjustment is not successful in every year, and brood reduction occurs in the Oulu area, e.g. in 1976 and 1977 (Orell & Ojanen 1983c). We cannot speak of "pure" clutch adjustment and brood reduction strategies, but rather of a "mixture" of breeding strategies, ranging from clutch adjustment when environmental uncertainty is low to brood reduction when it is high. This implies that the breeding strategies are not mutually exclusive (O'Connor 1978b).

The hatching period is somewhat longer in the Great Tit than in the Willow Tit, which indicates that the former species has a rapidly increasing size hierarchy, which leads to brood reduction when food is in short supply.

Growth rate

The growth constant K can be used in comparing the overall growth rates between different species if the same equations have been used for fitting the curves (Ricklefs 1967, 1968, 1973). Ricklefs (1968, 1969a, 1973, 1979) argued that the growth rate is related to the size of the adult birds, with small species growing faster than large ones. In birds of similar size the growth rate is related to the maturity of the offspring, altricial chicks growing faster than precocial chicks.

The exponential relationship $K=1.11A^{-0.278}$ (Ricklefs 1968) describes the dependence of the growth rate on the asymptotic weight in altricial birds. This equation gives the following growth rates for the Great Tit and Willow Tit in the Oulu

area (using the average adult weights from Table 7 as A):

| | |
|------------|-------|
| Great Tit | 0.495 |
| Willow Tit | 0.566 |

The observed values (Table 1) are much smaller, and the body size — growth rate relationship of these two species is inconsistent with that derived from more than one hundred altricial birds, i.e. the Willow Tit does not grow faster than the larger Great Tit.

Tiainen (1978) found that the growth rate of the Chiffchaff *Phylloscopus collybita* in southern Finland was slower than could be expected from Ricklefs' equation, and attributed this to the poor productivity of the spruce-dominated habitats preferred by this bird. The same explanation may be valid for the Great Tit in the Oulu area in view of the pronounced nestling starvation which frequently occurs (Orell & Ojanen 1983b). However, the overall growth rate in other Great Tit populations is also smaller than would be expected from the equation (Table 8).

The Great Tit is best adapted to living in broad-leaved woodlands; the first broods in Wytham Wood (mixed broad-leaved) and broods in Oosterhout (rich oakwood) hardly suffer at all from food shortage. The latter material even contained broods with no mortality (van Balen 1973). In the survey conducted by Rheinwald (1975) in a deciduous wood, however, the weight of the nestlings remained surprisingly low and some were poorly nourished, judging from the great range in weights within the age groups.

The Willow Tit and other *Parus* species also have a smaller growth rate (Table 8) than could be expected from the equation; the average rate calculated from the data in Table 8 is 0.410, which is much lower than the average for 18 passerine species with a size range of 11.0–20.0 g (0.501 ± 0.076 (SD), $N=21$; Ricklefs 1968).

The above equation shows only the average relationship between the growth constant (K) and the asymptotic weight. Hence the estimates calculated with this equation have certain standard errors. In spite of this, the growth constants estimated for different tit species were all considerably higher than the observed values. It is tempting to suggest that the growth rates of *Parus* species are lower than would be expected from the body size of the species.

Ricklefs (1968) estimated the growth constant for the Great Tit, Blue Tit and Black-capped Chickadee *Parus atricapillus* from the material of Gibb (1950) and Kluyver (1961), using the graphic method. The figures of 0.416 for the Blue Tit and 0.480 for the Black-capped Chickadee (first and second broods combined) were very close to those obtained here (Table 8) using Crossner's regression methods. In the case of the Great Tit, how-

Table 8. Growth parameters for five *Parus* species in different localities. The parameters were calculated by the present author.

| Species | Locality | Growth rate (K) | Asymptote (A) | Source |
|------------------------|----------------------------|-----------------|---------------|-----------------------|
| Great Tit | Oulu | 0.449 | 16.41 | This study |
| | Lahr | 0.383 | 16.66 | Rheinwald 1975 |
| | Oosterhout | 0.374 | 17.68 | Van Balen 1973 |
| | Wytham (1947) ¹ | 0.452 | 18.68 | Gibb 1950 |
| | Wytham (1948) ¹ | 0.433 | 18.73 | —" |
| | Wytham (1948) ² | 0.410 | 16.77 | —" |
| Willow Tit | Oulu | 0.406 | 11.66 | This study |
| | Wytham | 0.392 | 10.78 | Foster & Godfrey 1950 |
| | Near Moscow | 0.412 | 11.72 | Inozemtsev 1962 |
| | Changbai Shang Mts | 0.380 | 12.39 | Song 1980 |
| Black-capped Chickadee | Massachusetts ¹ | 0.500 | 11.02 | Kluyver 1961 |
| | Massachusetts ² | 0.439 | 11.74 | —" |
| Marsh Tit | Lahr | 0.330 | 11.58 | Rheinwald 1975 |
| Blue Tit | Lahr | 0.374 | 11.20 | Rheinwald 1975 |
| | Wytham | 0.413 | 11.55 | Gibb 1950 |

Note: ¹) First broods
²) Second broods

ever, Ricklefs gave confusing results, with growth rates varying between 0.382 and 0.480 in different tables. Rheinwald (1975) also used the graphic method for fitting the weight data, and obtained somewhat higher growth constants than those presented in Table 8 (0.404 for the Great Tit and Blue Tit and 0.352 for the Marsh Tit *Parus palustris*). Nevertheless, the different method of estimating the growth constants does not explain the difference observed between *Parus* and other passerine species.

Lack (1968) suggested that the development period in a bird species is a compromise between various selective pressures favouring slow or rapid growth, the main factors at work here being food supply and chick mortality. A slow growth rate means that the offspring require less intensive feeding and makes it possible for the parents to rear more young. This selection for slow growth is balanced by predation pressure, which favours fast growth. Lack (1968) found support for his view in the fact that species which have concealed nests have longer nestling periods (consistent with a lower growth rate) than do the open nesters (v. Haartman 1954, 1957, Nice 1957). Ricklefs (1969a, 1979, 1982) rejected the notion that nestling mortality selects for a high growth rate, arguing that the growth rate is inversely correlated with the adult body size. Although some hole nesters may grow at a slower rate than some open nesters, as suggested above, the difference in the nestling time is greater. The prolonged nestling time in hole nesters is due to the long interval between the day of attaining maximum weight and

the day of fledging (v. Haartman 1954, 1957).

Haftorn (1978) claimed that the relatively slow growth rate of the Goldcrest *Regulus regulus*, $K=0.409$, represents a level which matches the physiological limits of small birds. Owing to its small size, the Goldcrest must invest proportionately larger amounts of energy on self-maintenance, leaving less for its offspring. The same goal, lower daily energy expenditure, could have been attained by brood reduction or clutch size reduction, but growth rate reduction represents a finer adjustment (e.g. O'Connor 1978b, Drent & Daan 1980). The hypothesis that the comparatively slow growth rate of the nestlings is better suited to the food level and the parents' capacity, may also be put forward for the *Parus* species. Even so, this strategy proves inadequate for the Great Tit in the Oulu area in most years, and brood reduction is needed to match the energy expenditure to the availability of food.

Although growth rates are typical of individual species to a certain extent (e.g. Ricklefs 1968, 1979), their heritability is low as shown by Ricklefs & Peters (1981) for the Starling, which indicates that ecological factors are also involved (O'Connor 1977, Bryant 1978b). The variation in the growth rate of the Great Tit was high in years when there was marked nestling starvation; besides broods that grew at the normal rate, there were some that grew slowly. Under the most favourable conditions, i.e. in 1980, slow-growing broods were lacking. This suggests that, although the energy demands are limited by brood reduction, some pairs normally experience difficulty in

finding food for their nestlings, and the growth of their broods is delayed.

The relative safety of the nest site makes it possible for the chicks of hole nesters to stay in the nest for some time after attaining their maximum weight. This is an adaptive feature, allowing better development of the wings and tail at fledging than in open nesters (v. Haartman 1954, Tiainen 1978). The energy requirements of nestlings are apparently lower than those of fledglings, principally because the chicks huddle together in the nest to conserve heat (Royama 1966, Mertens 1969, van Balen 1973, O'Connor 1976), and this also makes it advantageous for them to stay in the nests as long as possible. The greater the maturity at fledging, the greater the fitness to face the critical post-fledging period (Perrins 1965, Lack 1966, Royama 1966).

The higher relative growth rate of the Great Tits compared with that of the Willow Tits may perhaps be explained by the hypothesis that in the latter species the parents invest less energy in siblings than in their own survival, or that the latter siblings invest relatively more in survival than in growth. The strategy of the Willow Tit is superior under the conditions prevailing in northern Finland, as judged in terms of nestling starvation. The chicks also tend to be slightly more developed at fledging than those of the Great Tit.

Weight and brood size

An inverse relationship between brood size and fledging weight has been reported in many studies concerning tits (Gibb 1950, Gibb & Betts 1963, Perrins 1963, 1965, 1979, Lack 1966, Lack et al. 1957, Minot 1981). Gibb (1950) showed that the increase in feeding frequency with brood size is not proportional. Gibb (1955), Royama (1966) and van Balen (1973) all pointed out that feeding frequency is not a good indicator of the amount of food brought to the nestlings, since it is inversely related to prey size. The estimated food intake per nestling per day is nevertheless larger in small than in large broods (Gibb & Betts 1963). However, late-hatching Great Tit and Blue Tit nestlings were fed more efficiently in large than in small broods, and thus gained weight more rapidly (O'Connor 1975b). This would at least partly compensate for the disadvantage of hatching late.

Feeding efficiently is not constant over the whole nestling period, however, and the parents usually begin to tire at the time of high energy requirement, when the chicks are about 12–14 days old (Royama 1966). Thus the weight of the chicks is lower in large than in small broods. This relationship may explain the trend for an inverse

relationship between asymptotic weight and the growth constant.

On the other hand, chicks in large broods have smaller energy requirements (heat loss) due to the smaller surface area/volume ratio. The inverse relationship between metabolic rate and brood size is not linear, however, and only the smallest broods (2–3 chicks) are at a disadvantage in this respect (Royama 1966, Mertens 1969, 1977, van Balen 1973, O'Connor 1975a). In spite of their smaller heat loss, chicks in large broods still suffer from food shortage. In the experiments of Crossner (1977), the chicks in the largest Starling broods weighed about the same as in the small ones, when the parents were provided with extra food for their young. In the control broods the weight decreased with brood size. Large broods may also suffer from hyperthermia at high temperatures (Mertens 1969, 1977, O'Connor 1975a), although the temperatures involved seem to be at the upper end of the normal range of the ambient temperatures (van Balen & Cavé 1970).

Although an inverse relationship tended to exist between initial brood size and asymptotic weight in the Oulu area, the large weight variation between broods of the same initial size shows that food affects the weight in many ways. There may be variation in feeding capacity due to differences in foraging efficiency between the parent birds, and the "quality" of the territory may also be involved (Askenmo 1973, Högstedt 1980), since not only the quantity but also the quality of the food has been shown to affect the growth rate (Berthold 1976). Hence, parents may have somewhat different strategies in raising their young, depending on the prevailing conditions and their own ability to find food. Similarly, size reduction is used in some broods to match the energy expenditure to the amounts of food which the parents can provide, while in others this level is attained by reducing the growth rate still further.

Importance of size at fledging for future survival

The size at fledging is important for subsequent survival, and recovery rates 3 months and more after fledging have been shown to be higher among large than among small Great Tit nestlings (Lack et al. 1957, Perrins 1963, 1965, Garnett 1976). The total fat content, lean dry weight and carcass weight explained nearly 90 % of the total variance of the 15th day body weight in this species (Garnett 1976), and the fat content alone 88 % in the Blue Tit (O'Connor 1976). The young hatching later carried less protein than did the early hatching siblings in the Great Tit (Garnett 1976), and the heavy fledglings thus had higher energy reserves when leaving the nest. Garnett

(1976) nevertheless estimated that fat reserves are not important for long-term survival since the amounts concerned would suffice for only one day on average. Even so a high fat and protein content must be of some survival value during brief periods of food shortage (see also Bryant & Gardiner 1979).

It is a disadvantage to hatch last when food is scarce, since the size hierarchy remains at fledging, provided that the later hatchlings are still alive. Under good feeding conditions the weight hierarchy disappears, though as shown here, there is still a difference in the wing and tail lengths (see also O'Connor 1975b, Garnett 1976). Post-fledging survival is evidently not greatly affected by the hatching hierarchy when there is plenty of food during the nestling period.

The weight of Great Tit fledglings is higher in early than in late broods, which is attributable to a shortage of food later in the season (Gibb 1950, Perrins 1963, 1965, Lack 1966, van Balen 1973). In coniferous habitats in the same areas, where food is abundant later in the season, the young in the later broods are heavier than in the earlier ones (Lack 1955, Lack et al. 1957, Gibb & Betts 1963, Perrins 1965, van Balen 1973).

Perrins (1963, 1965, 1979) and Lack (1966) argued that it is advantageous for tits to breed early in Wytham Wood because fledglings from early broods are better nourished and survive better after fledging than those from late broods. Even a smaller brood size later in the season is not enough to compensate for the decrease in the food supply, and the recovery rate among these fledglings is low. However, the Belgian and Dutch data analysed by Dhondt & Hublé (1968) did not reveal differences in survival between early and late broods. Moreover, Kluyver et al. (1977) showed that survival in late broods was better in a Dutch pinewood than in an oakwood.

No study has yet been made on the post-fledging survival of tits in the Oulu area, but a brief analysis suggests better survival among heavy fledglings than among light ones (own unpublished data).

The present results do not point out to any pronounced difference in the size of the fledglings between early and late broods (Table 3), but a preference for early breeding may still be regarded as an adaptive feature. This is due to the social relations among the young birds (Garnett 1976); in flocks of tits the offspring from early broods, being larger, tend to dominate over the newly fledged young from late broods.

The limited length of the season available for breeding and post-nuptial and post-juvenile moult also implies selection for early breeding in the Oulu area (Orell & Ojanen 1983a).

When food is short the hierarchy within broods

becomes rapidly marked and it is not adaptive to invest energy in the runts, whose chances of survival are small, at the expense of the larger siblings. Hence active reduction of the brood size by the parents is even likely to occur (Bumerl 1970, Neub 1979).

Comparison of the Great Tit and Willow Tit in the Oulu area, suggests that the young of the latter species may be more developed on leaving the nest. They are relatively heavier and tend to have slightly longer wings and tail. In the Blue Tit fledglings in Wytham Wood the wings were even better developed, their length being 79.8 % of that of the adults (O'Connor 1977). Although brood reduction occurs in the Great Tit in Oulu, there is still a great deal of variation in size among the fledglings of the same brood. The fledged broods of the Willow Tit are more uniform in size. In view of what was said above about the influence of energy reserves and body size on post-fledging survival, we may expect that in many years a much larger proportion of fledglings of the Great Tit will die soon after leaving the nest, and the Willow Tit thus seems better adapted to conditions in northern Finland. This may be interpreted as a better adaptation of the Willow Tit to the northern conditions.

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Selostus: Tali- ja hömötiaisen poikasten kasvu

Tali- ja hömötiaisen poikasten kasvua tutkittiin Oulussa kahdella tutkimusalueella Taskilassa ja Kuivasjärvellä vuosina 1969, 1977—1981. Poikaset punnittiin, siiven, pyrstön ja "nilkan" pituus mitattiin.

Molempien lajien poikaset kuoriutuivat usein eriaikaisesti. Talitiäisellä eriaikaisuus oli korostuneempaa kuin hömötiäisellä. Edellisen lajin ensimmäisissä pesyeissä kuoriutuminen yleensä tapahtui kahden vuorokauden sisällä, mutta joissakin tapauksissa kuoriutuminen kesti neljä vuorokautta (taulukko 3). Saman kesän toisissa pesyeissä kuoriutuminen kesti kauemmin kuin varhaisissa pesyeissä (keskiarvot 3.0 ja 1.9 vuorokautta). Joka neljännessä hömötiäispesässä poikaset kuoriutuivat samana päivänä ja loppuissa kahden päivän aikana.

Pesäpoikasten kasvu on esitetty kuvissa 1 (paino), 5 (siiven pituus), 7 (pyrstön pituus) ja 8 ("nilkan" pituus) sekä liitteissä 1 ja 2. Taulukossa 1 on esitetty painon kasvun logistiset kuvaajat. Hömötiäinen näyttää kasvavan hieman hitaammin kuin talitiäinen, mutta ero ei ole tilastollisesti merkitsevää. Talitiäisen kasvunopeudessa on vuosienvälisiä eroja. Vuonna 1980, jolloin poikasia kuoli vain satunnaisesti, poikueiden väliset kasvunopeuserot olivat pienimpiä. Samana vuonna poikaset olivat pesästä lähtiessään painavampia kuin muina vuosina. Vuonna 1977, jolloin poikaskuolleisuus oli erittäin suuri, poikasten painot jäivät alhaisimmiksi (kuva 3, taulukko 1). Vuonna 1969 talitiäisen poikaset kasvoivat uusintapesyeissä nopeammin kuin ensimmäisissä pesyeissä, mutta vuonna 1980 eroja ei ollut ensimmäisten ja toisten poikueiden välillä (taulukko 2). Yleensä suurissa poikueissa kasvu oli nopeampaa, mutta poikasten lopulli-

nen paino jäi alhaisemmaksi kuin pienissä poikueissa. Kaikkina vuosina poikuekoosta johtuvat erot eivät kuitenkaan olleet tilastollisesti merkitseviä. Vuosienvälisiä ja poikuekoosta johtuvia eroja ei voitu tutkia hömötiäisellä pienestä aineistosta johtuen.

Eriaikaisesta kuoriutumisesta johtuen poikaskuolisuus kohdistui valikoivasti pienimpiin, viimeisenä kuoriutuneisiin poikasiin. Mikäli nuorimmat poikaset selvisivät lentokykyisiksi niiden suuret ja pyrstö olivat lyhyemmät kuin vanhemmilla sisaruksilla. Painoltaan nämä poikaset eivät aina olleet keveimpiä. "Nilkan" pituudessa ei ollut kuoriutumisjärjestyksestä johtuvia eroja pesästä lähdön aikaan.

Tämän tutkimuksen tulosten ja kirjallisuustietojen perusteella täiasten kasvuopeus näyttää olevan hitaampaa kuin ennustettu arvo, joka saadaan yli sadan pesäviipyyisen lintulajin aikuislintujen painon ja poikasten kasvuopeuden välisestä riippuvuudesta. Tämä saattaa olla sopeutuma tuottaa suurempia poikueita kuin avopesijät. Kolopesijöiden pienempi predaatiopaine verrattuna avopesijöihin on ilmeisesti mahdollistanut hitaamman kasvuopeuden.

Hömötiäisen poikaset jättävät pesänsä suhteellisesti hieman kehittyneempinä kuin talitiäisen poikaset. Edelliset painavat yhtä paljon kuin emonsa pesinnän lopussa, mutta talitiäisten poikaset ovat saavuttaneet keskimäärin vain noin 90 % emojen painosta. Myös siipi ja pyrstö näyttävät olevan suhteellisesti hieman pitempiä hömötiäisen poikasilla (taulukko 7). Molempien lajien poikasilla "nilkka" saavuttaa lopullisen pituutensa jo pesäpoikasikana.

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Appendix 1. Weights (g) of nestling Great Tits and Willow Tits calculated from the material for 1969, 1977, 1978 and 1980, and for 1977—1981, respectively.

| Age (days) | Great Tit | | | Willow Tit | | |
|---------------|-----------|------|-----|------------|------|----|
| | Mean | ±SD | N | Mean | ±SD | N |
| 0 | 1.59 | 0.25 | 98 | 1.13 | 0.12 | 25 |
| 1 | 2.37 | 0.38 | 166 | 1.67 | 0.24 | 25 |
| 2 | 3.55 | 0.56 | 179 | 2.28 | 0.34 | 26 |
| 3 | 5.04 | 0.72 | 170 | 3.14 | 0.49 | 26 |
| 4 | 6.72 | 0.94 | 244 | 4.14 | 0.58 | 26 |
| 5 | 8.33 | 1.16 | 225 | 5.23 | 0.86 | 25 |
| 6 | 9.95 | 1.43 | 213 | 6.45 | 1.06 | 25 |
| 7 | 11.49 | 1.67 | 239 | 7.48 | 1.07 | 26 |
| 8 | 12.69 | 1.81 | 227 | 8.58 | 1.06 | 26 |
| 9 | 13.88 | 2.00 | 237 | 9.32 | 1.08 | 26 |
| 10 | 14.76 | 2.29 | 256 | 9.94 | 0.98 | 26 |
| 11 | 15.54 | 2.30 | 212 | 10.62 | 0.88 | 26 |
| 12 | 15.96 | 2.31 | 237 | 10.98 | 0.93 | 26 |
| 13 | 15.80 | 2.31 | 248 | 11.27 | 0.86 | 25 |
| 14 | 16.48 | 2.07 | 246 | 11.34 | 0.82 | 26 |
| 15 | 16.48 | 1.83 | 234 | 11.36 | 0.66 | 26 |
| 16 | 16.01 | 1.86 | 208 | 11.53 | 0.81 | 17 |
| 17 | 15.49 | 1.73 | 93 | 11.16 | 0.56 | 11 |
| 18 | 15.61 | 1.30 | 97 | — | — | — |
| 19 | 15.83 | 1.32 | 12 | — | — | — |

Appendix 2. Wing lengths (mm) of nestling Great Tits and Willow Tits calculated from the material for 1978 and 1980, and for 1978—1981, respectively.

| Age (days) | Great Tit | | | Willow Tit | | |
|---------------|-----------|------|-----|------------|------|----|
| | Mean | ±SD | N | Mean | ±SD | N |
| 0 | 5.28 | 0.40 | 21 | — | — | — |
| 1 | 6.14 | 0.45 | 53 | 5.16 | 0.43 | 9 |
| 2 | 7.55 | 0.50 | 41 | 6.57 | 0.55 | 14 |
| 3 | 9.15 | 0.86 | 47 | 7.68 | 0.58 | 14 |
| 4 | 11.23 | 1.01 | 61 | 9.46 | 0.69 | 14 |
| 5 | 13.51 | 1.68 | 49 | 11.68 | 0.93 | 14 |
| 6 | 18.15 | 2.06 | 49 | 14.96 | 1.28 | 14 |
| 7 | 22.65 | 3.47 | 52 | 19.00 | 1.80 | 14 |
| 8 | 27.44 | 3.18 | 66 | 22.32 | 1.65 | 14 |
| 9 | 31.58 | 3.48 | 77 | 26.32 | 2.20 | 14 |
| 10 | 36.67 | 3.14 | 90 | 30.50 | 2.24 | 14 |
| 11 | 39.49 | 3.86 | 113 | 34.36 | 1.86 | 14 |
| 12 | 44.49 | 2.95 | 128 | 37.86 | 1.70 | 14 |
| 13 | 46.75 | 4.25 | 129 | 40.78 | 1.53 | 14 |
| 14 | 49.79 | 4.31 | 131 | 43.36 | 1.45 | 14 |
| 15 | 52.81 | 4.02 | 145 | 45.86 | 1.35 | 14 |
| 16 | 54.04 | 4.23 | 109 | 48.42 | 1.08 | 12 |