

Nestling growth and breeding biology of Great Tit, Blue Tit, Willow Tit and Crested Tit

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Abstract

The correlative relationship of growth rate constant, environmental variables and life history traits was studied in the nestlings of the great tit, the willow tit, the crested tit and the blue tit in the Oulu area of northern Finland in 1969, 1977-1981 and 2017. All the species reached their species specific asymptotic weights by the age of 13-14 days. The asymptotic weight of the great tit was relatively lower than the adult weight compared with the other parids studied. The mortality rate of the nestling great tits was higher than of the crested and willow tits in 2017. Large initial brood size pose a negative impact on the great tit mass growth. It is possibly related to the high energy maintenance from the parents and unpredictable weather reduces food supply. The high number of hatchlings seems to be related to increasing nestling mortality in the great tit. After the brood reduction, parents can better nourish the rest of the nestlings which leads to a positive association between the number of fledged chicks and the growth rate constant. We did not find any significant relationship between the ambient temperature and growth rate constant in any of the species. It can be associated with the method of collecting the temperature data. However, the amount of rainfall during the nestling period was positively related to the wing growth rate constant in great tits. The late hatched willow tit nestlings grew faster than the early nestlings. There was a trade-off for the timing of breeding in the willow tit. The early nestling might be able to prepare themselves into breeding population while the late nestling might receive better nourishment from their parents. Besides, the brood size at hatching were markedly related to the growth rate constant in the willow tit. This possibly reflects the female quality and habitat quality in the Oulu area. The growth rate constant of different species was related to the body size, clutch size, and species specific breeding strategies.

Introduction

The study of nestling development presents the diversity of growth patterns among birds associated with their morphology, ecology, and behavior (Ricklefs 1968). The shape of the growth curve reflects the wide range of selective pressure driving adaptation for reproduction (Ricklefs 1968). The altricial-precocial spectrum describes the difference in the developmental trajectory of hatchlings, parent-chick relationship, and interaction between the environment and chicks (Ricklefs & Starck 1998). The earliest description goes back to Oken (1837), state that “altricial birds come naked and blind into the world, needing to be fed in the nest, while precocial birds come from the egg with sight and feathered; not being fed, but soon running about and searching for their food by themselves”. At the present, the basic distinction between altricial and precocial has not changed yet.

Parids are generally classified as altricial with regard to their intensive parental care throughout the nestling period. They breed in nest holes, which is relatively safer than open nesting and allow them to grow slower. The growth rate of nestling is influenced by habitat quality, availability, and quality of food, brood size and weather condition etc. Habitat type is highly correlated with the beak shape (Snow 1954). Coniferous forest species have relatively long and fine beaks, which are practical for probing among conifer needles and the invertebrates on conifer trees should be smaller than in broad-leaved trees (Snow 1954). Species living in broad-leaved habitats have relatively short and stout beaks (Snow 1954). For example, the great tit (*Parus major*) prefers to live in broad-leaved woodlands and has the largest beak. Most studies of breeding biology concentrate on species living in broad-leaved woodlands. The great tit is one of the most extensively studied species in ornithology because it is common in human settlements. Data focusing on the pattern of weight of the crested tit (*Lopophanes cristatus*) is insufficient. The breeding biology of the crested tit is poorly known due to the difficulties in collecting data.

The blue tit (*Cyanistes caeruleus*) and the great tit are commonly widespread in rural and urban habitats of Europe (Cramp & Perrins 1993). They occupy similar habitats surrounded by human settlement as they provide stable food sources and breeding resources (Schmidt 1988, Orell 1989). From early March, their breeding season starts across Europe (Cramp & Perrins 1993). Both species are insectivorous during the breeding season and raise their young mostly with caterpillars. At the beginning of the 20th century, the population of the blue tit in southern Finland was extremely scarce (Hildén 1986), but the population density of the species was as abundant as of the great tit by the end of the century (Hildén 1990) due to intensive artificial winter feeding (Hildén 1990). Both species vary in size and euryoecious, but where they reside together, the great tit is always larger than the blue tit (Snow 1954). The blue tit becomes more stenoecious towards its northern limit (Snow 1954). However, the broad-leaved forests are rare in northern Finland and it brings up the question regarding the adaptability of the great tit and the blue tit. Species colonized new habitats or gradual changes in vegetation can lead to selection for adaptation to the new habitat (Snow 1954). The blue tit has demonstrated its adaptability in the pine forests on the Canary Island before (Snow 1954).

Compared with the aforementioned species that reside in man-made habitats, the willow tits (*Poecle montanus*) prefer mixed forest of spruces and birches, pure coniferous forests, and deciduous woodlands (Palmgren 1930). The distribution of the willow tit is throughout much of the Western Palearctic and extends over the northern parts of Eurasia (Cramp & Perrins 1993, Snow & Perrins 1998). In Siberia, the nestling diet of the willow tit mostly consists of Diptera and Lepidoptera (Pravosudova & Pravosudova 1996). With the fast response to the warmer weather and short breeding period, willow tits lay eggs slightly earlier than great tits and blue tits (Orell & Ojanen 1983a). Replacement and second clutches are rare in the willow tit (Orell & Ojanen 1983d).

During the 1940-1950's and the 1970's, the large-scale clear cuttings on old growth forests lead to a drastic decline in crested tit population in northern Finland, by up to 95% (Järvinen & Väisänen 1978). Old growth forests provide suitable nesting holes and protection for crested tits and willow tit to breed. Deforestation heavily affects the breeding parameters, which have caused the delay in laying and smaller clutch size (Orell & Ojanen 1985). In the Scandinavian coniferous forest, the crested tit is the pioneer regular breeder that starts to lay eggs in April (Ekman & Askenmo 1986). The length of the breeding season of the crested tit in Oulu was 38 days, which is comparatively shorter than of the willow tit (65 days) (Orell & Ojanen 1983c). Crested tits rely on the spiders, adult insects, and conifer seeds by storing them on tree trunks and branches to survive through the winter and prepare for the early breeding season. (Cramp & Perrins 1993). Some observations claim that they feed seeds to the nestlings and make it possible for them to breed in early spring (Cramp & Perrins 1993, Eeva et. al 2011). A notable contrast with willow tits, blue tits and great tits that feed their chicks with caterpillars.

Studies on passerines birds regarding the breeding biology have been conducted for some decades in Oulu (Orell & Ojanen 1985, Orell 1983). Various breeding strategies have adopted to cope with the unpredictable climatic event in northern Finland. Synchrony between the timing of caterpillar biomass peak and the breeding phenology of passerine birds creates selection pressure on breeding success (Blondel et al. 1993, Noordwijk et al. 1995). Matching the peak of caterpillars can increase the likelihood of nesting success. The great tit is generally more opportunistic than the other Parids, therefore it often lays large first clutches and produces also second clutches (Orell & Ojanen 1983b). Brood reduction in the great tit is facilitated by nestling starvation and unpredictable adverse weather. The large first brood commonly suffers from intensive nestling mortality (Orell & Ojanen 1983c). Deserting nestlings in unfavorable condition and investing in future young appear to be more prevalent in the willow tit (Orell & Ojanen 1983c). On the other hand, willow tit parents invest relatively more energy in their own survival than in reproduction. The initial brood size of willow tits attains substantial nesting success by adopting the clutch adjustment strategy in Oulu (Orell & Ojanen 1983d). The crested tit responded rapidly to the warmer weather and lays egg relatively earlier in oulu than in the southern part of Finland (Orell & Ojanen 1985), an inverse relationship between clutch size and the degree of latitude (Orell & Ojanen 1985). In Orell & Ojanen (1985), it has exhibited the similar breeding success of the crested tit and the great tit in Oulu area.

The diversity of growth patterns provide insight into selective forces at different stages of the life history cycle as well as ecological and social factors such as predation pressure, energy budget and parental care (Ricklefs 1968, Lack 1968). In this study I examined four passerines species regarding their patterns of growth. Great tit is the largest tit species with largest beak and being the widest distributed Palearctic species (Snow 1954). Great tit and blue tit

together extensively occupied broad leaved habitats in the western Palearctic (Snow 1954). Crested tits and willow tits are classified as vulnerable in the 2015 Red List of Finnish Bird species (Tiainen et al 2015). Snow (1954) states that “species occurring together in the same habitat are generally more similar to one another than to those from other habitats”. It constructs a hypothesis that nestling growth in the great tit and the blue tit are similar to each other, and the same happens with the willow tit and the crested tit. I also expected differences in the nestling growth pattern in the great tit and the blue tit, newcomer species in the north, compared with willow tits and crested tits. Based on the population increase in the blue tit and the great tit gives us a hint on how well they have adapted to the north. On the other hand, the crested tit breeding in early spring with lower food availability and quality, is assumed to have a lower nestling success than other Parids. The primary aim of this study is to document and gather quantitative and qualitative information regarding the nestling growth of the blue tit and crested tit in Oulu area. It is important to learn about the ecology and growth rate constant of the crested tit through a comparative study as the start of laying and food sources are distinct. I will model the growth trajectories of these four species and identify the significant factors associated with them. Growth patterns are correlated with life-history traits and environmental factors to evaluate the relationships in great tit and willow tit. Using the past 50-year data on the great tit, I tried to measure the annual variation in their growth curves and find some general outlines of the situation during nestling the growth period. By this empirical and descriptive approach, my attempt was to get some insight on the growth pattern and breeding strategies of these four species through a correlative and comparative analysis of their growth rate constant.

2. Method

2.1 Study areas

The study was composed of data provided by Professor Markku Orell in 1969 and from 1977 to 1981 in Taskila and Kuivasjärvi and the second set of data collected in May-July 2017 in Rusko, Oinaansuo and Uikulaisjärvi at Oulu (65N, 25.3E) (Orell, 1983). All the habitat description and procedure of data collection between 1969 to 1981 was based on Orell and Ojanen (1983a). In Taskila, deciduous tree, birch, alder (*Alnus incana*) and aspen (*Populus tremula*) are abundant throughout the area. In the eastern part, private houses and abandoned field are located. The under canopy was rich in dwarf shrubs and grasses. Kuivasjärvi was dominated by spruce forests. Scots pine, birch, and aspen are relatively less abundant compared to Taskila. The study sites are moist forests constituted spruce and pine bogs, supplying decaying woods for willow to excavate the natural nest hole. In addition, artificial nest holes tied onto tree trunk are provided. Only a fraction of willow tit nest will breed in nest boxes with rotten wood.

The nests of great tit and blue tit in this study were concentrated on the Rusko area and Oinaansuo area with the size of 1.3 km² and 0.9 km² respectively (Karvonen et al. 2012). Oinaansuo area occupied with 150 nest boxes, and was surrounded by moist spruce forest and spruce bogs (Rytkönen & Orell 2001). Willow tit and crested tit nests were located at the empty spaces between Oinaansuo and Uikulaisjärvi area. The habitat types were dominated by dry pine forest (Rytkönen & Orell 2001).

2.2 Material and Fieldwork

The material consisted of 4 willow tit broods, 11 great tit broods in 1969 and 1977 to 1981. 3 blue tit broods, 3 crested tit broods, 4 willow tit broods and 4 great tit broods were examined in 2017. In total, this study includes 179 nestlings and 26 broods (Table 1). All the dead chicks were excluded from the analysis. Once a week, each site was visited from mid-April onwards to search for crested tit and willow tit nest.

Great tit nests were recorded from May until August. With the assistance of a small mirror and torch, clutch size was estimated and later verified when the chicks hatched. The number of eggs and chicks were recorded during each visit. If the nest was destroyed, the regular visit will monitor the activity of the parents and check the presence of the second nest. The majority of clutches were visited before laying had ended. An assumption of one egg laid per day was made to estimate the day of laying when several eggs were laid during the first visit. The transparency and size of the air bubble in the eggs were taken into account to determine the start of laying (Ojanen & Orell 1978). The age of chicks was determined based on the previous experience from the selected brood that had been followed daily. The estimation of hatching day was referenced to the age of chicks.

All great tit and blue tit broods were nested in wooden nest boxes. Willow tit and crested tit broods were located in natural holes that parents excavated with wire protection. The nestlings of great tit and blue tit were carefully taken out through the roof by removing the wood cover on the box. Willow tit and crested tit nest cavity were accessed through a hole which was cut at the level of the nest and the entrance then covered with birch bark. Parents can enter the nest through the main entrance that has no any sort of coverage. The age of chick was recorded as day 0 on the hatching day and day 1 as the following day, etc. Each brood was visited either in the morning or afternoon. All the nestlings studied in 2017 were individually marked with water-proof dye on the leg on the first day except one crested tit nest, which was marked at the age of 4. Nestling was weighed with 50g electronic balance (accuracy 0.1g). The wing was measured starting from day 3 with a ruler to the nearest 1mm. The method described by Svensson (1970) was applied, a flattened wing was placed straightened sideways on a ruler. Tail and tarsus began to be recorded on day 6 since the tarsus was fragile in newborn chick and the tail started to emerge between 4 to 5 days. The measurement of the tail was obtained according to the "right angle" method of Busse & Kania (1970), to an accuracy of 1mm. The standard method described by Svensson (1970) was performed to measure the length of tarsus with sliding calipers to the nearest 0.05 mm. Young was subjected to the measurement until the age of 15 days to 17 days depending on the species. Several retarded nestlings died during the measuring period. All the nestlings were marked with aluminum rings at the age of 10 days. Regular visits were undertaken until all nestlings fledged and checked for the possible dead chicks left in the nest.

2.3 Grofit model

According to Ricklefs (1976), the growth curves of passerines fitted the logistic equation better than the Gompertz or von Bertalanffy equations, which was more suitable for species only raise one chick. Logistic equation is a three parameters equation, typically given as:

$$M = \frac{A}{1 + \exp(-k(t - T_i))}, \quad (1)$$

where M is body mass, A is the final weight or asymptote, K is growth rate constant, and T_i is the age at the inflection point of the growth curve (days), where $M = A/2$. The logistic model is relatively inflexible because of the symmetrical around inflection point is fixed at 50% of the upper asymptote, $M = A/2$.

The grofit package (Kahm & Kschischo 2015) in R 3.1.0 (R Core Team 2015) offers three parameters, maximum of the curve (A), maximum slope (μ) and lag-phase (λ). Maximum of the curve (A) represents the asymptote. Growth rate constant (K) can be obtained by using μ and A, and the equation is $K = 4 \mu/A$.

2.4 Statistical analysis

The linear mixed model (LMM) was adopted and analyzed in the lmer package (Bates, Maechler, Bolker, and Walker 2015) in R 3.1.0 (R Core Team 2015) as the data set is in a normal distribution. Linear mixed model (LMM) is used to perform analysis of variances (ANOVA) in growth rate constant and mortality rate of great tit among different years. Each nestlings served as a sampling unit in the test.

Variance Inflation Factor (VIF) was used to analyze for controlling multicollinearity of explanatory variables. If the VIF value was larger than 4, we rejected to use those explanatory variables together in selecting the model. The impact of year and brood variation on growth rate constant is uncertain. That is the reason why they are the random factors in the model. Only brood ID was the random factor and species was the explanatory variables in testing the growth rate constant of different species in 2017. Linear mixed models were developed using growth rate constant of four morphological characters (mass, wing length, tail length and tarsus length) as the response variable for the analysis in great tit and willow tit. Clutch size, first egg day, number of hatched chicks (initial brood size), number of fledglings, hatching day were then used as explanatory variables. Ambient temperature and rainfall were the environmental variables, which were the average daily temperature and rainfall during the growth period of each nest (day 1-20). The climatic data were collected from monthly reports of the Meteorological Institute of Finland, which took place at the Oulu airport. In total, 5 models featuring optimal correlation and variance structures were presented regarding the lowest values of Akaike information criterion (AIC) (Appendix 1).

3. Result

3.1 Growth pattern

3.1.1 Weight

In all the graphs and calculations, chicks that died before fledging were excluded in all measurements. This exclusion can provide a more accurate result of growth rate constant. Great tit nestlings weighted about 1.35 – 1.84 g while willow tit chicks weighted 1.08 – 1.33 g at hatch. At the age of 15, great tit had some weight recession before fledging (Fig.1a). Fledging took place at the age of 18 days in Oulu area (Orell & Ojanen 1983a). In willow tit, there was no sign of weight recession before fledging (Fig. 1b). Orell (1993) recorded the weight recession of willow tit on day 17 and no sign of weight recession on day 15 and 16. Weight variation in great tit was remarkable compared to willow tit. At the age of 10 – 13 days, great tit chicks had the highest weight variation, and those of the willow tit were at the age of 6 – 9 days. The most underweight great tit chick weighted only 8.7-9.9 g, while the heaviest young weighted 20.5 g at the age of 13 days. The average coefficient of variation in weights ($CV = 100 \times SD/mean$) at day 10 -16 was more than twice as high in the great tit (15.3%) as in willow tit (7.8%). The inter-individual variation in weight was higher in the great tit than in willow tit. Besides, great tit had relatively low fledging weight in comparison to adult body weight, whereas willow tit fledglings reached almost the adult weight.

In great tit, the absolute growth rate (g/day) was the highest at the age of 3 – 6 days (Fig. 1c). The largest daily increased in grams is 1.8 g at day 6. The same happened in willow tit that the age of day 6 was the peak daily increase of 1.6 g. In compare to great tit, willow tit daily increase progressively dropped until day 15, while great tit daily increase in weight gradually decreased and fluctuated. The peak relative weight increase was on the first day of life on both species and then progressively decline (Fig. 1d) . At the first 4 days, the relative weight increase was higher in great tit and the reserve situation happened on day 6, meaning that great tit nestling grew faster in the early period.

According to Orell (1983), many irregularly growing broods occurred in 1969 and 1977. In 1980, great tit showed the highest growth rate and asymptotic weight (Fig. 1e). The same case happened on willow tit in 1980 (Fig. 1f). The overall growth rate constant (K value) in great tit nestlings was 0.432 (Table 1). The result of the mean weight graph was not consistent with the growth rate constant result. The growth rate constant in 1969 was higher than 1978 and 2017. The result in growth rate constant and asymptotic weight in willow tit was consistent with the graph that 1979 had the lowest growth rate. During the first 11 days of life, great tit weight increased normally in 1969 but thereafter growth was markedly slowed down. However, the final weight of both nestlings in 1969 and 1978 were very similar, and they were both lower than 2017.

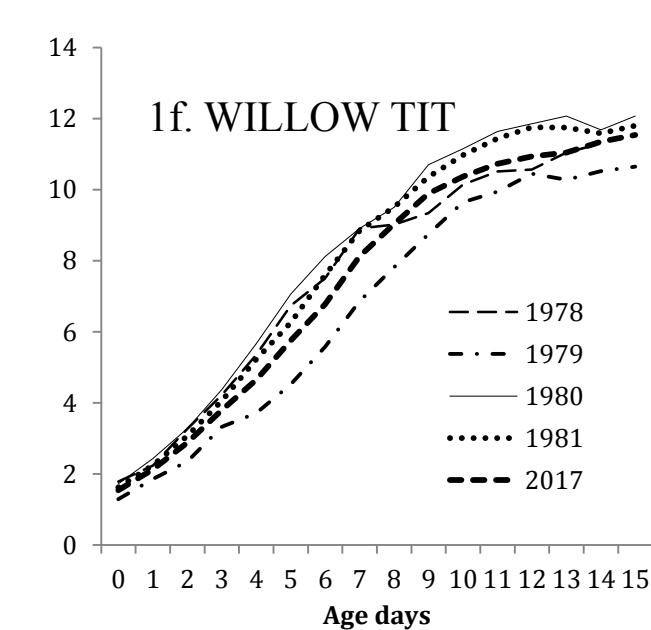
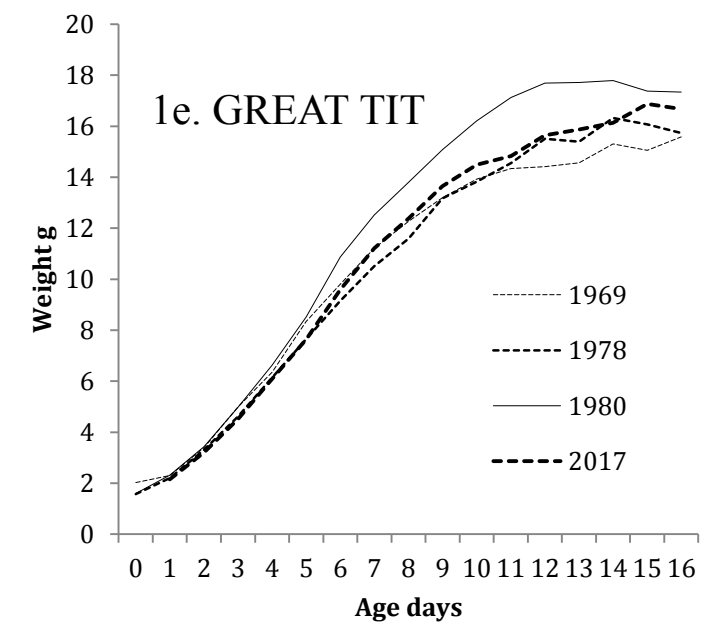
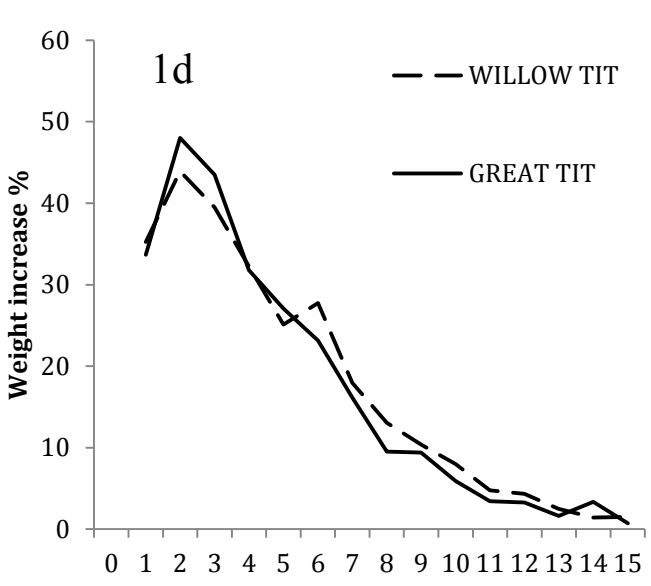
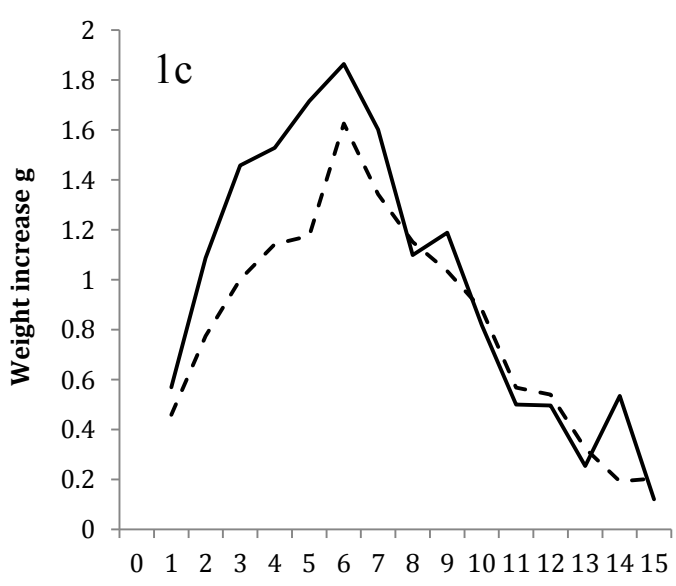
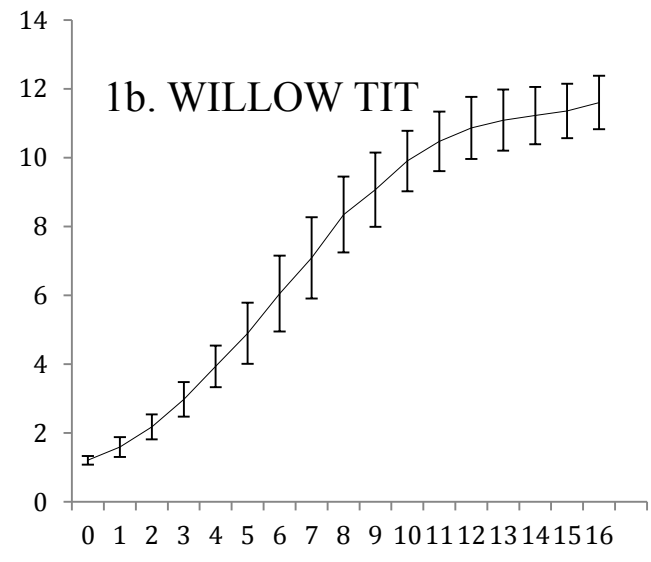
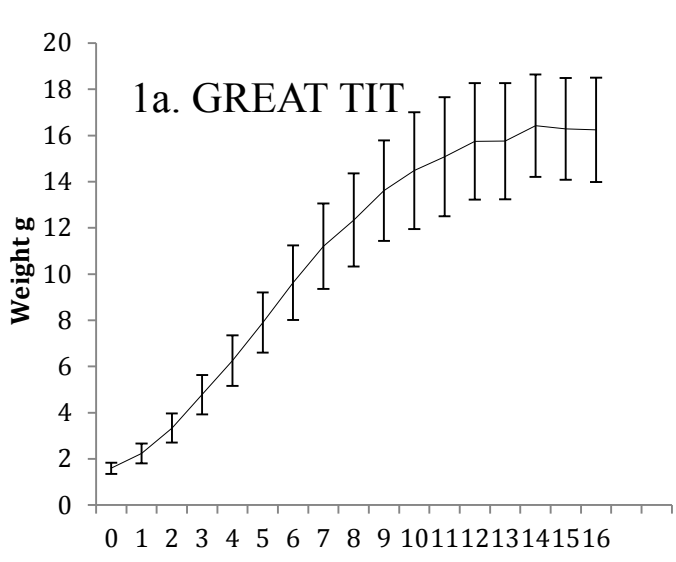


Fig. 1a & 1b Increase of weight in nestling Great tit and Willow Tit Fig. 1c & 1d Mean daily increase and percentage increase in Great Tit and Willow Tit Fig. 1e & 1f Mean weight curve of different years in Great Tit and Willow Tit

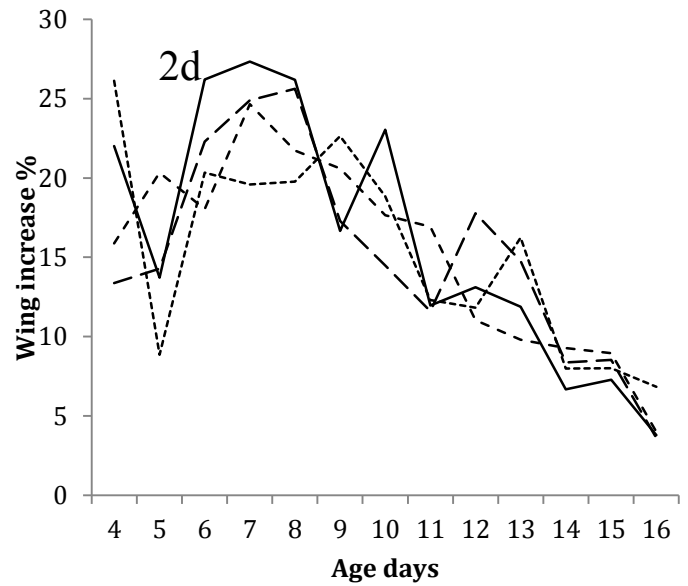
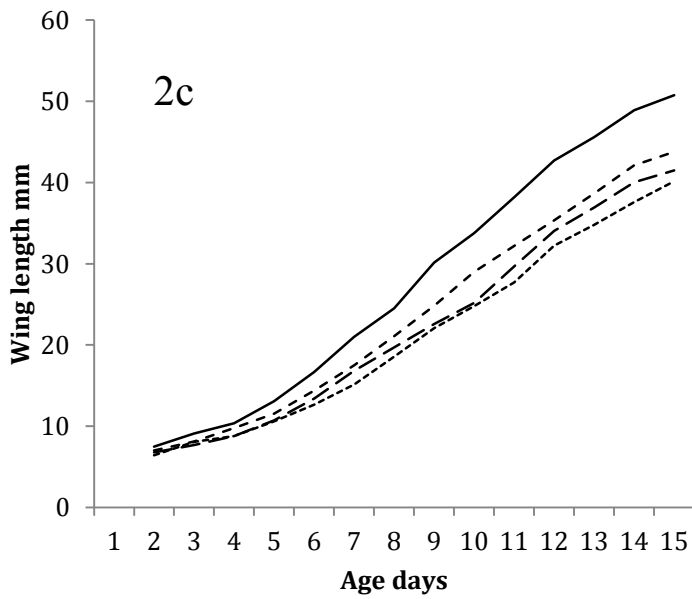
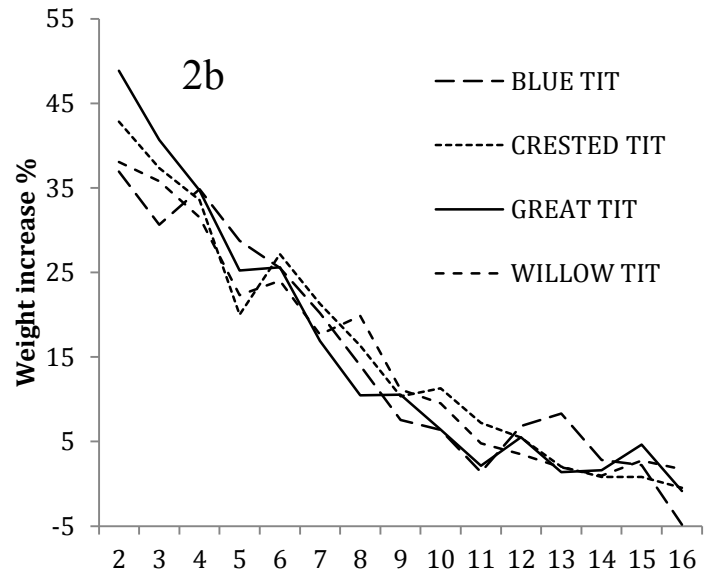
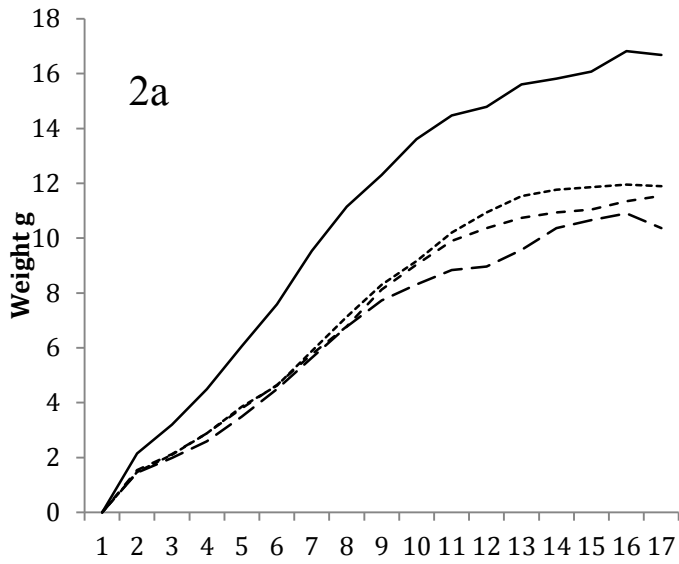


Fig. 2a & 2b Increase of weight and mean daily percentage increase of weight in nestling Great Tit, Blue Tit, Crested Tits and Willow Tits (2017). Fig. 2c & 2d Increase of wing length and mean daily percentage of the wing length in the Great Tit, Willow Tit, Blue Tit and Crested Tit nestlings (2017).

In blue tit, relative weight increased gradually until the age of 16 days, and thereafter it experienced a higher weight recession before fledging than in the other tits (Fig. 2a). The other three species experienced a continuous increase in weight increase until day 15-16, after which growth levelled at about the final fledging mass. In all species the relative growth (weight increase %) decreased throughout the nestling period (Fig. 2b).

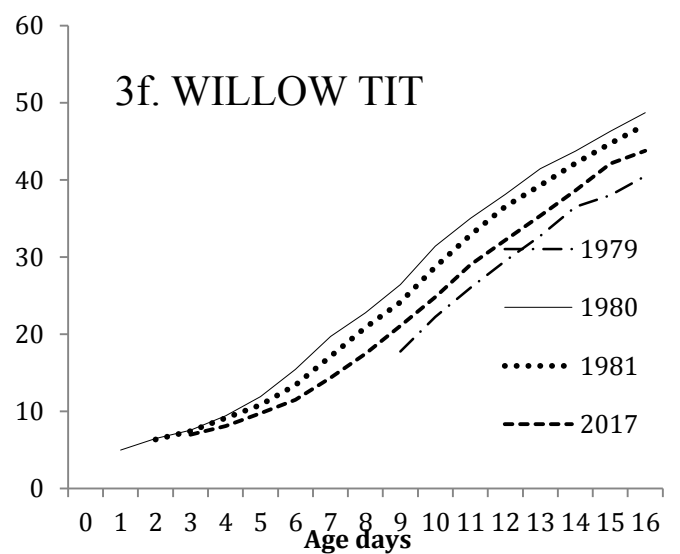
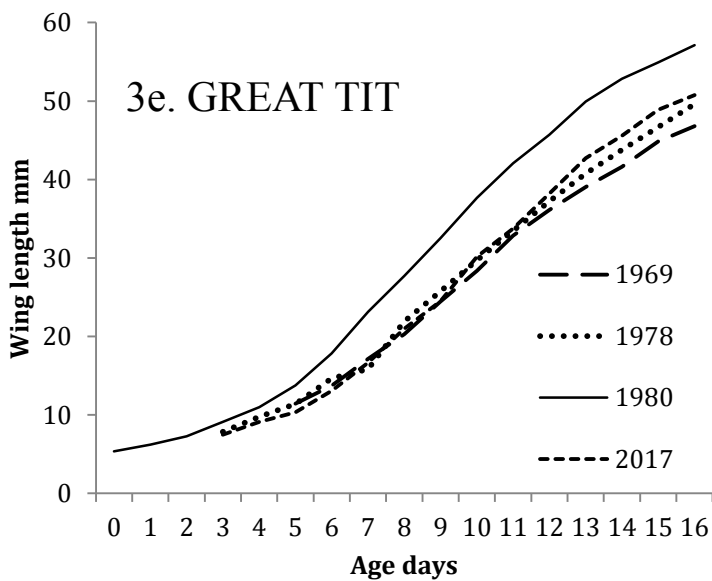
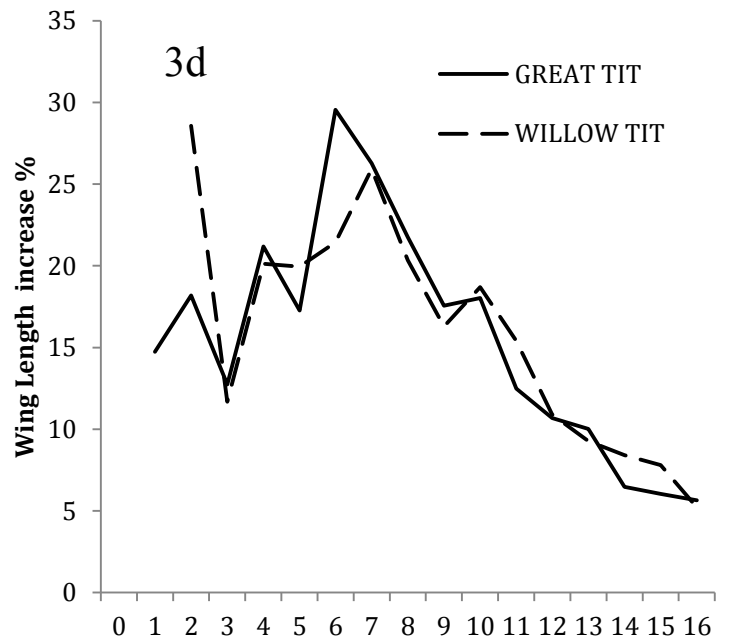
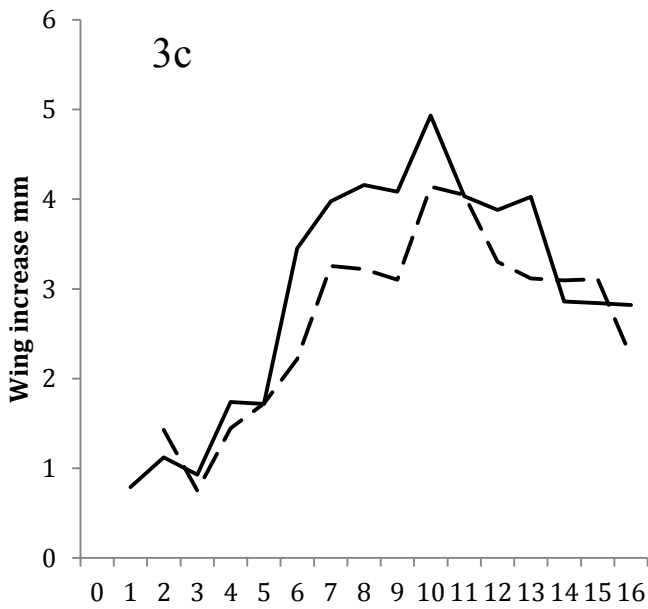
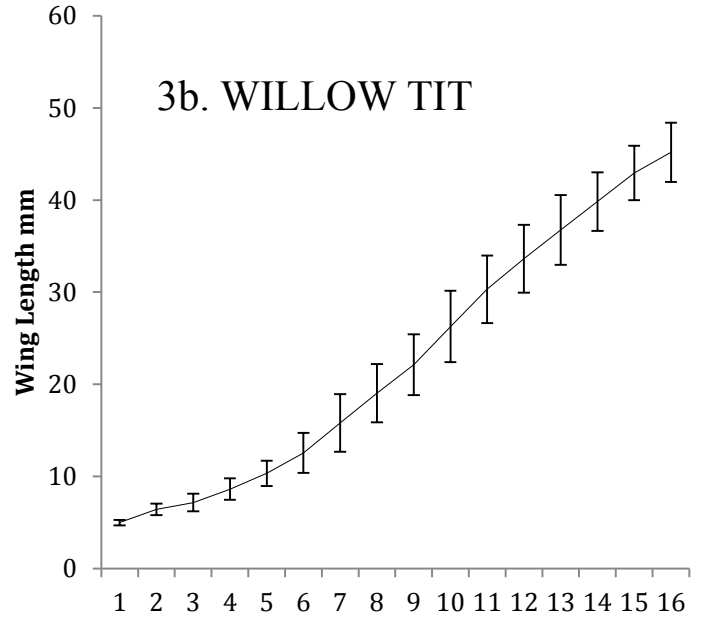
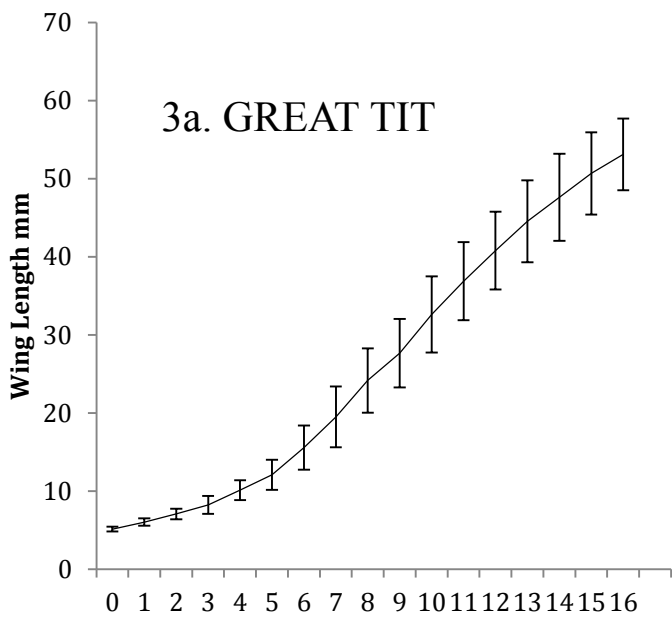


Fig. 3a & 3b Increase of wing length in nestling Great Tit and Willow Tit Fig. 3c & 3d Mean daily wing length increase and percentage increase Fig. 3e & 3f Mean weight curve of different years in Great Tit and Willow Tit

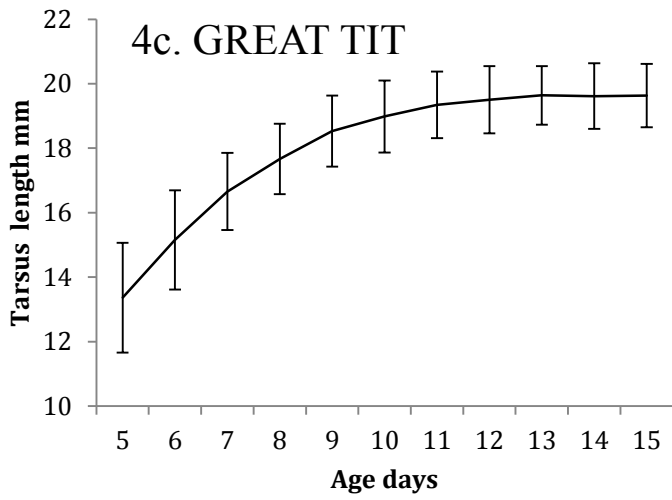
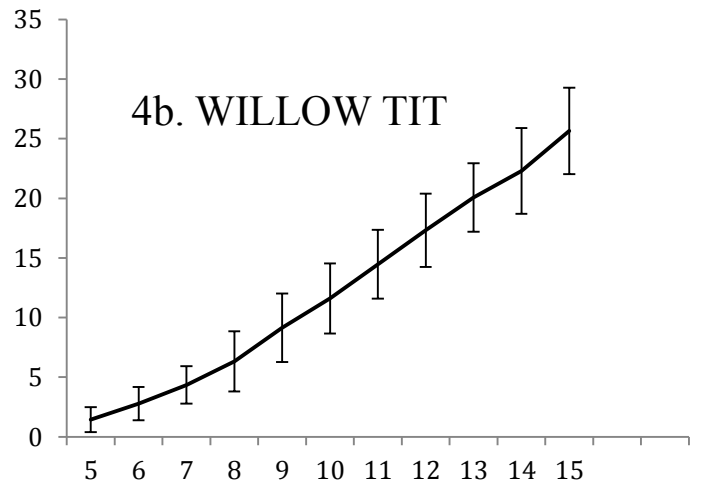
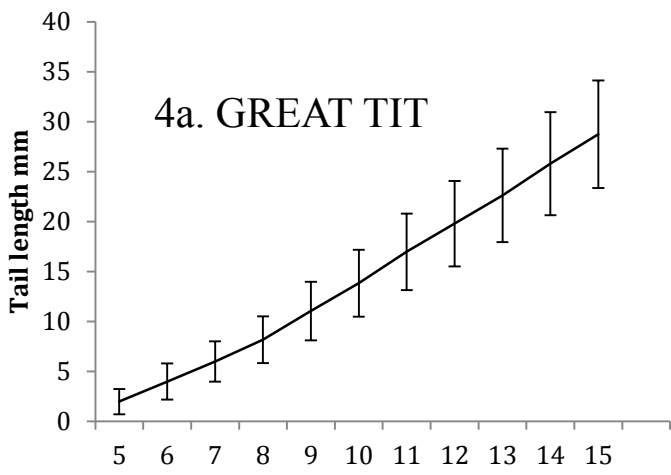


Fig. 4a & 4b Increase of tail length in Great Tit and Willow Tit nestlings. Fig. 4c & 4d Increase of tarsus length in Great Tit and Willow Tit nestlings.

3.1.2 Wing length

In both great tit and willow tit, the increase in wing length was relatively slow compared to that in weight for the first five days. The growth pattern was linear (Fig. 3a, b). Great tit only grew 1.0 to 2.0 mm/day at the age of 1 to 5 days old (Fig. 3c). From the age of day 6 to 10, it grew 4.0 to 5.0 mm/day and the average growth rate is 4.13mm/day. The growth of wing length never stopped at the fledging, being then still 2.4 mm/day.

Willow tit had consistent wing growth pattern with great tit. In the first 5 days, wings grew 0.7 to 1.72 mm/day and rapidly changed to 2.2 - 4.1 mm/day at the age of 6 to 10 days (Fig. 3c). Before fledging, it dropped to 2.2 mm/day. The highest intraspecific variation on wing growth on both great tit and willow tit were at the age of 6 to 7 days, the coefficient of variation was 17-19%.

Wing length in 1969, 1978 and 2017 in great tit was about 1.5 to 2 days delayed compared to 1980 and was already seen at the age of 6-7 days (Fig. 3e). A one-way ANOVA test was run to test the final wing length difference in years. The asymptotic weight in 1980 was significantly higher than 1969 and 1978 (ANOVA, $P < 0.05$). There was a significant difference between 2017 and 1969 in the asymptote (ANOVA, $P < 0.05$).

Absolute growth rate (mm/day) of great tit and willow tit continuously grew until the age of 10 days (Fig. 3c). The largest daily wing length increase of great tit was 1.67 mm at the age of 6 days. In willow tit, the highest daily wing length was 1.03 mm at the age of 7 days. Relative wing length increase (%) was the highest at the age of day 6 in great tit while for willow tit, the peak was at day 7 (Fig. 3d). After the peak, the relative increase rate gradually slowed down until fledging in both species.

Great tit had the highest growth rate constant and asymptote in wing length and weight in 2017 (Table 1). On day 4, both great tit and crested tit had experienced a big drop in daily percentage increase and rapid growth in the next day (Fig. 2d). The peak of wing increase in crested tit was at day 4 while for great tit, it was at the day 7. For blue tit, the peak was at day 8, and day 7 in willow tit. Among all species, at the age of day 15, they had similar relative wing length increase with the previous day.

Crested tit had higher daily weight gain, final weight and growth rate constant than willow tit and blue tit. However, in wing growth, it had the smallest value. Compared to the weight growth in 2017, Blue tit grew faster than willow tit, however, the opposite situation happened on weight growth. All the species continued to grow their wings during fledging.

3.1.3 Tail length

Tail started to penetrate through the skin at the age of 5-6 days. All the species showed a linear tail growth. At the age of 13 to 15 days, CV averaged 19.7% and 14.8% in the great tit and willow tit respectively. The highest tail length increase in great tit nestling was 3.18 mm/day at the age of 14 days, while for willow tit, it was 3.35 mm/day at 15 days. Great tit growth rate constant on tail in 1969 was significantly larger than all other years (ANOVA, $P < 0.05$). In table 1, crested tit tail growth rate constant was the highest. The average tail

growth in the blue tit and crested tit at the age of 13 -15 days in 2017 was 2.5 mm/day and 2.6 mm/day respectively. Tail growth did not stop until fledging.

3.1.4 Tarsus length

In order to prevent injury to the tarsus, we measured it only until the age of day 6. It is obvious that all the species slowed down or even stopped growing tarsus at the age of 12 days, and the peak of tarsus growth was about the age of 7 – 9 days (Fig 4c, d). In fact, studies have reported that passerines reached their final tarsus length before fledging (O’Connor 1977). The growth rate constant of tarsus in great tit and willow tit were very similar, however, the great tit had larger asymptotic length. In 1978, it has the highest significant growth rate constant on final length in tarsus (ANOVA, $P < 0.05$).

3.1.5 Mortality rate

The equation of mortality rate is $\log(\text{number of hatched}/\text{number of fledged})$. Mortality rate was similar in 2017 and 1978, 0.12. The mortality rate in 1980 was significantly lower than in all other years, only 0.018 (ANOVA, $P < 0.05$). In 1969, the mortality rate was at highest, 0.18. Both clutch size and the number of hatched chick were significantly smaller than all other years, only 7.9 egg/nest and 6.69 hatched chicks/nest. In 2017, great tit had significantly higher mortality rate than crested tit and willow tit (ANOVA, $P < 0.05$). Crested tit had the lowest mortality rate, 0.027, among all species. Crested tit was the earliest breeder among the study species and supposedly bred in the hardest period of time.

Biometric measurement	Mass		Wing		Tail		Tarsus		Brood	Nestling
	A	K	A	K	A	K	A	K		
Great Tit										
all data	17.12	0.425	61.05	0.29	31.58	5.72	19.94	0.2	14	94
1969	16.19	0.411	56.59	0.27	24.65	N/A	N/A	N/A	5	26
1978	16.08	0.416	58.91	0.28	28.56	5.49	20.48	0.26	2	14
1980	18.81	0.448	63.56	0.31	38.97	5.78	20.38	0.22	4	46
2017	16.91	0.425	62.33	0.29	30.97	5.88	19.38	0.2	4	28
Willow Tit										
all data	11.76	0.4	56.06	0.28	29.68	5.78	16.42	0.2	6	50
1978	11.3	0.4	N/A	N/A	N/A	N/A	N/A	N/A	1	7
1979	11.14	0.37	50.63	0.3	28.77	5.12	15.95	0.23	1	4
1980	12.29	0.41	55.2	0.3	34.21	5.53	17.82	0.22	1	7
1981	12.15	0.42	58.02	0.29	30.11	5.79	16.53	0.2	1	7
2017	11.74	0.4	56.06	0.27	28.44	6.04	16.09	0.18	4	25
Blue Tit										
2017	11.24	0.39	60.53	0.25	23.28	6.45	16.7	0.16	3	21
Crested Tit										
2017	12.26	0.41	54.83	0.25	25.59	6.7	17.6	0.15	3	14

Table 1. Parameters of the logistic equation of biometric measurement of all species in 1969, 1978-1981 and 2017, and numbers of broods and nestlings.

A represents the asymptotic weight and K is the growth rate constant.

Note. Only fledged nestlings included

3.2 Linear mixed model result

3.2.1 Mass growth

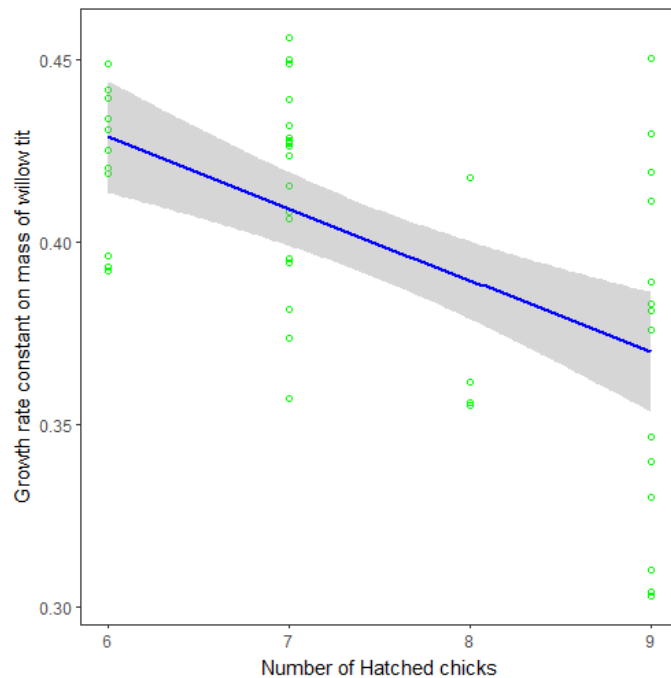


Fig. 5 Best model of growth rate constant on mass of Willow Tit

The best model of mass growth rate constant included number of hatched and number of fledged in great tit. Growth was negatively related to number of hatched chicks, but positively to number of fledglings. This may indicate that in the early nests, the larger number of hatchlings will negatively affect the mass growth. While, at the end of the nesting period, the higher number of fledged chicks will benefit of the increased food resources.

For willow tit, the best model explaining weight growth included only the number of hatched (Fig. 5, Appendix 2, $P < 0.05$). The effect was negative, meaning that the larger number of hatched chicks in the nest decreased the mass growth.

3.2.2 Wing growth

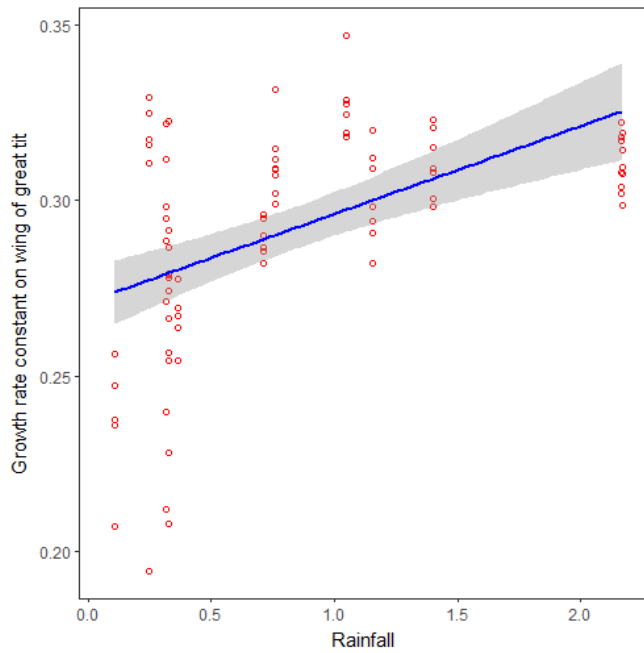


Fig. 6 Best model of growth rate constant on wing length of Great Tit

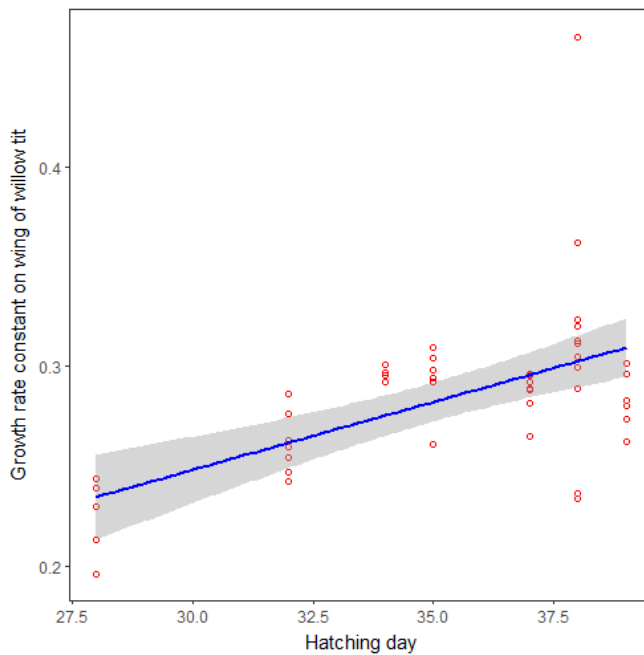


Fig. 7 Best model of growth rate constant on wing length of Willow Tit

Wing growth rate constant in great tit was positively related to the amount of rain (Fig. 6, Appendix 1, $P < 0.01$). The higher amount of rain benefited the wing growth during the growing period. Wing growth rate in willow tit had a positive relationship with the hatch day (Fig. 7, Appendix 2, $P < 0.05$). This indicated that the late hatched nestling had higher growth rate on the wing.

3.2.3 Tail growth

The tail growth rate in great tit was negatively correlated with the number of hatched chicks and the amount of rain (Appendix 1, $P < 0.05$). The larger number of chick in the initial brood decreased tail growth. The relationship with the amount of rain in tail growth rate constant was completely opposed with the result in wing growth. However, the P value in wing growth model was highly significant compared to tail growth model. We can not find any model in willow tit tail growth.

3.2.4 Tarsus growth

We can not find any significant model in great tit and willow tit tarsus growth.

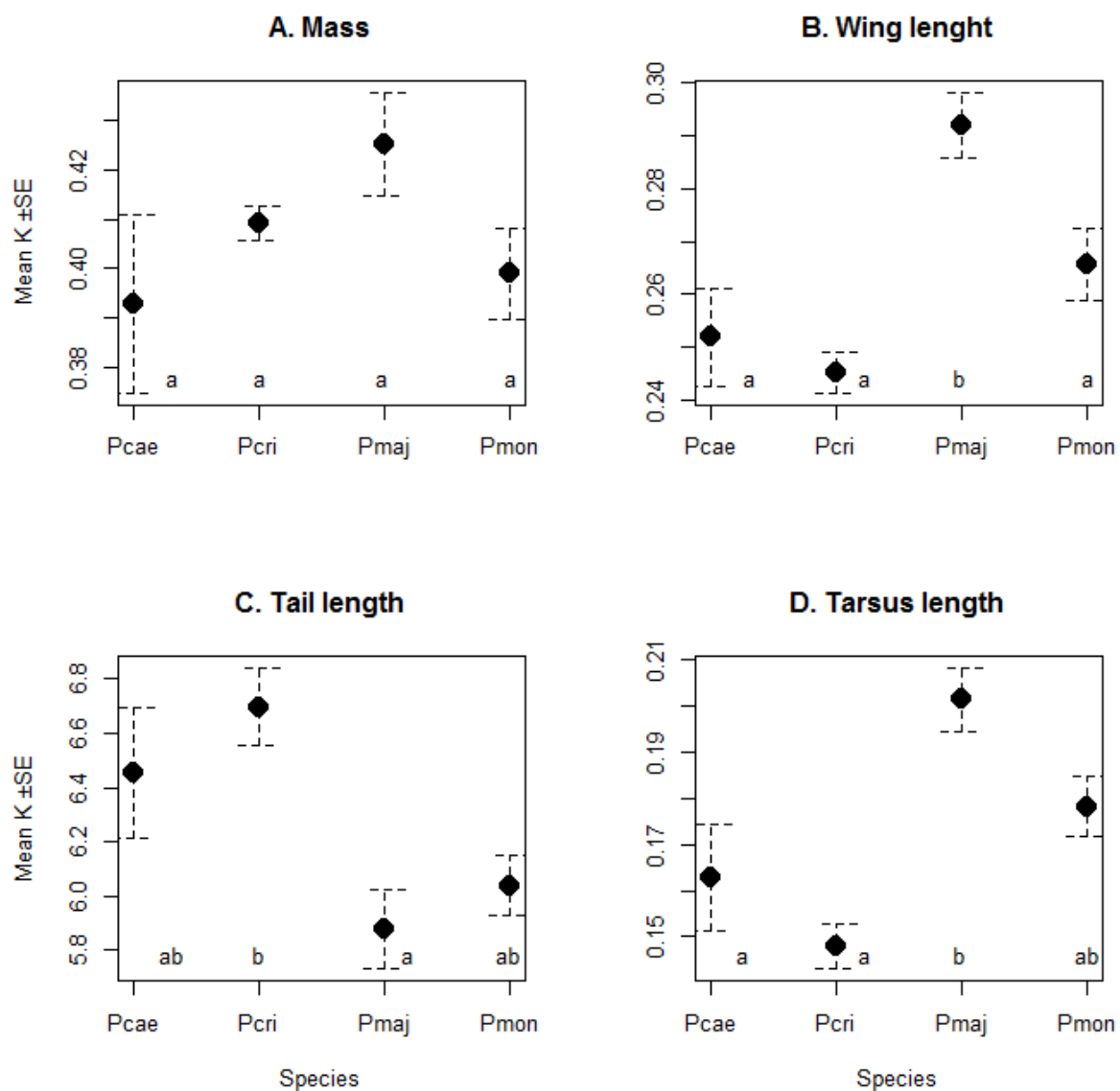


Fig 8. Growth rate constant (K) of mass, wing, tail and tarsus in Great Tit (Pmaj), Crested Tit (Pcri), Blue Tit (Pcae) and Willow Tit (Pmon). Small letters connected to species indicate

homogenous groups, i.e. different letters show significant difference between species at 95% risk level.

3.2.5 The comparative study in 2017

Great tit is significantly higher on growth rate constant in mass, wing and tarsus than other three species (Fig. 8, ANOVA, $P < 0.05$). Crested tit had significantly higher tail growth rate constant compared to great tit (Fig. 8). Blue tit had the lowest on K value in mass growth. Crested tit had the lowest K value in wing and tarsus growth.

Growth was affected by the number of chicks in initial brood in both great tit and willow tit. The number of hatched chicks were negatively correlated with the growth rate constant. This implied that each chick could have a better development with a smaller number of siblings. Each of them could receive more food and nourishment. The only significant relationship regarding the weather factors was rainfall in the growth of great tit. Surprisingly, it was positively related to the growth rate constant. The hatched day also showed a strong correlation with the growth rate constant in willow tit. Great tit had the highest growth rate constant in the weight, wing length and tarsus length. It gives a hint that it might be related to the body size. In the following, I will discuss the findings in more detail with previous studies.

4.1 Effect of brood size on great tit

In the great tit, the variation in growth rate could be related to so-called brood reduction strategy (Orell 1983). It is known that in unpredictable and adverse condition, brood reduction often occurs in many passerine birds (Lack 1954, 1966; Ricklefs 1965, 1976; Löhrl 1968, Van Balen 1973). Brood reduction facilitates energy expenditure matching the amount of food that parents can supply (Orell 1983).

A negative relationship between brood size and asymptote weight has been demonstrated before (Gibb 1950, Gibb & Betts 1963, Nur 1984). An inverse relationship between initial brood size and fledging weight experiences higher nestling mortality were reported in Oulu (Orell 1983, Orell & Ojanen 1983c). Starvation on nestlings is particularly pronounced in the great tit (Orell 1983). Compared to willow tits in Oulu, great tits have large brood size and a higher risk of brood reduction. Large clutch size of the great tit is probably related to the gene flow from the southern populations, which prevents them to optimally adapt in the north (Rytönen & Orell 2001). Intra brood competition can cause less food intake per nestling in larger brood (Gibb & Betts 1963). However, the chick can get benefit from staying in large brood by the lower amount of energy required.

All the great tit nest in 1969 experienced severe brood reduction. Only 25% of the pairs could adjust their broods to food resources in 1980. Pairs that had more than 9 nestlings in the initial brood lost at least 2 chicks until fledging. The pairs having more than 10 nestlings lost at least 4 chicks. There were no pairs that had more than 9 nestlings surviving until fledging in 1980. It is clear that a larger number of hatched chicks can lead to higher mortality when food resources are scarce. After brood reduction, parents can nourish the rest of the nestlings better and each of the nestlings will receive less intra brood competition for food.

4.2 Effect of environmental factor

Temperature

Temperature can influence avian growth in two different ways, via food availability (Avery & Krebs 1984, Tinbergen & Dietz 1994) and thermoregulation (Yapp 1970). Tits are insectivores when they raise their chicks. Caterpillars are available at the time of tree budburst and their timing is highly correlated with the temperature (Van Balen 1973, Thessing 2000). The brooding time of a female is negatively correlated with the brood size in the first half of the nestling period, meaning that large brood size can help the chick to stay warmer and allow the female to invest more time in foraging (Rytönen et al. 1995). Higher ambient temperatures can directly reduce energy loss and facilitate foraging. The ambient temperature may have a larger impact on willow tit than great tit since willow tits breed earlier in spring. The summer in 1980 was warm and led to highest growth rate constant and lowest nestling mortality among all the years (Orell & Ojanen 1983c). However, we did not find any correlation between growth rate constant and ambient temperature. This might be related to the period of time that we choose to analyze. We only used the mean temperature during the 20 days nestling period, from day 0 to day 20, while in other studies the mean temperature of the whole season, e.g. from May to June, was used (Orell & Ojanen 1983c). The earlier studies found a negative relationship between nestling mortality and the temperature of May and June (Orell & Ojanen 1983c). The parents can get benefit from the warm weather during incubation and egg-laying period. They can prepare better for themselves to resist any unfavorable period encountered during the nestling period. The scale of our climatic data might not be large and representative enough to show this relationship.

Rain

Cold or rainy weather can reduce the amount of food by making caterpillars inactive and thus more difficult for birds to detect, or by increasing caterpillar mortality (Thessing 2000, Avery & Krebs 1984). Heavy rain (>20mm) will reduce average hourly parental visitation rates by ~22% and is thus an important factor explaining daily variation in parental visitation rate (Öberg et al. 2014). Some other studies have shown a decrease in parental visitation rate with increase in daily rainfall (Radford et al. 2001, Arlettaz et al. 2010). Chicks will receive less food from parents during heavy rain, which may reduce the nesting success. However, the female can spend more time in brooding to compensate the thermoregulatory demands of ectothermic young (Radford et al. 2001). The decrease in visitation rate can be compensated by increased load size (the amount of food delivered per visit, Grieco 2002). However, the insects are less active during heavy rain, and they are hard to detect by birds typically resulting in decreased load size (Dawson & Bortolotti 2000). Overall, increase in rainfall should reduce the food supply and fledging success.

The impact of rainfall related to nesting success can differ depending on the developmental stage of the chicks (Low & Pärt 2009), the amount of rainfall (Dawson & Bortolotti 2000), the number of rain days (Öberg et al. 2014) and temperature. There is a number of reasons why the age of altricial chicks can affect their energy demands. These include an alternation from the ectothermic state at hatchling to endothermic and the reduce in surface to volume ratio with increasing body size and the growth of feathers, which both can reduce heat loss

(Dawson & Whittow 2000). Besides, the change in body size and growth rate (Low et al. 2012) and less brooding time on older chicks (Conder 1989) alter the energy demand from the female. In the passerine birds, nestling period can be divided into two periods based on the growth curve (Conder 1989). During the first period from day 0-7, chicks are ectothermic and highly dependent on brooding. During the second period from day 8-15, nestlings are endothermic and requires less brooding time. The basal metabolic rate is higher in the second period.

The number of rain days (>10mm per day) explained most of the variation in fledging and recruitment success of Northern Wheatears (*Oenanthe oenanthe*) in Sweden (Öberg et al. 2014). The number of days with rain was negatively related to juvenile survival in blue tit in Northern Italy and the growth rate was significantly higher in the non-rainy days (Morganti et al. 2017). However, in Oulu area, neither willow tit nor great tit nestling mortality was related to the amount of rainfall (Orell & Ojanen 1983c). In 1981, the exceptionally rainy summer did not have a significant impact on nestling mortality (Hilden et al. 1982, Orell & Ojanen 1983c).

In my result, the amount of rainfall during nestling period was positively related to the growth of nestling wings. We did not include the number of heavy rain days in our data, since these were so few in our study periods. There was only one day in 1980 that exceeds 10 mm rainfall in all of our data. The amount of rain in Oulu is not particularly high compared to other studies (Öberg et al. 2014). In 1980, a warm and comparatively wet summer had the highest growth rate constant and lowest nestling mortality. Early nests suffered more than late nests because of the higher number of rain days and amount of rain. In late nests, there were only 2-3 rain days and the maximum amount of rain was 7.3 to 8.8 mm. Heavy rain days only happened at the age of 18 to 20 days, which was the period of reaching the final weight. In 1978, heavy rain days (5.2 – 6.3 mm) only occurred at the age of 9 or 16-18 days. The number of rain days was very low, only 1 to 4 days. In 2017, rainfall mostly occurred in the second period of growth and the number of rain days was relatively higher than in other years. In 1969, the mortality rate was the highest and growth rate constant the smallest. Overall, the amount of rainfall was not high, but mostly happened at the first period of nestling growth and the number of rain days was 3-8 days. This may imply that the impact of rainfall might be lower when the number of rain days is low and occurs in the second half of the nestling period. During that time chick becomes endothermic and required less brooding time from the female. Females can invest more time in foraging to compensate the heat loss and food supply. Even if the amount of rain was low, the high number of rain day occurred in the first nestling period can cause high mortality rate and low growth rate constant.

4.3 Effect of initial brood size and hatch day on willow tit

Hatching day

The hatching day in willow tit was positively correlated with the growth rate constant in wing. This indicates that the late nestlings grew faster than the early nestlings. The timing of breeding has been considered as a life-history trade-off between benefits of early breeding and later emerging richer food resources (Pravosudov & Pravosudov 1996). The timing of breeding is dependent on the ability of the female to lay the eggs (Perrins 1996). In a study in Siberia, mass and fifth primary of willow tit nestlings grew significantly faster in late than early nests, suggesting that there is be a trade-off between early and late breeding

(Pravosudov & Pravosudov 1996). In both Oulu and Siberia, when the willow tit starts to breed, there was still snow cover and food became more abundance later in summer. In 2017, the spring was late for 3 weeks and there was still snow cover in late May in Oulu. Female need to be able to synchronize the peak of the caterpillar and find enough food to prepare the right nutritional state to start egg laying. Willow tit has a mechanism to survive through cold winter by being in hypothermia at night and store food early (Haftorn 1972). Eggs that are laid earlier might experience periodic chilling and postpone the hatch day. On the other hand, the early nestlings might be able to prepare themselves into breeding population while the late nestling might receive better nourishment from their parents (Pravosudov & Pravosudov 1996).

Initial brood size and clutch size

Lack's hypothesis suggests clutch size in birds is limited by the parental ability to provide food and evolved towards the size, which produces the most surviving offspring (Lack 1947, 1948, 1954, 1966). In many altricial birds, parents adjust and produce the maximum number of young that they can feed (Orell 1983, Murphy & Haukioja 1986). This clutch adjustment strategy is possible when food source is reliable and predictable (O'Connor 1978). Slagsvold and Lifjeld (1990) showed that the clutch size determination is purely decided by female tits, not by their mates. Breeding period of the willow tit is shorter than that of great tit in Oulu area (Orell & Ojanen 1983a). Late breeding willow tits in Oulu area do not lay replacement clutches and actually no second clutches has recorded. Therefore, in the willow tit, the size of the first clutch is relatively important to determine the number of fledged chicks in that year (Orell 1983).

Data shows the clutch size and number of hatched chicks were highly related in willow tits. The number of hatched chicks in 1978 – 2017 were 6-9 per nest. In 1978 and 1979, there was no unhatched egg, while in 1980 and 1981, only one egg has not hatched. Only one nest in 2017 had two unhatched eggs. There is a sign of clutch adjustment strategy in willow tit, which has been demonstrated before in Oulu (Orell 1983, Orell & Ojanen 1983a). Nest who has small number of hatched chicks can have better opportunity to accelerate growth rate in the result. Each chick can receive better nourishment from the parents. Unpredictable extreme weather can also cause brood reduction in willow tit, for example in 1979, when half of the hatched chicks died.

The results of growth rates may reflect the female quality and habitat quality in Oulu area. Habitat quality is one of the important factors for parents to decide how many eggs to lay. Experimental evidence from passerines suggests that females adjusted the clutch size in relation to habitat quality (Högstedt 1980, Slagsvold and Lifjeld 1988, Slagsvold 1986). A high habitat quality encourages female to lay a larger number of eggs. In Oulu area, a study has shown that poor habitat quality, for example, densely populated area, was related to smaller clutch size (Orell 1983). Female willow tit in our study adjusted their clutch size due to unfavorable environment and their own nutritional status, which do not allow them to produce a larger clutch. After the chicks have hatched, a further brood reduction might occur because of unpredictable adverse weather.

4.4 Comparative study

According to Ricklefs (1967, 1968, 1973, 1979), the growth rate is inversely correlated with body size. The clutch size of raptors and large passerines, which weight over 100g, generally decrease with increasing body size and slow growth (Ricklefs 1967). Lack (1968) suggests that slow growth nestlings can be compromised by larger clutch size. Parents can feed more young with less food intake per each nestling. Besides, predation can also increase nestling growth and shorter nestling period regarding the type of nest. The length of nestling period generally correlates with the nesting success, as the young will be willing to stay longer in a protected nests (Lack 1948, Nice 1957). The mean duration of nestling period for Central European passerines in hole-nester, roofed-nester and open-nester are 17.3 d, 15.9 d and 13.2 d respectively (Lack 1948, 1968). The survival rate for open nester (45 %) is particularly low compared to hole-nester (67 %) (Lack 1954).

The exponential relationship $K=1.11A^{-0.278}$ was applied in altricial birds including passerines and raptorial birds (Ricklefs 1968). The equation gives the following growth rate constant result of great tit, blue tit, willow tit and crested tit in 2017:

Great tit	0.50
Willow tit	0.56
Blue tit	0.57
Crested tit	0.55

The body size - growth rate relationship is inconsistent with our result, as the values are much higher than our observed values. The figure 6 in Ricklefs (1968) tried to demonstrate a linear relationship between asymptote and the inverse index of growth rate in passerines and raptorial birds. However, the linear relationship only shows in raptorial birds but not the passerines. There is no clear linear relationship between asymptote and the inverse index of growth rate constant in passerines, if we excluded the raptorial birds in the graph. Therefore, our results do not agree that growth rate constant is inversely correlated with body size.

Studies of small passerine birds (7-20 g) with 17-22 days of nestling period (including our study species) found that the results are inconsistent with Ricklefs' results (Orell 1983, Haftorn 1978). In the study of Goldcrest (*Regulus regulus*), the smallest European passerine bird, the K value (0.409) was well below the mean value of growth rate constant in Ricklefs' (1968) results (Haftorn 1978). The observed value of great tit and willow tit in Oulu was 0.449 and 0.406 respectively (Orell 1983). In Siberia, the nestling growth rate constant was 0.331-0.436, which was very similar to willow tits in Oulu (Pravosudova & Pravosudova 1996). Besides, the growth rate constant of blue tit Oxford was 0.413 respectively (Gibb 1950). Blue tit in our study has the lowest K value on mass (0.39). Those studies have shown a positive relationship between adult body size and growth rate constant. In our study, the body size of blue tit was slightly smaller than willow tit and crested tit, and great tit was the largest. The result of growth rate constant on mass and wing are consistent with the body size.

In small passerine species, like blue tits and goldcrests, the daily energy expenditure used to obtain enough food to feed a large clutch is pushed to the maximum physiological limit (Haftorn 1978). The blue tit has fairly large clutch size (8.3 eggs) and often lays second broods, while the Goldcrest lay two relatively large clutches (9.8 eggs) in an overlapping

period of time (Haftorn 1978). Small birds require a relatively large food supply to maintain themselves because of the higher heat loss. Haftorn (1978) suggests that natural selection will favor moderate daily energy expenditure accompanied by the low growth rate constant and long nestling period. The interspecific competition between great tit and blue tit has been demonstrated in different studies (Minot 1981, Dhondt 2010). In low-quality habitat and oak-dominated plots, the intensity of competition was higher (Dhondt 2010). Nests of great tit and blue tit were very close to each other and shared a similar habitat in Oulu. The breeding density of great tit in Oulu area was between 2.8 to 4.6 pairs / 10 ha (Orell & Ojanen 1983d). In Oxford, the mean fledging weight of nestlings in great tits is inversely correlated with the population density of blue tit. All the above factors that have mentioned might be the cause of low growth rate constant of blue tit in Oulu area.

Both crested and willow tits had significantly smaller growth rate constant on mass and wing than great tits. Crested tits had the lowest number of eggs, on average 5.14, and willow tit had a slightly higher clutch size, on average 7.3. Crested tits tend to lay smaller clutches due to the nest predation by woodpecker (Ekman & Askenmo 1986). Both species rarely lay second clutches in Oulu. Parents can put more effort to raise one brood with the smaller amount of young and provide better nourishment. In Gothenburg, Sweden, less than 5% of breeding pairs will lay second clutches (Brömssen & Jansson 1980). Perrins (1970) conveys that birds start breeding as early as the food is available for them to form eggs. Crested tit is the earliest breeding passerine in Scandinavian forests, meaning that they breed in cold weather (some few degrees above zero) and in conditions of low food availability and quality. Insects with high fat content is hard to obtain during that period of time. In an experimental study, additional food was provided during the breeding period of willow and crested tits. Both of the species started to lay eggs significantly earlier, and the frequency of second clutches was higher with food addition, but the clutch size was not affected (Brömssen & Jansson 1980). Early breeder allows their nestlings to have longer preparational time before winter comes again (Brömssen & Jansson 1980). Both crested tit and willow tit prefer to stay in holes that were excavated by themselves, which requires lots of energy from the parents. The average density over 7 years (1975-1981) was 1.1 pairs/10ha in Oulu (Orell & Ojanen 1983d). The population was relatively stable in the past. Due to the low number of decayed tree and loss of old forest habitat in Oulu area, the population density in Oulu has been declining. Therefore, we can assume that the interspecific competition between crested tit and willow tit is less intense even though they shared a similar habitat. It is because of the low breeding density, difference in breeding time and food sources.

Brood adjustment strategy and second clutches are common in great tit (Orell 1983). Being the largest tit species in size in this study, higher growth rate constant in young is necessary to keep up with the time to lay the second broods since the nestling period is only 17-22 days. Great tit fledging weight is relatively lower than adult body size. It implies that they will continue to grow after fledging, while for the other three species, their fledging weight is closer to adult body weight. The difference of nestling period with other smaller tit species is minor. In our study, dead chicks were not included in the analysis. Even though great tit has high mortality rate due to brood reduction, its nestlings were still possible to maintain high growth rate constant. Larger body size gives an advantage to great tit to have low self-maintenance and contribute more to the nestlings.

5. Conclusion

The results presented in this thesis indicate that a multitude of variables influence the growth rate constant of the studied four tit species. The growth rate constant of great tit was significantly affected by the brood size and the amount of rain. Surprisingly, the amount of rain had a positive relationship with the growth rate constant. However, other key factors, for example, the number of rain days and the age of the chicks, also need to be taken into consideration. The amount of hatched chicks was inversely related to the growth rate constant, which is consistent with many previous studies in great tits. In willow tits, the number of hatched chicks and hatch day were the major factors affecting the growth rate constant. Though willow tits breed relatively early, delayed breeding was related to higher growth rate in wing length. The results of willow tit are consistent with their clutch size adjustment strategy documented also in earlier studies. Great tit nestlings had the fastest absolute growth rate because of their large body size. In addition, the brood reduction strategy of great tits may result in higher growth rate in comparison to clutch adjustment strategists, like the crested and willow tits. Correspondingly, the nestlings of blue tits had the slowest absolute growth rate due to the smaller body size, large brood size and the weaker tendency for brood reduction than in the great tit. Growth rate constants in crested tit and willow tit were similar since they have similar body size, the same number of clutches and because they breed relatively early. Ecologists predict that climatic change will have an impact on the synchronization between the peak of food availability and breeding time. Insectivorous birds might have to change their clutch size and adjust their incubation period to respond to the climatic change, which may affect how much they should optimally put effort on their offspring. If the warming results in relatively early emerging food resources, investing in smaller but higher quality broods might be favored. By identifying the important factors affecting the growth rate constant of small insectivorous passerine, this can be used to predict the potential changes in their life history traits. The results can be facilitated in the conservation work by putting more focus on important factors in the future.

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Appendix 1.

Great Tit mass model		All variables				Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	0.278273	0.146379	9.393	1.901	0.0884					
NbrHatched	-0.029943	0.009543	7.244	-3.138	0.0157	-0.0132	0.01014	11.433	-1.302	0.21868
Hatchday	-0.007749	0.007538	7.851	-1.028	0.3345					
Temperature	-0.009554	0.00588	6.302	-1.625	0.153					
Rain	-0.029902	0.022491	7.352	-1.329	0.2235					
FirstEgg	0.011324	0.006942	7.831	1.631	0.1423					
ClutchSize	0.036149	0.01172	7.337	3.084	0.0167					
NbrFledged	0.048647	0.011008	8.362	4.419	0.002	0.02045	0.01397	11.998	1.464	0.16894
Great Tit wing model		All variables				Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	0.1049312	0.1550334	5.158	0.677	0.5277					
NbrHatched	0.0007654	0.0058967	4.939	0.13	0.9018					
Hatchday	0.0001645	0.0041291	5.898	0.04	0.9695					
Temperature	0.0003546	0.0033286	4.748	0.107	0.9195					
Rain	0.0299477	0.0127597	5.063	2.347	0.0652	0.02498	0.007794	11.256	3.205	0.00815 **
FirstEgg	0.0002139	0.0037268	5.894	0.057	0.9561					
ClutchSize	0.0047628	0.0067248	5.196	0.708	0.5093					
NbrFledged	0.0147024	0.0100647	5.141	1.461	0.2024					
Great Tit tail model		All variables				Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	11.8578	4.4791	22.93	2.647	0.01441					
NbrHatched	-0.5177	0.1726	14.51	-2.998	0.00927	-0.4826	0.1613	8.358	-2.992	0.0164 *
Hatchday	-0.1052	0.1229	43.64	-0.856	0.39672					
Temperature	-0.234	0.1389	1.07	-1.685	0.32798					
Rain	-1.4475	0.493	2.13	-2.936	0.09195	-1.0623	0.4726	10.147	-2.248	0.048 *
FirstEgg	0.141	0.115	25.54	1.226	0.23143					
ClutchSize	0.3705	0.1977	20.32	1.874	0.07539					
NbrFledged	0.1751	0.2892	67.73	0.606	0.54683					
Great Tit tarsus model		All variables				Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	-0.20971	0.157506	1.54	-1.331	0.34614					
NbrHatched	0.013587	0.011566	47.47	1.175	0.24598					
Hatchday	0.011105	0.0042	52.98	2.644	0.01074					
Temperature	0.011582	0.010034	1.01	1.154	0.45256					
Rain	0.086441	0.034921	52.03	2.475	0.01661					
FirstEgg	-0.012533	0.003753	52.4	-3.34	0.00155					
ClutchSize	-0.014754	0.008408	41.34	-1.755	0.08672					
NbrFledged	-0.003192	0.00668	52.9	-0.478	0.63472					

Appendix 2.

Willow Tit mass model All variables						Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	-0.020815	0.292373	42	-0.071	0.9436					
NbrHatched	-0.036581	0.019001	42	-1.925	0.061	-0.019859	0.007228	6.133	-2.747	0.0327 *
Hatchday	0.014723	0.016153	42	0.912	0.3672					
Temperature	-0.006188	0.012677	42	-0.488	0.628					
Rain	-0.014523	0.018194	42	-0.798	0.4292					
FirstEgg	-0.004247	0.010323	42	-0.411	0.6829					
ClutchSize	0.036193	0.01668	42	2.17	0.0357					
NbrFledged	0.006993	0.009797	42	0.714	0.4793					

Willow Tit wing model All variables						Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	-0.274018	0.350161	41	-0.783	0.438					
NbrHatched	-0.002659	0.022695	41	-0.117	0.907					
Hatchday	0.012625	0.019244	41	0.656	0.515	0.006417	0.001424	3.068	4.508	0.0194 *
Temperature	0.002412	0.0151	41	0.16	0.874					
Rain	-0.002786	0.021682	41	-0.129	0.898					
FirstEgg	-0.002553	0.012298	41	-0.208	0.837					
ClutchSize	0.019979	0.019873	41	1.005	0.321					
NbrFledged	-0.002955	0.011679	41	-0.253	0.802					

Willow Tit tail model All variables						Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	7.86125	7.84569	41	1.002	0.322					
NbrHatched	-0.28712	0.5085	41	-0.565	0.575					
Hatchday	-0.02316	0.43119	41	-0.054	0.957					
Temperature	-0.12454	0.33833	41	-0.368	0.715					
Rain	-0.22137	0.48582	41	-0.456	0.651					
FirstEgg	0.02106	0.27554	41	0.076	0.939					
ClutchSize	0.15208	0.44526	41	0.342	0.734					
NbrFledged	0.1954	0.26168	41	0.747	0.459					

Willow Tit tarsus model All variables						Best model				
	Estimate	Std. Error	df	t value	P value	Estimate	Std. Error	df	t value	P value
(Intercept)	-0.5614478	0.7469627	41	-0.752	0.457					
NbrHatched	0.0270153	0.0484124	41	0.558	0.58					
Hatchday	0.010733	0.0410519	41	0.261	0.795					
Temperature	0.0086975	0.032211	41	0.27	0.789					
Rain	0.0008896	0.046253	41	0.019	0.985					
FirstEgg	0.0013072	0.0262335	41	0.05	0.961					
ClutchSize	0.0124577	0.0423921	41	0.294	0.77					
NbrFledged	-0.0066221	0.0249139	41	-0.266	0.792					