

The influence of the environment on growth parameters of great tits (*Parus major*)

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Abstract. The data from previous studies on the ontogeny of *Parus major* were used in this study. Allometry of growth characters was compared at three independent sites and at different times. A total of 186 young were measured in three habitats: Low Tatras - an ecotone between a mountain meadow and forest community; High Tatras - forest habitat near the road; Šúr - a habitat of a wetland alder forest. In terms of allometric characteristics such as tarsometatarsus growth, wing skeleton (ulna/radius), and weight, it can be concluded that the best environment for development is the border of forest and meadow habitats (Low Tatras). The forest with a network of transport roads represents a lower quality environment. In waterlogged alder forests, the trajectories of juvenile development were different than in the mountain environment of spruce forests. Rather, they indicated more difficult development conditions for the nestlings, which suggests that the wetland alder forests are not the optimal habitat for the breeding of *P. major*.

Key words: *Parus major*, environment, trajectories of juvenile development

Introduction

The study of avian life history holds an important position in various areas of ecological research (Ye *et al.* 2021). The life history theory explains the general features of the life cycle, (i.e., lifespan, growth rate, number of offspring, and reproductive attempts), which are connected with constraining relationships among each other and specific environmental requirements (Wawrzyniak *et al.* 2020). Environmental conditions during early development stages can have long-term effects on an individual's life history (Lindström 1999; Monaghan 2008). In altricial birds, the nestling period is an especially sensitive time within the life cycle that strongly influences their further survival and general reproductive success (Langham 1972; Bryant 1978; Amiot *et al.* 2014). The studies of nestling develop-

ment and growth present the diversity of growth patterns among birds associated with their morphology, ecology, and behavior (Ricklefs 1968; Nilsson and Svensson 1996; Bize *et al.* 2006), parental effort (Gilby *et al.* 2011), as well as other life-history traits (Remeš and Martin 2002; Mainwaring *et al.* 2010). The body condition of birds is related to their survival, reproductive success, behavior, and evolutionary ecology, but also provides the knowledge necessary in wildlife management and conservation biology (e.g., Bustnes *et al.* 2002; Blums *et al.* 2002, 2005; Bachman and Widemo 1999). In studies with regard to body condition, morphological and physiological measurements replace direct measurements (Labocha and Hayes 2012). Quantitative measures of nestling growth and development are important for understanding avian breeding biology and reproductive strategies (Fernaz *et al.* 2012). Determining the exact age of nestlings is an important prerequisite for determining the nesting strategy, and helps identify the impact of environmental variables on body condition, growth, and reproductive success (Shaffer 2004; Jongsomjit *et al.* 2007).

The great tit (*Parus major*, L. 1758) is a widespread and common species across most of Europe, the Middle East, Central Asia, and east across the Palearctic to the Amur River. Their population in Europe accounts for less than half of its global range. Its European breeding population is extremely large (> 46,000,000 pairs), and was stable between 1970–1990. Although there were declines in a handful of countries during 1990–2000, populations were stable across the vast majority of Europe (BirdLife International 2021). The most common occurrence of the species is in open deciduous and mixed forests and edges and clearings in dense forests, including conifer forests and boreal taiga. It is also found more widely in plantations, hedgerows, orchards, parks, gardens, the edges of cultivation, and almost any group of trees or bushes (Gosler *et al.* 2013; Hinsley *et al.* 2008). It feeds on a wide variety of insects, especially caterpillars and larvae as well as spiders, seeds and fruit (Perrins 1991; Snow and Perrins 1998; Seki and Takato 1998).

The egg-laying period differs mainly among latitudes. In Europe, laying begins in March and April in southern lowlands, and in May in the north (Snow and Perrins 1998). The great tit is a typical cavity nester, breeding in a hole that is usually inside a tree, (although occasionally in a wall or rock face) and it frequently uses nestboxes for nesting (Gosler *et al.* 2013). They are monogamous breeders, and establish breeding territories (Krebs 1971).

Though clutch size can vary, it is most often 6 to 12 eggs. The incubation period is between 12 and 15 days. As altricial birds, they hatch unfeathered and blind, and chicks are fed by both parents. The nestling period is between 16 and 22 days, with chicks being independent of the parents eight days after fledging (Gosler *et al.* 2013). Great tits are seasonal breeders. The exact timing of breeding varies based on a number of factors, including location, sunlight, and daytime temperatures (Van Noordwijk *et al.* 1995; Gosler *et al.* 2013). The start of nesting may also be influenced by individual factors such as the age of the female, as younger females tend to start laying later than older females (Jarvine 1991). The timing of hatching is synchronized with peak availability of prey, but can be manipulated when environmental conditions change after the laying of the first egg by delaying the beginning of incubation, laying more eggs, or pausing during incubation (Cresswell and McCleery 2003).

Postnatal development is an important period in the life history of birds. Birds with high postnatal growth rates (altricial species) are characterized by the rapid early development of “supply” organs, such as digestive organs (Blom and Lilja 2005). The difference in growth rate, (an increase of mass and size), mainly at fledging, depends on external environmental factors (season, nest location, food availability) as well as on the individual predispositions of the individual (e.g., might be sex-specific, Tilgar and Mänd 2006). The rates of biological processes measured in extrinsic time or on an astronomic time scale may fluctuate within growing birds according to environmental conditions (Janiga 1986). Several studies have confirmed that in the great tit population, the growth rate of nestlings between broods is related to some reproductive parameters, such as hatching date or brood size (e.g., Ricklefs and Peters 1979; Murphy 1983; Orell 1983; Skagen 1987; Singer and Yom-Tov 1988), as well as to external variables, such as ambient temperature or food supply (e.g., Quinney *et al.* 1986; Blancher and Robertson 1987; Skagen 1987).

Body mass (weight) is a variable that can be easily and reliably measured and is a good indicator of condition index (Labocha and Hayes 2012). Weight of nestlings is the criterion generally used as a measure of body size, and is dependent on brood size, season, and habitat (Orell 1983). The study of nestling development presents the diversity of growth patterns among birds associated with their morphology, ecology, and behavior (Ricklefs 1968). The growth rates of birds are species dependent and can vary within a certain range (Ricklefs 1968, 1973, 1976). In great tits, the growth rate is most obvious in the first days of life, as the absolute growth rate (g/day) increases during the first days of life and is highest at 3-7 days (Orell 1983). Eight day old nestlings weigh about ten times their hatching weight. After 7 days, the daily weight increase becomes smaller, and between the 10th and 14th days the weight curve begins to level off as nestlings approach adult weight (Gibb 1950). Slight weight recession may occur before flying (Gibb 1950; Orell 1983).

Wing length. During development in nestlings of great tits, weight increase is more rapid than increase in wing length. The growth rate is low during the first several days (0-4), increasing from 1.0 to 2.0 mm per day, and became linear at a much

higher rate, (4.5-5.0 mm per day) at 5-10 days. Toward the end of the nestling period growth slows down, but the wings are still growing during fledging, at a rate of about 2.5 mm per day (Orell 1983).

The tarsus length is one of the basic input parameters for calculating fitness index (i.e., physical condition, Velký and Kaňuch 2008). In the great tit, the tarsus stops growing at the age of 12 days and has even been found to shorten in many chickens just before flying out (Orell 1983). This is because the ankle joints are not as swollen at this age as in younger chickens. General growth curves of *P. major* tarsus indicate that a size of about 12 mm was found in 6-day-olds from different environments (Gosler 1993).

In this study, we tried to evaluate the impact of environmental conditions on the growth curves of great tit nestlings in three different habitats. Two of them represent a forest zone in a submontane area. One of these localities is congested by traffic (nests near roads), which represents a burden due to the environmental impact of lead from motor fuel mixtures (Kočvara *et al.* 2021). The third habitat is at a lower altitude, in a waterlogged alder forest. We assumed that the trajectories of development and the success of reproduction would be different in all localities.

Material and Methods

Study sites and data collection

Research was conducted at three different locations in Slovakia. Data were collected in different years as part of previous research on the nesting biology of birds (see Paliesková *et al.* 1990; Kočvara *et al.* 2021).

The first locality was in the submontane area of the High Tatras (at 850 to 1350 m a.s.l.). The nest boxes were placed at a height of 2.5-3.0 m above ground near the road leading to the cities of Štrbské Pleso, Starý Smokovec, and Tatranská Lomnica. Nest boxes were placed 100 meters apart over 1.5 km. The habitat presents a typical forest community with a dominant representation of spruce (*Picea abies*). The research was carried out from May to July during the years 1995 and 1996. The second locality was in the Low Tatras, in the Brankov nature reserve (about 900 – 1100 m a.s.l.). This study area is characterized by various types of forest, from spruce monocultures to mixed fir (*Abies alba*), beech old wood (*Fagus sylvatica*) and meadow communities. The location of the nest boxes was similar to the most frequent observations of *P. major*, as reported in the study by Janiga and Korec (2019). The research was carried out from May to July during the years 1985 and 1987. The third locality was in the Šúr National nature reserve (130 m a.s.l.), located in the northwestern tip of the Danube plain between Svätý Jur, Bratislava-Vajnory and the Chorvátsky Grob at the foot of the Little Carpathians. The area is represented by original communities of peat alder (*Alnus glutinosa*) forest with characteristic barrel roots. The nest boxes were placed on trees similar to the previous sites. The research was carried out from May to July during the years 1985 and 1986.

At eachy site, boxes were monitored regularly during the nesting period, and every 2-3 days af-

ter hatching. During monitoring, the following parameters of hatchlings were consistently measured: length of tarsometatarsus, length of wings skeleton (ulna/radius), and weight of nestling.

Age of the nestlings

During postnatal development, there is a disproportionate growth of internal organs, bones, muscles, and weight gain. In altricial birds, this disproportion in size and weight gain is evident during the first days of life and continues until the nestling leaves the nest. The concept of heterochrony in the study of growth trajectories deals with changes in growth rate and timing of developmental processes, and therefore includes time as an essential component. (McKinney and McNamara 1991). Allometry only refers to time implicitly, with respect to the rate at which growing organisms move through the space of the morphological characters (Teather and Weatherhead 1994; Badyev and Martin 2000). Because heterochrony deals with changes in the rates and timing of growth processes, the most useful way to study it is to compare the actual curves depicting measures of size or shape as a function of physical time (Alberch *et al.* 1979). The age scale is calibrated with a measure of physical time (measured usually in days). In altricial and semi-altricial birds, the age (physical time) does not increase linearly with many growing variables, and the scale of age may be very wide to detect important proportional changes in the growth of organs of birds (Paliesková *et al.* 1990; Janiga *et al.* 1993). As an alternative, the concept of physiological age (intrinsic time) may be used (Lebeau *et al.* 1986). Strauss (1987) suggests that overall body size is preferable as an estimate of biological age because it is more directly tied to growth than chronological time. In this sense, physical time (age in days) is replaced by physiological age (body size) in this study.

Statistical analysis

Statistical analysis of the obtained data was performed in the software Statistica Ver. 12. To determine the growth curves at specific localities, linear graphs were made, taking into account the dependence of growth factors on tarsometatarsus length, wing bones (ulna/radius), and weight.

Results

In total, 186 great tit nestlings were measured (Low Tatras: $n = 51$; High Tatras: $n = 88$, Šúr: $n = 47$). Growth curves depending on tarsometatarsus size and weight (Figs. 1 and 3) confirm that the nestlings in the Low Tatras locality achieved the best development due to their earlier departure from the nest. The higher weight due to tarsometatarsus rates in the second half of nest care suggests better feeding by adults and a more suitable habitat (fir-beech forests). A comparison of the growth curves of wing length and weight (Fig. 2) confirms that nestlings developed best in the Low Tatras. In the second half of nest care, the nestling wings in the High Tatras developed slightly better than in Šúr, unlike tarsometatarsus measurements.

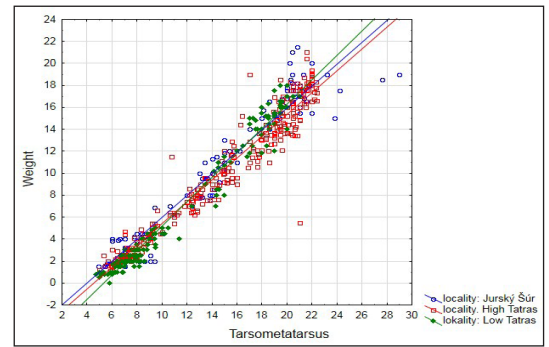


Fig. 1. Comparison of tarsometatarsus growth depending on weight in *P. major* nestlings in three different localities.

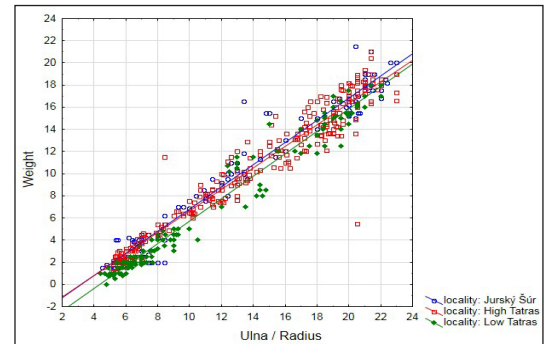


Fig. 2. Comparison of wing bone (ulna, radius) growth dependent on weight in *P. major* nestlings in three different localities.

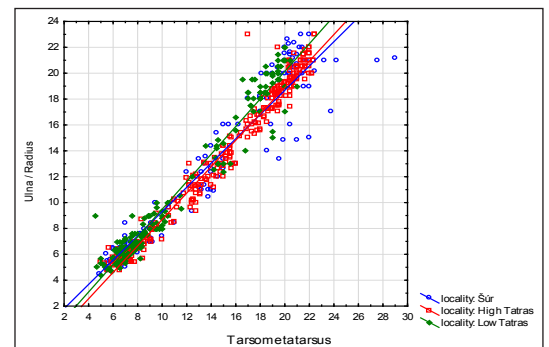


Fig. 3. Comparison of tarsometatarsus growth depending on wing bone (ulna, radius) growth in *P. major* nestlings in three different localities.

Discussion

Birds are generally considered to be suitable indicators for detecting the effects of many environmental factors acting simultaneously since they may respond to subtle changes in the environment which would otherwise remain undetected (Koskimies 1989; Furness *et al.* 1993). In this study, we tried to compare the growth curves of nestlings of great tits from different habitats in order to determine the impact of the habitat on the quality of development. Our results confirm that the growth curves in the three different tit populations are very similar, but show slight differences. However, additional studies have confirmed differences in growth rates among populations of great tits from different geographical areas or altitudes (Barba *et al.* 1993; Bor-

djan 2013). Changes in growth rates will show up as differences in slopes of the growth curves, either upward (acceleration) or downward (retardation) McKinney and McNamara (1991). The development period in a bird species is a comparison between various selective pressures favoring slow or rapid growth, the main factors at work here being food supply and chick mortality (Lack 1968). Birds developing at a slower rate of growth have less frequent feeding, which allows parents to raise more juveniles. On the contrary, rapid growth is balanced by predation pressure (Orell 1983). Growth rates are optimized among species that occupy different environmental conditions (Remeš and Martin 2002) and can vary considerably between different populations (Barba *et al.* 1993). The difference in growth rate might be limited by physiological limitations and subjective predispositions of the individual, such as sex (Ricklefs 1969; West *et al.* 2001), and/or is year-dependent (Tilgar and Mänd 2006), relating to external environmental variations (season, nest location, food supply) (Remeš and Martin 2002). Although the nestlings from warmer and lower altitude areas (Šúr) hatch with a larger tarsometatarsus, in the second half of nest development, the growth rate slows down. Juveniles from the High Tatras lag behind the most in development (Fig. 1). As we compared the growth of tarsus with weight gain, we can say that nestlings from the Šúr and the High Tatras had lower quality or less food, or worse environmental conditions. Differences in populations caused by the environment are also documented in the studies by Gil-Degado *et al.* (2005); Biard *et al.* (2017); and Ye *et al.* 2021.

Overall body size is preferable as an estimate of biological age because it is more directly tied to growth than chronological time (Strauss 1987). Rates of biological processes measured extrinsic time or using an astronomic time scale may fluctuate within growing birds according to environmental conditions (Janiga 1986). Chronological time is usually replaced by size as a measure of intrinsic time (Strauss 1987). In studies evaluating the influence of several factors on the development of the organism, it is, therefore, more appropriate to use the physiological age of the young (expressed by changes in size) than the chronological age. It is, however, appropriate to use more than one morphometric measurement to estimate age (Brown *et al.* 2011). Because individual birds have a remarkable capacity to vary their mass and volume depending on their nutritional status (Emlen *et al.* 1991), it is biologically most meaningful to define size from skeletal measurements, and therefore, independent of nutrient reserves (Piersma and Davidson 1991). Morphometric data have been used to estimate the nestling age of various species (see Wails *et al.* 2014).

To compare growth rates from different populations of great tits, we chose only three basic measures. Tarsometatars length and wing bone length are endogenous factors that are individual for each individual. Weight gain is an exogenous factor that correlates most with the availability of food resources and thus with the benefits of the habitat. The primary growth pattern can be hypothetically defined as rapid tarsus growth with weight gain in the first days of development (tarsus growth stabilizes around day 10, see in Orell 1983). In the sec-

ond half of nesting development, weight gain and tarsal growth are both slower, while the growth of the wing is accelerated. The high energy costs of development are offset by a sharp increase in weight within the first 10 days (Barba 1993). Early lower limb development is important for nest mobility, which may be related to eating behavior or hygiene. The development of the wing is related to the ability to fly earlier and leave the nest. The parts of the body which are essential for mobility, the wing and tarsus, are much more developed at the fledging stage than is the tail, which a bird can manage without for short periods (Orell 1983).

Wing feathers of juveniles grew faster relative to tarsus bones in localities with the best environmental conditions (Kočvara *et al.* 2021). If juveniles in the Low Tatras have the fastest wing development relative to tarsus, this could indicate development and fledging. Thus we can infer that conditions for leaving the nest quickly are the most satisfactory in the Low Tatras locality and the least satisfactory in the Šúr locality (Fig. 3). Acceleration of growth is important for the success of the growth strategy, but is also crucial to maturation, with respect to the degree of functional maturity Bjorklund (1996). Relatively heavier nestlings with longer wings (in our study in the Šúr locality, Fig. 2) should, according to Orell (1983), be more developed due to their more advanced maturity. The prolonged nesting period in hole nesters is due to the long interval between the day of attaining maximum weight and the day of fledging (Haartman 1954, 1957).

Individual growth rate and fledging mass is determined by food intake (Gill 1994; Keller and Van Noordwijk 1994), and can be reflected in the difference between two environments (Richner 1989). Thus, the growth curve may be used for comparing differences in quality between breeding environments within the range of species (Janssens *et al.* 2003; Eeva *et al.* 2009). Great tits are altricial nesters and all food consumed by juvenile is provided by the parents (Tanner *et al.* 2007).

The quality and quantity of food resources is determined by food availability in the breeding territory (Gibb and Betts 1963), and can be further influenced by unfavorable conditions such as weather or competition (Minot 1981; Keller and Van Noordwijk 1994). There may be variation in feeding capacity due to differences in foraging efficiency between the parent birds, and the “quality” of the territory (Askenmo 1973; Högstedt 1980), as both quantity and quality of food has been shown to impact growth rate (Berthold 1976).

Variation in growth rate of the great tit can be high in years when there was marked nestling starvation, or when some pairs experience difficulty in finding food for their nestlings, resulting in delayed brood growth. It was found that chicks hatched in years that were poor in food have a shorter tarsus than those that hatched in years when food was sufficient (Horak 1994). The difference between the two environments can be reflected in fledging mass (Richner 1989), thus growth curve may be used for comparing the quality difference between breeding environments within the range of species (Janssens *et al.* 2003; Eeva *et al.* 2009). Differences in the growth curves in our monitored habitats can be explained by the different nesting environments of tits.

In Šúr, vegetation is comprised of high barrel alder forests, often flooded with water, which is perhaps a more suitable habitat for such hole-nesting species as *Ficedula albicollis* (see Paliesková *et al.* 1990). This species catches insects out of the air, whereas tits feed on larvae and small insect caterpillars that are better represented in spruce and mixed forests. Habitats poor in food sources or offering more uniform food equate to higher daily energy expenditures of feeding parents (Veľký and Kaňuch 2008).

Altitude is an important factor in reproduction success. The effect of altitude on breeding phenology and clutch size of tits in Europe has been confirmed (Gil-Delgado *et al.* 1992; Kremetz and Handford 1984; Sanz 1998). Individuals breeding at the limit of species distribution show markedly different breeding parameters than their counterparts in more optimal environments (Orell and Ojanen 1980, 1983; Veistola *et al.* 1994). Bordjan (2013) confirmed that at lower altitudes, weight curves are approximately the same, and differ only at higher altitudes (approximately 1000 m a.s.l.). Our results confirm that the growth curves within areas at the same altitude are similar. It can be assumed that the nestlings in the High Tatras localities, which were at approximately the same altitude as in the Low Tatras locality, were impacted in their development due to proximity of the road and the associated pollutant loads (e.g., lead; Kočvara *et al.* 2021).

Another negative environmental factor in the Šúr area is higher temperatures and waterlogged and flooded areas. This factor is crucial for the development of insects that hatch in water (e.g., mosquitoes), but is also a vector of various parasites - particularly haemosporidian. It is known that the type of nesting affects the occurrence of blood parasites specifically as well as parasites in general. Open nest birds are prone to more haemosporidian parasites and longer developing chicks have a higher prevalence (longer nest time results in more parasites) (Dunn *et al.* 2017). An extremely high number of vectors can have the same effect on hole-nesting birds. Although the prevalence of haemosporidian has not been studied, it can be assumed that the increased presence of vectors encountered in the Šúr locality during research may have increased its occurrence, which could negatively affect the condition and growth of nestlings.

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