

Allometric analysis of developmental adaptation of Collared Flycatcher (*Ficedula albicollis* Temm.)

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Abstract. By the method of comparison of statistically equalized allometric curves the seasonal difference in postnatal development was clearly revealed without knowledge of age of nestlings. The nestlings of females of greater clutches exhibited more progressive postnatal development. More young in a nest (4 and more) developed better during the first days of ontogeny. Latter in the second half of nest care the probable advantage was the presence of fewer young in a nest. Young also differed in postnatal development according to the order of hatching in a nest. Nestlings of weighty females exhibited better quality of postnatal development. Development of nestlings also slightly reflected the negative influence of parasitism of *Ixodes arboricola* in the last days of nest care.

Key words: intraspecific allometry, adaptation, natality, regression

Introduction

Presented study on Collared Flycatcher is based mainly on these known results:

1. Nestlings of altricial birds reared by their parents in favourable conditions are heavier during the nesting care but their plumage starts to develop relatively latter (Belskij 1948).
2. Mainly in the second period of nest care the plumage in growing burden the metabolism of altricial birds, which is connected with a slowing down in the growth of other organs such as the cranial bones, the legs and also the total weight (e.g. Novotný 1958).

The plumage is more preferred in this time. In the second half of the nest care also skeleton of the wings grows relatively more quickly to the skeleton of legs (e.g. Kramer 1959).

Comparison of allometric curves – skeleton versus weight (in the time of active increments, what meant the first half of the nest care), skeleton versus rectrices (what meant mainly the second half of the nest care) and length of tibiotarsus versus length of antebrachial skeleton – made possible to analyze the following problems during the nest ontogeny of Collared Flycatcher:

1. Connection between the clutch size of a female and her mate ability to rear the young in a nest.
2. Connection between the success rate of fledging and the quality of postnatal development in a nest.

3. Difference between the types of postnatal development of earlier and latter hatched young – siblings.
4. Quality of the postnatal development of young from the nests situated more colonially and from more isolated nests.
5. Seasonal influence on postnatal development.
6. Nest places (net boxes), repeated year nesting and postnatal development.
7. Does any connection exist between predisposal female reproduction ability, i.e. amount of nest material and quality of postnatal development of her young?
8. Do the morphological characters (weight) of female connect with the quality of development of her offspring?
9. Influence of the parasite *Ixodes arboricola* on the postnatal development of the nestlings.

Material and methods

The study area was situated in the region of alder woodland of Jurský Šúr reserve near Bratislava. The area is the ancient swamplike refuge in the agricultural country with the typical spring and pre-spring inundations. In the middle of woodland 49 nest boxes were situated in the “T” – shape in approximate distance of 50 m. Records were made in the years of 1985 and 1986. Nest boxes were inspected every 3 – 4 days during the breeding period. For each nest we recorded the first day of laying, clutch size, number of nestlings and fledgings, difference in the time of hatching of young, presence of parasites *Ixodes arboricola*, height of nest material in the nest box. Chicks after hatching were coloured, older nestlings were ringed by colour plastic rings. Females were caught during the incubation, measured, weighed and ringed by aluminium rings.

Females and young were weighted by the Pesola spring balance, rectrices and 13 bones (skeletons) for skeleton sum were measured with a caliper. Selected bones (skeletons): 2nd, 3rd, 4th toe, tarsometatarsus, tibiotarsus, femur, width and height of beak, humerus, antebrachial skeleton, skeleton manus, width and length of the head (in detail see Janiga 1986). The ratio of bone length was approximately 2:1 in favour of skeleton which grows more quickly in the first half of nest care as opposed to the wing skeletons. For an allometry the weights of young were used only till the value of 13 gms (10 days of age), i.e. till their strong active increments (see also Král 1982). The comparison characterized mainly the development in the first phase of nest care. The second half was analyzed by the comparison of rectrices against skeleton sum (KS). Because the weight and the plumage more strongly

correlate the exogenous factors and because mainly the weight is very variable during the first days of life (Král 1982, Paliesková 1987) the development was also analyzed by the allometry of bones (antebrachial skeleton versus KS). Allometric increments were evaluated by the linear regression analysis (microcomputer Commodore 16). The power function of allometry was used in decadic logarithmic form. For the control the untransformed data were evaluated by the t-test (t_{ab}) for difference between two regression coefficients (b) – Sokal and Rohlf (1969) and by the t-test (t_{sa}) for difference between two regression constants (a). Before the comparison the data were statistically equalized by the test of the difference between two X – means, by the test of their variances (Sokal and Rohlf 1969) and by the test of two residual variances (Anděl 1985). Values of these tests had not to exceed the level of probability $P = 0,025$ for the adequate data (df). This statistical homogeneity of data was the first assumption for an allometric comparison. The second one was the biological heterogeneity of data. For example the data for the comparison of the development of earlier or latter hatched young were selected by the help of microcomputer from the mixed years, clutches, nest boxes, etc. for the purpose of exclusion of their influences.

Mainly in 1986 we also analyzed the age of young. We were capable to recognize the interval of one day but the temporal analysis showed to be very rough against allometric one, which did not require the age. Time interval of 24 hrs is very long sometimes to indicate some growth changes. In allometry the measured characters correspond and so temporal mistake is excluded. The calculated days have only the orientation character in figures presented in the results. They were computed according to the equations:

$$\text{Skeleton sum} - \ln(\text{age}) = \frac{\ln(\text{KS}) - 4,428}{0,319}$$

where r (correlation coefficient) = 0,95, df = 216.

$$\text{Tibiotarsus} - \ln(\text{age}) = \frac{\ln(\text{tib.}) - 2,304}{0,362}$$

r = 0,95, df = 216.

Because every type of postnatal development (type of the course of allometric curve) is an adaptation and reaction on momentary exogenous and

endogenous factors the term “more progressive development” is judged from the viewpoint of fitness of a population. Clear differences between the summer and winter generations of pigeon juveniles (Janiga 1987) helped us to analyze the types of curves in Collared Flycatcher and to understand them.

Results

Natality and the postnatal development

Number of eggs per clutch is presented in Table 1. Clutches consisting of 6 eggs were most frequently encountered. Analysis presented in Figure 1 shows the connection between the clutch size of female and the postnatal development of her nestlings. Nestlings were divided according to the clutch size into two groups: young from clutches of six and fewer eggs and young from clutches of seven and more eggs. In the comparison of bones the regression analysis only of untransformed data shows the significant differences (Fig. 1b). Young of greater clutches developed more progressively. Comparisons with weight or rectrices (Figs. 1a, 1c), more indicating the exogenous factors, show better postnatal development of young of greater clutches at the start (significant only in logarithmus) and mainly at the end of nest care. In the middle of nesting (7 – 8 days old young) the curves run slightly oppositely. But finally, at the end of nest care, the greater clutch of female relatives to better development of her nestlings.

Success rate of fledging and postnatal development. Division into groups according to the number of fledged young showed the opposite results. Average numbers of fledgings per nest were 3,9 ex. in 1985 and 3,4 ex. in 1986. Group of fewer young contained 3 and fewer fledgings, group of large brood 4 and more ones.

We calculated that majority of large brood nests had been represented by the nests of low clutch size (approximately 60%). Great clutch size nests produced approximately 25% of nests with 3 and fewer fledgings. And so the allometric comparisons reveal that in the first and second third of the nest care the young from large brood developed more progressively (Fig. 2). The phenomenon probably connects with better thermoregulation of young in a nest. Fewer nestlings

Year	Number of clutches							Sum	Mean clutch
	3 eggs	4 eggs	5 eggs	6 eggs	7 eggs	8 eggs	9 eggs		
1985	1 4.3%	1 4.3%	4 17%	9 39.0%	7 30.0%	-	1 4.3%	23	6.04
1986	-	1 5.2%	6 31.5%	7 36.8%	5 26.3%	-	-	19	5.8
Total	1 2.3%	2 4.7%	10 23.8%	16 38.0%	12 28.5%	-	1 2.3%	42	5.95

Table 1. Number of eggs in a clutch.

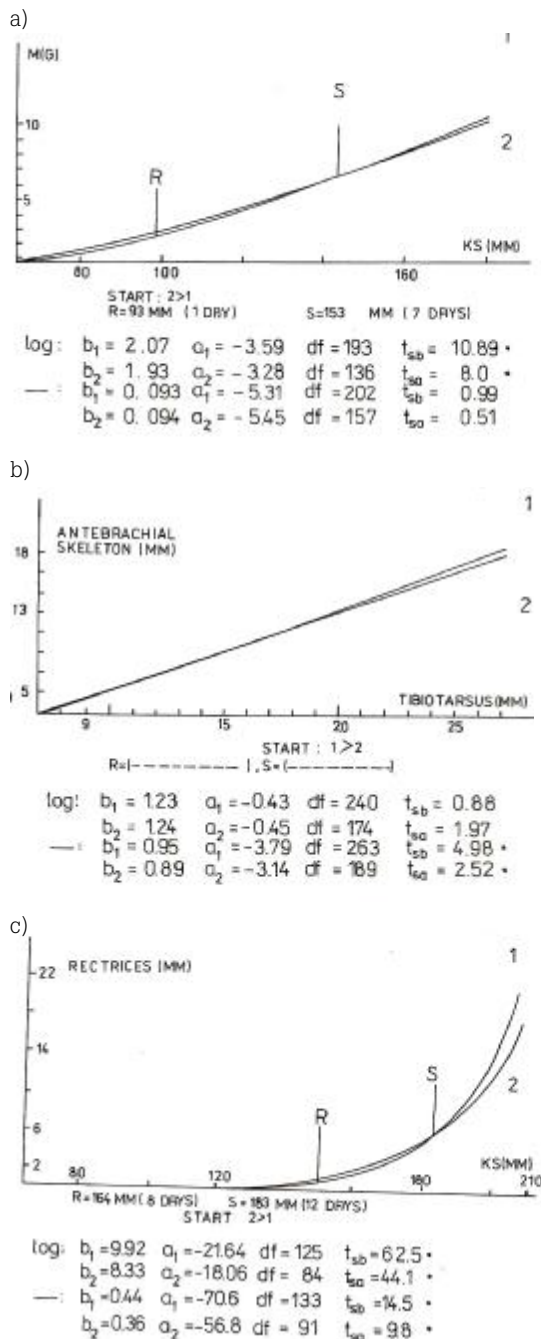


Fig. 1 Allometric analyses of the development of nestlings from high (2) and low (1) clutches. **R** – moment of change of allometric „speed“ in increments, **S** – moment of crossing of allometric curves. Statistically significant tests are marked by the points. Other symbols see Material and Methods.

in a nest is probably the advantage for parents at the end of nest care when the care for food is very intensive and in that time fewer young developed more progressively (Figs. 2b, 2c).

Developmental differences of young in a nest

Order of hatching of chicks in a nest was controlled visually or analyzed according to the biometric characteristics during the first visit in a nest after hatching. Significant differences between the allometric curves of bone comparisons (Fig. 3b) describe the more progressive postnatal development of 4th and latter hatched young in the first half of nest care. First three

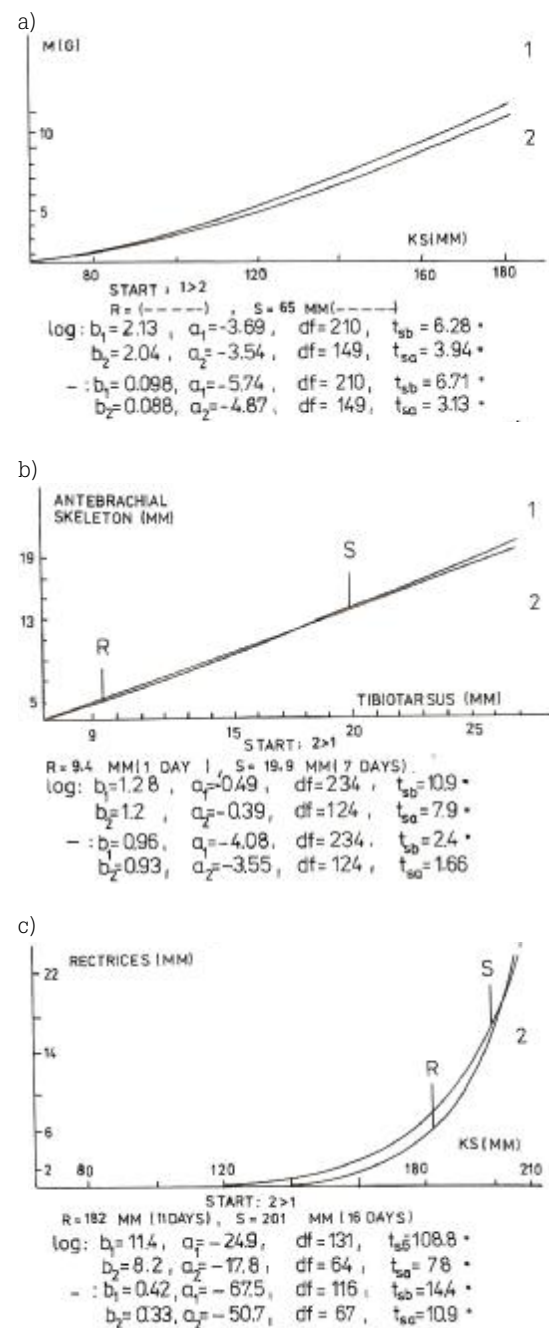


Fig. 2 Allometric analyses of the development of more (1) and fewer (2) young in a nest. Explanations see Fig. 1 and Material and Methods.

hatched nestlings have been running up to their siblings in the second half of nest care. Comparisons with the weight and the rectrices exhibit the more progressive development of latter hatched young mainly in the middle of nest care (Fig. 3a) and less progressive at the end of nest care (Fig. 3c).

Seasonal and topic influences on postnatal development

Breeding adults did not select the nest holes randomly. Selection started from three centres (Fig. 4). One developed in the large colony (nest boxes 31 and more), in the others the birds bred more

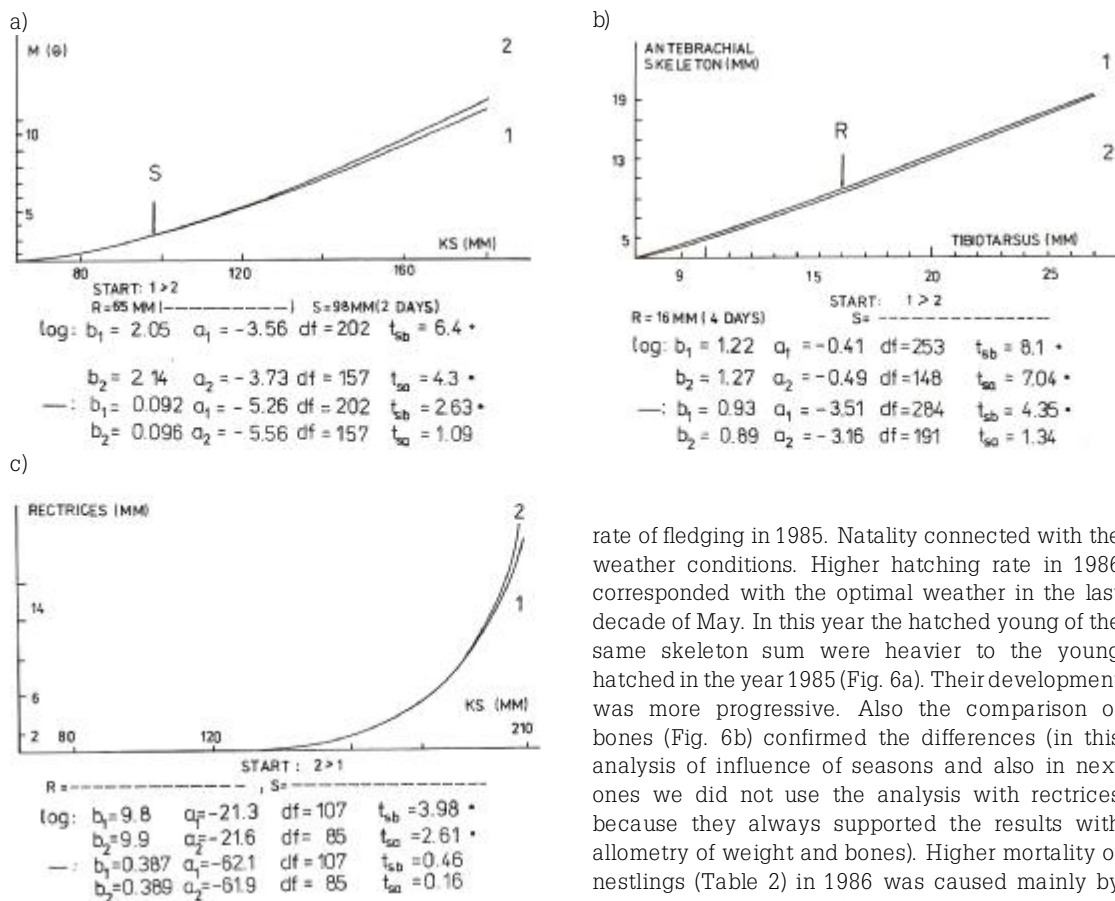


Fig. 3 Allometric analyses of the development of the first three (1) and latter (2) hatched young in a nest. Explanations see Fig. 1 and Material and Methods.

separately and so the postnatal development of young in “colonial” or “separate” nests may be influenced by environment as well as by territorial dispositions of breeding adults. Analyses with weight (Fig. 5a) and partially with bones (untransformed data) bring out that in the first half of nest care the marked differences did not exist between the quality of development of selected groups. In the second half the nestlings of “separate” nests (Figs. 5b, 5c) developed more progressively but at the end of care the types of development approximately equalized. Because differences did not occur in the first days of life of chicks, we presume that development of young was more influenced by environmental conditions of nest places than by the dispositions of adults.

Review of the breeding success of Collared Flycatcher is presented in Table 2. Success rate of hatching was higher in the year 1986, but success

rate of fledging in 1985. Natality connected with the weather conditions. Higher hatching rate in 1986 corresponded with the optimal weather in the last decade of May. In this year the hatched young of the same skeleton sum were heavier to the young hatched in the year 1985 (Fig. 6a). Their development was more progressive. Also the comparison of bones (Fig. 6b) confirmed the differences (in this analysis of influence of seasons and also in next ones we did not use the analysis with rectrices because they always supported the results with allometry of weight and bones). Higher mortality of nestlings (Table 2) in 1986 was caused mainly by the higher number of rainy days with lower temperature. Changes in the courses of allometric curves and calculated results (Figs. 6a, 6b) reflect these seasonal situations. At the end of the nest care the young born in the year 1985 exhibited more progressive development.

Topic environmental influence was analyzed by the acceptability of the nest boxes per two years. We compared the postnatal development of young from once or twice used nest boxes per two years. Individual influence might be probably excluded because in the year 1986 we had never found anyone of 10 females at the same nest which had been ringed in the year 1985. Also we did not find their ringed offspring. Figure 7 shows slight differences between the developments. Calculations shows that at the start of nest care the chicks of “two year” nest boxes developed better but at the end of care the courses of developments equalized. Most of computed tests were not significant or slightly significant. We could not satisfactorily confirm that young of the groups differed in postnatal development. The connections between the climatic factors and the growth of nestlings were analyzed by the

Year	No. of clutches	No. of eggs %	No. of hatchlings	No. of fledglings %	Total success rate %
1985	23	139	104 74.8	91 87.5	65.5
1986	19	111	90 81.1	64 71.1	57.7
total	42	250	194 77.6	155 79.8	62.0

Table 2. Success rate of breeding of Collared Flycatcher.

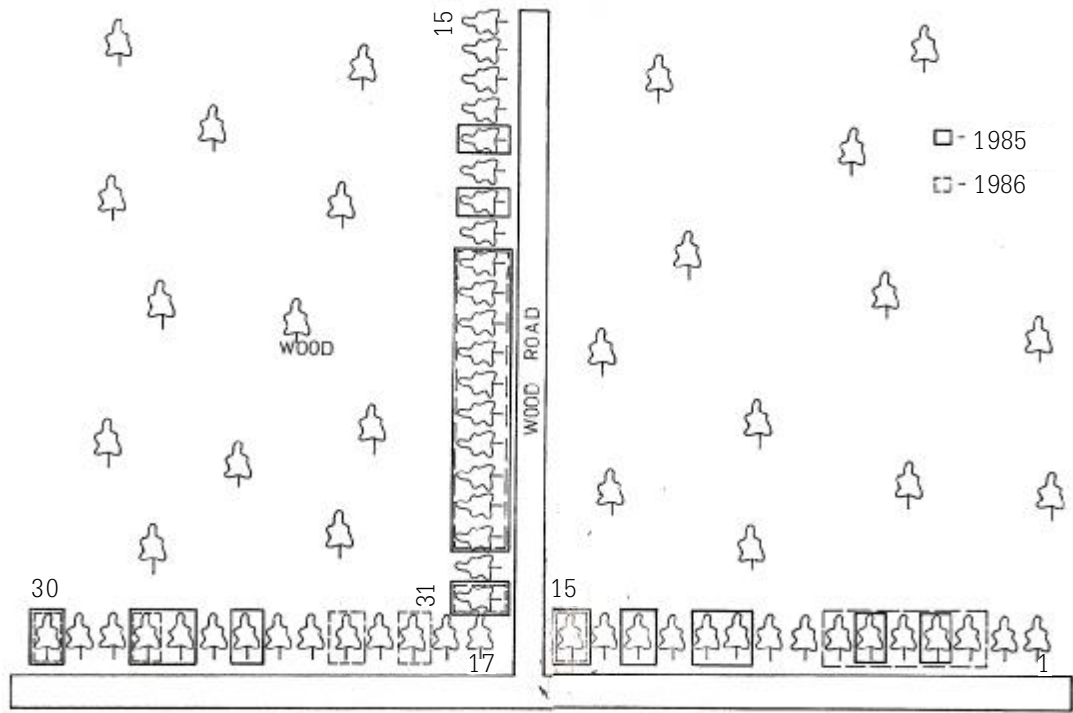


Fig. 4 Occupation of nest boxes by Collared Flycatcher (Two nests in the year 1986 were abandoned).

correlation between the morphological characters of young of the same age and the weather conditions (temperature, sunshine, relative humidity, speed of the wind) in the previous day of the measurement of young (Table 3). Meteorological information was obtained from near situated Bratislava airport. Data on age of nestlings were taken from the year 1986 when

we took greater interest in the age of young. Table 3 shows the momentary hatching was not influenced by the weather beside the speed of wind. Wind negatively correlated to the skeleton sum. The stronger wind in the previous day, the smaller skeleton sum of hatching in the next day. 7 days old young represented the nestlings still partially depended on thermoregulation of female

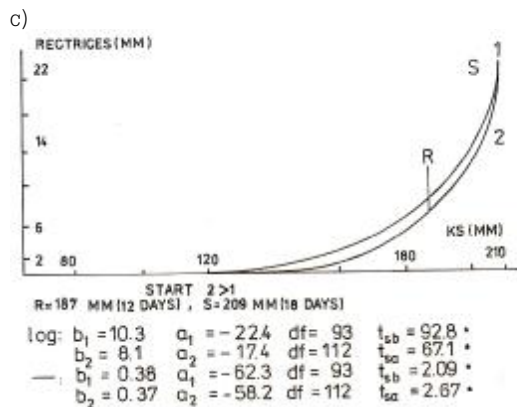
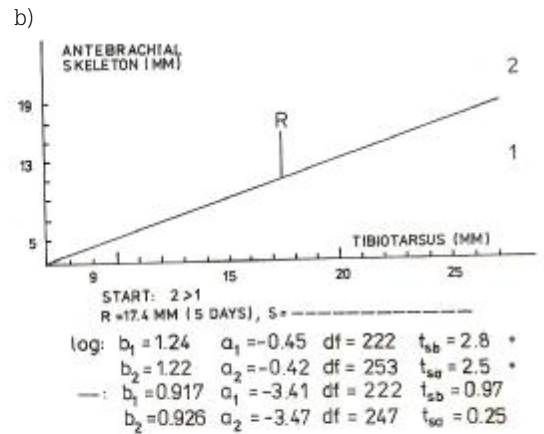
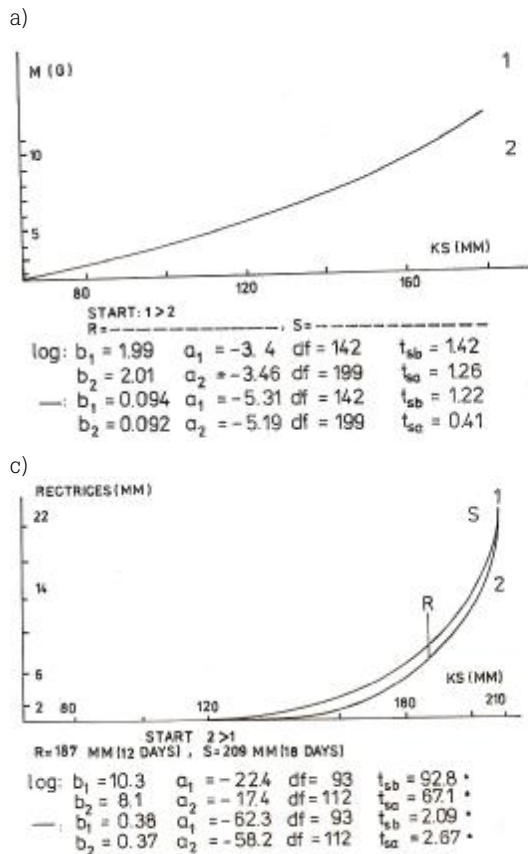


Fig. 5 Allometric analyses of the development of nestlings according to their origin from colonially (2) or more separately (1) situated nests. Explanations see Fig. 1 and Material and Methods.

and of course on the food. In this age the weather in the previous day more correlated to the growth of rectrices and skeleton. Higher speed of wind positively influenced the growth of bones and rectrices. The fact probably connected with the food as well as with the thermoregulation function of wind in warm days. Growth of 11 day old young did not correlate to the weather in previous day. Low correlations

Age	Morphological character	Speed of wind (kms/h)	Average temp. (° C)	Sunshine (hrs)	Relative humidity (%)
0.5 (27)	skeleton sum	- 0.61	0.29	0.16	- 0.23
	weight	- 0.06	- 0.19	0.21	- 0.21
7 (29)	skeleton sum	0.33	0.40	0.40	- 0.40
	rectrices	0.52	0.45	0.40	- 0.44
	weight	0.18	0.06	0.04	- 0.05
11 (26)	skeleton sum	- 0.09	0.26	0.28	- 0.29
	rectrices	0.01	0.14	0.17	- 0.35
	weight	- 0.03	0.06	0.06	- 0.03

Table 3. Correlation values between the climatic factors and morphological characters of nestlings of Collared Flycatcher.

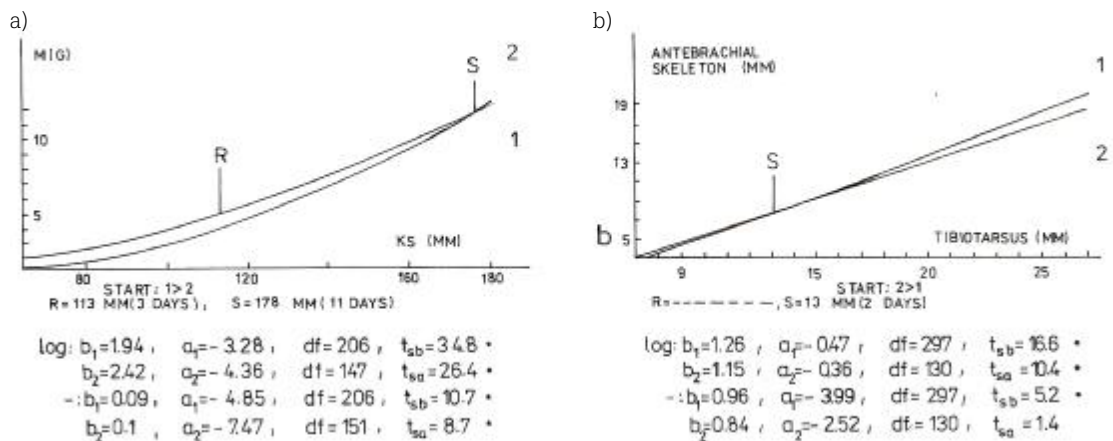


Fig. 6. Allometric analyses of the development of nestlings from the years 1985 (2) and 1986 (1). Explanations see Fig. 1 and Material and Methods.

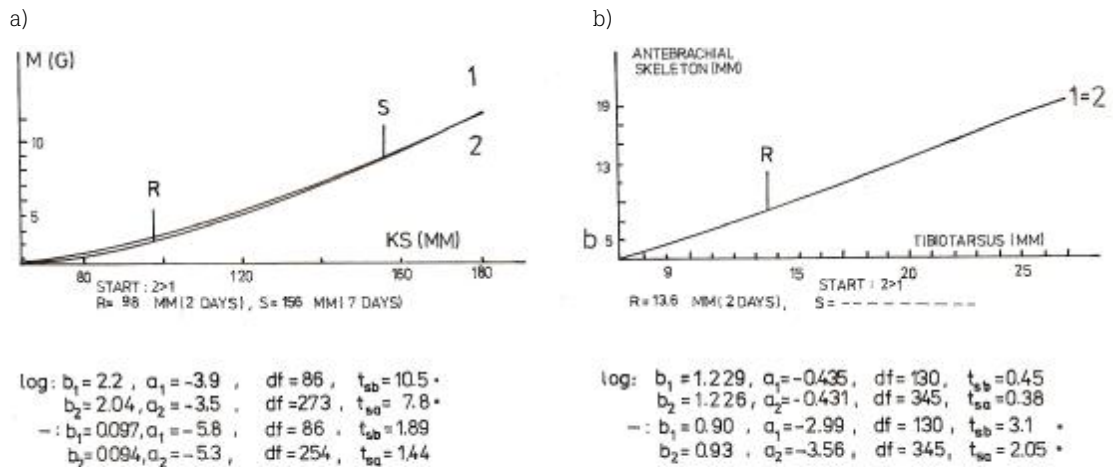


Fig. 7. Allometric analyses of the development of nestlings in the different nest boxes (1 – nest boxes occupied one year, 2 – nest boxes occupied two years). Explanations see Fig. 1 and Material and Methods.

between weight and climatic factors confirm that the weight is the most variable character very depended on momentary feeding and weather in the same day.

Disposition characters of female and postnatal development of young

By the measurement of the height of nests we found that the construction had lasted from 5 to 7 days. Latter nested females built the nests only from 3 to 4 days. We

devided the nests according to their height into two groups: high nests (85 – 134 mm) and low ones (50 – 70 mm). Figure 8 shows more progressive development of young of low nests but the differences are not very high and occur only in logarithms. Quality of the postnatal development of nestlings of a female did not reflect the predisposal reproduction ability of female to accumulate the nest stuff.

For an analysis whether the morphological characters of female might connect with the development of her nestlings we devided the females

according to their weight into two groups: light females of weight of 16, 9 gms and less and weighty females of weight of 17 gms and more. Calculated results (Fig. 9) clearly revealed the positive connection between the greater weight of a female and better development of her nestlings. Comparison of bones showed this difference during all nest care (Fig. 9b) and allometric analysis with weight showed the difference approximately from the age of 5 days (S – Fig. 9a).

Parasitism of Ixodes arboricola and postnatal development of young in a nest

In the year 1986 we revealed 6 nests where the ticks *Ixodes arboricola* had occurred. Mainly older nestlings suffered from the parasitism of two to four specimens of ticks. In the year 1985 we did not find the ticks. According to the presence of ticks we divided the nestlings into two groups and compared their development. The development of young with and

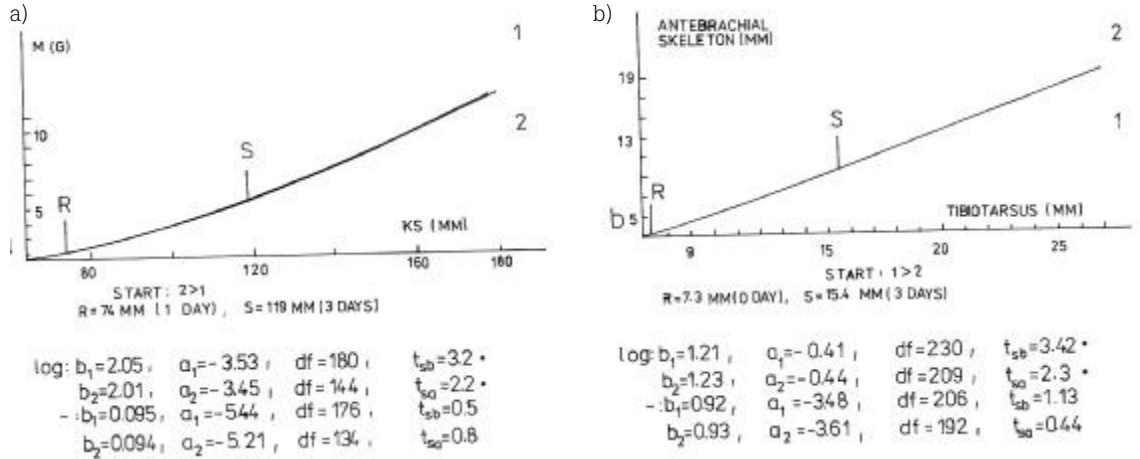


Fig. 8 Allometric analyses of the development of nestlings from different nests (1 - low structure, 2 - high structure). Explanations see Fig. 1 and Material and Methods.

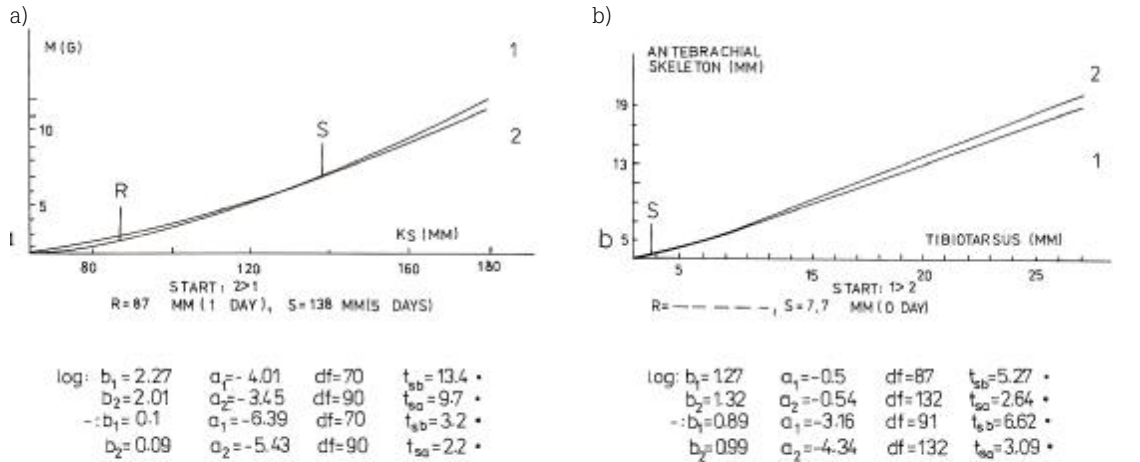


Fig. 9 Allometric analyses of the development of nestlings in relation to the weight of female (1 – weight of a female = 17 gms and more, 2 – weight of a female = 16, 9 gms and less). Explanations see Fig. 1 and Material and Methods.

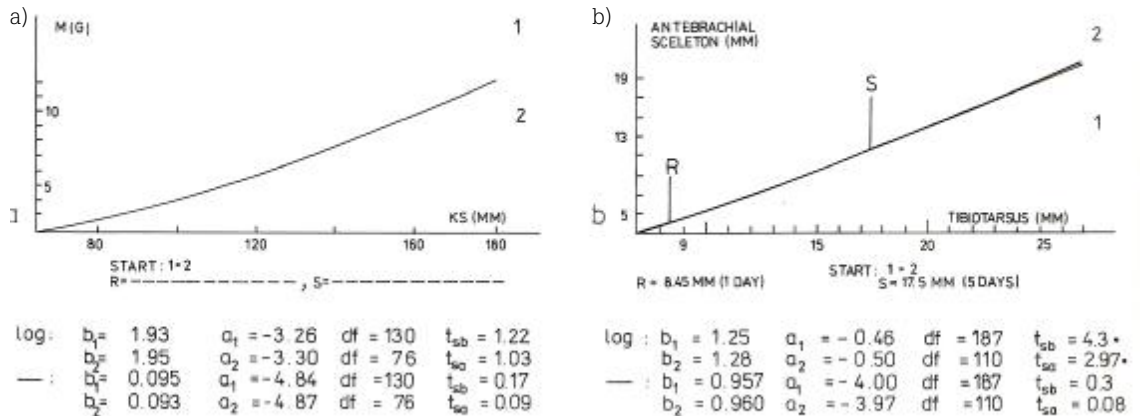


Fig. 10 Allometric analyses of the development of nestlings with (2) and without (1) *Ixodes arboricola*. Explanations see Fig. 1 and Material and Methods.

without ticks differed only at the end of nest care and only in logarithmic data (Fig. 10b). Earlier the courses of curves (mainly with weight – Fig. 10a) were the same with non significant tests of coefficients. Quality of postnatal development of nestlings reflected the parasitism of *Ixodes arboricola* very slightly after several days of nestling presence in a nest mainly at the end of nest care.

Discussion

The average clutch size of *Ficedula albicollis* in Europe is approximately 6 eggs (Löhl 1957, Balát 1971, Glowaciński 1973, Král 1978). Differences in the quality of postnatal development of young may connect with differences in females. Clutch size is seemingly indicative value of a female. Individual constancy in a clutch size of Collared Flycatcher is high (Löhl 1957) and only slightly depends on age of female (Löhl 1957), on environmental conditions (Balát 1971) but may reflect the abilities of female, e.g. to select the optimal nest box after male finding. Females lay smaller clutches in small nest boxes (Gustafsson and Nilsson 1985). Fledging is more influenced by environmental factors (Löhl 1957). Our analysis of postnatal development confirmed this fact. We did not confirm the result of Löhl (1957) or Gustafsson (1985) that greater clutch produced greater number of fledged young, when we divided them into two groups (4 and more and 3 and fewer) according to the fledging. At the end of care we found better development of young of greater clutches. Gustafsson (1985) also found that young of large broods had not become inferior quality when they were selected and judged according to the clutch size. On the other hand Gustafsson (1985) showed that there was a trade – off between number and quality of fledging weight and their tarsi length was shorter than average. We found less progressive development in large broods at the end of nest care. There is great probability that in worse momentary conditions (mainly of weather) the adequate part of natural large broods became enlarged in sense of Gustafsson (1985). Type of nest environment greatly affects the trophic base of Collared Flycatcher and the richness of the trophic base is also expressed in a very low mortality rate of young (Bureš 1983). Where the trophic supply is limited, the birds exploit the supply at the ground level, but this often means a very active search (Bureš 1986) sometimes also for plant food (Bureš 1986, Král 1986). In that time the mortality of young increases (Bureš 1986). Fewer young in a nest may be more oftenly fed by parents. One young was fed 8,4 times per hour in the nest of two young, in the nest of seven young one young was fed only 6,2 times per hour (Maštálka and Stárek 1978). Number of fledgings may be influenced also by interspecific competition. Collared Flycatchers breeding under reduced Great and Blue Tit competition contributed more recruits to the breeding population. The number and mass of young at 13 day of age increased (Gustafsson 1987). Interspecific competition affects the mortality among nestlings and among fledglings (Gustafsson 1987). The average niche breadth for food composition of Collared

Flycatchers is greater than that of Great and Blue Tits (Török 1985, 1986) but it need not be the advantage because Collared Flycatchers feeding strategy is very depended on the weather (Bureš 1985, 1986, Král 1986), on the type of environment (Löhl 1957, Bureš 1986) and on the time of a day (Bureš 1985). The nestlings are fed the most intensively in the evening, male brings food more oftenly (Marisova and Kholina 1959). From a year to year the total niche breadth is more conservative in Flycatcher than in the Tits (Török 1985) and feeding competition occurs mainly in the worse conditions. In that time the Flycatchers apply the same feeding strategy like Tits (Bureš 1985), but in prolonged periods of rain also many young die mainly till the age of 7 days (Bureš 1983). Less food to the young may be provide also by polygamous males of secondary females, some of the young in the secondary nests starve (Alatalo, Gustafsson and Lundberg 1986). Sometimes the young of secondary female may be fed by the third unmated male (Löhl 1976). Some influence on reproductive success may be expected from hybrids of *F.hypoleuca* x *F.albicollis*. Offspring – hybrids (mainly females – Štastný 1971-72) have low reproductive success and reduced fertility (Alatalo, Gustafsson and Lundberg 1982).

Order of young in a nest. Female starts to incubate the eggs after laying of the third or fourth egg (Marisova and Kholina 1959), sometimes after laying of the last egg (Král 1982). Latter laid embryos develop more quickly, but the difference in the speed of development of embryos is not very high (Bolotnikov et al. 1985) and among young after hatching are visible the developmental differences. The period of incubation may be extended by the rainy days (Löhl 1976) and by the greater clutch size (Král 1982). Also after nest care the young do not always leave the nest at the same time (Löhl 1976). Our analyses of postnatal development confirm described knowledge on young in a nest. Latter hatched chicks developed better in the first phases of nest care, at the end of care earlier hatched young developed more progressively.

Territory. Male characters certainly interact with territory and nest place quality as cues for female mate choice (Alatalo, Gustafsson and Lundberg 1986, Eriksson and Wallin 1986, Wallin 1986). If a female approaches a mate's territory, the male begins to sing more intensely, with increasingly longer songs as the female moves closer (Gelter 1987). Also faithfulness to the place of brooding is stronger in young males than females (Löhl 1957). Average distance between natural nest holes is 37m (calculated by Marisova and Kholina 1959). Protected place of nest box and type of tree play also the important role during postnatal development. In moist nest boxes young lost more energy for thermoregulation (Bureš 1983). In open country or in the open part of wood the nest boxes are less protected (Löhl 1957) and probably it was cause that young in more "colonial" nest had slightly different. Larger males (tarsus length) are at an advantage in terms of acquisition of superior nest sites, females do not differ (Gustafsson 1985). In dominant polyterritorial males the benefit of becoming polygamous may be counteracted by an increased risk of being cuckolded, because two territories of other males (Alatalo and Lundberg

1985). The most likely male – cuckolder is the nearest neighbour (Alatalo, Gustafsson and Lundberg 1984).

Years. Comparably to Löhrl (1957) we found great influence of different years on fledging and postnatal development of nestlings. If we summarize knowledge of Löhrl (1957), Glowaciński (1973), Král (1982), etc., on influence of different years on nesting of Flycatchers we make sure of great importance of some years on breeding success, from the first arrival to breeding area to the fledging.

Dispositions of female. Female builds the nest (Eriksson and Wallin 1986). Entirely the nest is built of dry grass, dead leaves, stalks and it is lined with fine grass (Löhrl 1976). The stuff is from near surroundings (Maštalka and Stárek 1978) and nest building prolongs 7 – 12 (Marisova and Kholina 1959), 3 – 6 days (Král 1982). We did not find the positive connection between ability of a female to accumulate the nest stuff and latter developmental quality of her young. Nest building is probably more affected by momentary weather (see Löhrl 1957). Morphological characters of females seem better to characterize the breeding success. They have higher heritability values than values for lifetime reproductive success (Gustafsson 1986) and they may also indicate the time of nesting of a female (Löhrl 1957). We confirmed more progressive development of nestlings of weighty females.

Summary

In the course of 1985 and 1986 the postnatal development and growth from 194 hatched to 155 fledged nestlings of *Ficedula albicollis* were observed in the alder woodland of Jurský Šúr reserve near Bratislava. By comparison of linear regression and comparison on the basis of intraspecific allometry we found the following:

1. Young of females of greater clutches exhibited more progressive postnatal development.
2. More nestlings in a nest (4 and more) developed better during the first days of ontogeny. Latter in the second half of nest care the advantage was the presence of fewer young in a nest.
3. Chicks hatched latter developed more progressively in the first half of nest care. At the end of care the earlier hatched nestlings caught them.
4. Differences which existed in development of young of more colonially or more separately nesting pairs were probably more conditioned by environmental factors than the dispositions of parents.
5. Allometric comparison clearly revealed the influence of seasons on postnatal development. Without knowledge of age the analyses showed more progressive development of young in the year 1985. Comparison of success rate of nesting confirmed those results.
6. Quality of the postnatal development of nestlings of a female did not reflect the predisposal reproduction ability of female to accumulate the nest stuff.
7. Nestlings of weighty females exhibited better quality of postnatal development.
8. Postnatal development of nestlings slightly reflected the parasitism of *Ixodes arboricola* mainly in the last days of nest care.

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