Oecologia Montana 1992,
1, 21-30

Growth allometry in the Ring Ouzel, *Turdus torquatus.* Multivariate study.

M. JANIGA
National Park High Tatras, Research Coordination Centre, 059 60 Tatranská Lomnica, Czech and Slovak Federal Republic

Abstract. The five-year study presents the results of statistical multivariate techniques which extend our knowledge on intraspecific differences in the growth pattern of Ring Ouzels. Because the chronological time has only an approximate relationship to biological age, the data is evaluated by the multivariate allometry without knowledge of nestling age. The allometric - first principal component from PCA is used to evaluate the influence of clutch adjustment, hatching asynchrony and brood size on the growth pattern of nestlings. Patterns of growth differ between the earlier and later hatched nestlings. Younger nestlings tend to be underweight for their primaries. Comparable analysis of different breeding responses shows that the allometric magnitude of developmental slowing is greatest among younger nestlings within a brood. The effect of brood reduction on the growth pattern is almost identical to this but the effect is probably less important than the effect of asynchronous hatching. The examination of the effect of clutch adjustment on the growth pattern shows that the growth described in the form of body weight versus size skeletal index reflects the influence of exogenous factors, most likely because of the seasonal change in food.

Key-words: Growth allometry, *Turdus torquatus*, breeding responses, PCA, Low Tatras, Carpathians

Introduction

The life of birds can be divided into distinct sequential phases: e.g. embryogeny, ontogeny, adulthood. The time required from start to finish of one phase is normally measured in physical time units like days, months or years. Due to genetic, physiological or environmental fluctuations, the degree of development may correlate poorly with physical time (e. g. Dunn 1976, 1979). Besides the physical time there is another time scale ticking away as cycles of energy consumption, reproductive events, etc. The cyclic nature of these parameters allows the definition of a physiological or relative time scale which may be more relevant to characterizing biological systems than is the physical time scale (Lindstedt and Calder 1981). The observations that developmental rates are highly nonlinear, are temperate-dependent, and can be modified by a host of other environmental variables and metabolic states, indicate that chronological or physical time has only an approximate relationship to biological age (Strauss 1987).

One important goal of biological morphometry is the quantitative comparison of organisms as ontogenic trajectories that react to short-term ecological effects (Strauss and Fuiman 1985). To attain this we need an operational basis for treating different life stages within the same mensural scheme. Because we cannot assume that data on absolute (physical time) developmental rates represent „true" rates of biological change (Strauss 1987), the concept of physiological age may often be more suitable than chronological age or physical time in morphometric studies (Lebeau *et al.* 1986). In altricial birds, the usefulness of intraspecific growth allometry may arise from the fact that there are so many sets of biological data for which the age or day of hatching are unfortunately impossible to evaluate, particularly when the birds are sampled in the wild and great distances exist between nests or colonies. When the age is unknown, some analytical techniques, for example PCA (Lebeau *et al.* 1986), may extract more variance, revealing more variation in growth than techniques using age.

This paper presents chronological data on the growth of Ring Ouzel nestlings in the Low Tatras, Carpathians. The effect of clutch size, brood size and asynchronous hatching on nestling growth was examined by the method of multivariate ontogenic allometry.

Material and methods

This study was made at Veľký Brankov Peak, Low Tatras, Slovakia from May 1985 to July 1989. Ouzels bred normally in coniferous forest (800 - 1,200 m), preferring margins of the forest near moist open grass (Fig. 1). Fieldwork began in early May with the arrival of the birds and finished at the end of July with dispersal of the young

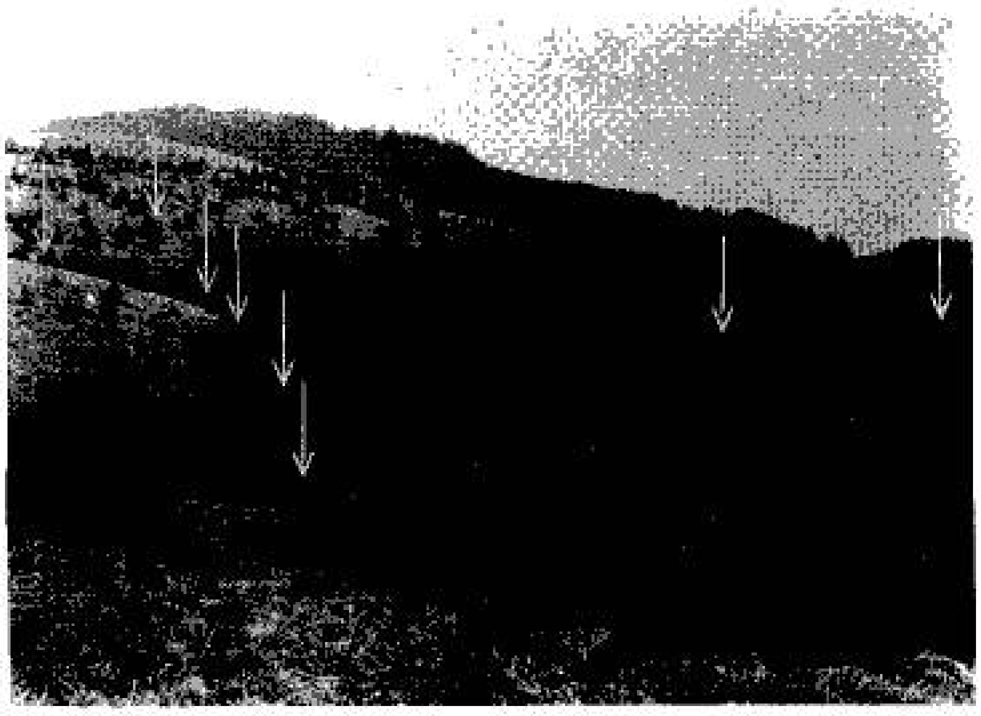

Fig. 1. Habitat and some nest sites (arrows) of Ring Ouzel.

and adults. Nests were found by searching for and watching the adults and were visited regularly during incubation and at two-day intervals from hatching onwards. All of 30 nests (used for this study) were found in spruce trees, placed close to trunk.

Data collection

As all the morphometric data were collected by me, variation due to difference in technique has been largelly avoided. I recorded the hatching order in siblings at my first visit after the chicks hatched and designated the day of hatching as day 0. Nestlings were uniquely marked with a felt-tipped pen and older nestlings were ringed with a combination of colored plastic rings, so that each individual was identifiable. In all, the data comprise 110 hatchlings. Measurements of many nestlings were excluded from the chronological description of the Ouzel growth because the young were of unknown age (Table 1). Some hatchlings were also excluded from the allometric analysis because they were of unknown origin (e.g. earlier or later hatched sibling in a nest) or died. I measured the length of the following skeletal indicators: tarsometatarsus, tibiotarsus, antebrachial skeleton, skeleton manus and width of the head (for details see Janiga 1986). The longest primary was measured from the point the fleshy sheath emerged from the skin to the tip of the feather, the primary vane was measured from the superior umbilicus to the tip of the feather. Tail length was taken from the insertion of the middle rectrices to the tip of the longest retrix. Each individual was measured to the nearest 0.1 mm with dial calipers and weighed to the nearest 0.1 g with a Pesola spring balance.

Developmental landmarks

The data were recorded between two „discrete" developmental events: emergence of the first quills on the alar tracts (primary was measured) and attainment of the peak weight during the postnatal development. The body weight data were initially displayed on a computer and the peak weights for tested groups of young were then found. The measurements after the attainment of the peak weight were excluded from the allometric analyses. That means, that young were measured to about ten days of their age.I recognize that the characterization of these events as discrete is arbitrary in that they represent recognizable points along a developmental continuum. I use the term merely to imply an unambiguously observable landmark in the development of an animal (Creighton and Strauss 1986). Each individual was measured approximately four times for allometric purposes; hence the interdependece among data points was equal in the groups compared.

Age (days)	HW,AS,SM TI, TA	TL	PR	PV	M
0	19	-	-	-	19
1	24	-	-	-	24
2	22	-	2	-	22
3	20	-	16	-	20
4	18	3	16	-	18
5	18	13	18	-	18
6	19	16	19	6	19
7	30	30	30	24	29
8	31	31	31	25	29
9	29	29	29	14	28
10	19	19	19	7	13

Table 1. Sample sizes of nestlings for each age-groups and growth parameters. HW = head width, AS = length of antebrachial skeleton, SM = length of skeleton manus, TI = tibiotarsus length, TA = tarsus length, TL = tail length, PR = primary length, PV = primary vane length, M = body weight.

Statistical methods and physiological age

Because individual birds have a remarkable capacity to vary their mass and volume depending on their nutritional status (Emlen *et al.* 1991, Janiga 1992), it si biologically most meaningful to define size from the skeletal measurements and as the nutrient reserve-independent size of a bird (Piersma and Davidson 1991). Principal component analysis (PCA) is a multivariate technique that may be used for summarizing data sets combining large numbers of variables. The first pricipal component ($PC1_S$) of a set of linear skeletal measurements provides an appropriate structural size measure (Rising and Somers 1989). The following variables were used: head width, length of skeleton manus, length of antebrachial skeleton, length of tibiotarsus, and length of tarsus. I represented structural size in my comparisons by a vector summarizing the joint size increase in all important morphometric traits. The $PC1_S$ was largely structured from the bones of the head and legs and also the bones of the wing. It is generally known that in many birds the head develops more rapidly than the rest of the body after hatching, and less rapidly after birth and that growth rates in the wing bones are not isometric to growth rates of the leg bones (Kramer 1959). A parameter composed of measurements of many bones summarizes the amount of total attachment surface available for muscle and connective tissue, and also the amount of support structure for internal organs. There is also another theoretical ground on which to defend the assumption that the $PC1_S$ was the best possible measure of „true" nestling body size. This parameter was composed of many different characters, and it should be less prone to variance caused by developmental abnormalities or measurement errors in a single character (Freeman and Jackson 1990). $PC1_S$ calculated from the covariance matrix of log-transformed data is little affected by measurement errors (Lougheed *et al.* 1991)

Comparisons of specific growth rates between two groups must be done at similar ontogenic stages in the two groups (see Blackstone 1987). In this study I used the concept of physiological age. I mentioned above that the measurements were done between two ontogenic landmarks. PCA of all young together produced a common size component. Subsequently, the mean and mean variance of the $PC1_S$ - scores were calculated between the two landmarks for a selected group of young (e.g. for the earlier hatched siblings in the Ouzel nests). A measure of the ontogenic equivalence of the size vectors between two groups was identified with one-way ANOVA ($P>0.05$) of the component scores (Sommers 1986). Before proceeding with one-way ANOVA, tests of the equality of the two variances (Sokal and Rohlf 1969) were used to evaluate the equality of group variance of the data.

Body weight and plumage length are not reliable indications of body size but they present information about quality of a bird growth and may vary due to food quality, reproductive activities and other variables. $PC1_S$ provides a standart measure against which growth of body weight and plumage length can be compared. For this comparison, I again used the PCA. Principal components of mensural data (structural skeletal size [$PC1_S$], body weight, primary length) were computed from the covariance matrix of logarithmically transformed data. The logarithmic transformation preserves allometries, standardizes variances, and produces a scale-invariant covariance matrix (Jolicoeur 1963, Strauss 1985). My preference for the lognormal model is also based on the reasons described by Mosimann and James (1979). The eigenvector (PC1) extracted from such a covariance matrix describes relative changes in the measured characters during growth and can therefore be interpreted as a general growth vector. For example, if the proportions of an *ith* variate to a *jth* variate were remain to constant as the size of a living organism increases, that is, if the relative growth of the two dimensions were isometric. In my case the hypothesis that *ith* variate is isometric could thus be expressed as - eigenvector (component weight) = 1/sqr (3) = 0.577 (see Jolicoeur 1963), because I use three variables. The nature of the growth variation corresponding to PC1 can thus be judged from the numerical values of its component weights. The development of body weight is completed earlier than that of the structural skeletal size ($PC1_S$ includes wing bones) and the development of primary length is completed later than that of the skeletal index (e. g. Kramer 1959). Subsequently, in nestlings from better environmental conditions, body weight has a higher growth rate and primary length a lower growth rate than in young from poorer conditions (Bel'skii 1947, 1948, Novotný 1970, O'Connor 1978, Janiga 1992). The importance of the second principal component in this allometric study can be judged from the amount of variance associated with this component. This variation is independent of general growth vector and is most easily attributed to fat deposition (O'Connor 1978). In the second principal component, the weight elements tend to have the opposite sign to that of feather elements (O'Connor 1978).

Results

Growth, chronological age and relative age determination

The growth curves for head width, tarsus, tibiotarsus, skeleton manus and antebrachial skeleton lengths are presented in Figures 2, 3, 4, 5 and 6. The sample sizes on which the growth curves are based are given in Table 1. After hatching, there is a general tendency for the head to grow more rapidly than the bones of leg or wing. A sudden increase in lengths of wing and leg bones is seen from the fourth to fifth day, when the sheaths of the remiges emerge (Fig. 11c). The age of feather splitting and the age of feather fringing are presented in Figures

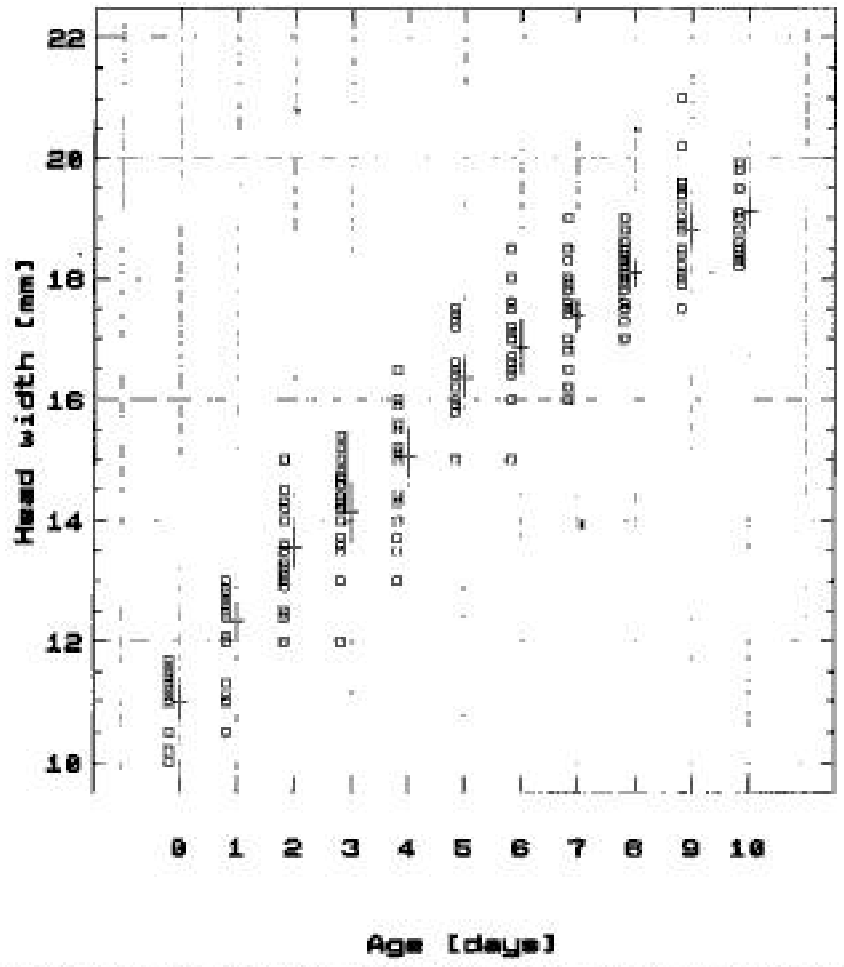

Fig. 2. Relationship between age and increase in the head width of Ring Ouzel.Horizontal lines represent mean values, vertical lines 95% confidence limits, symbols indicate samples. Sample sizes are shown in Table1.

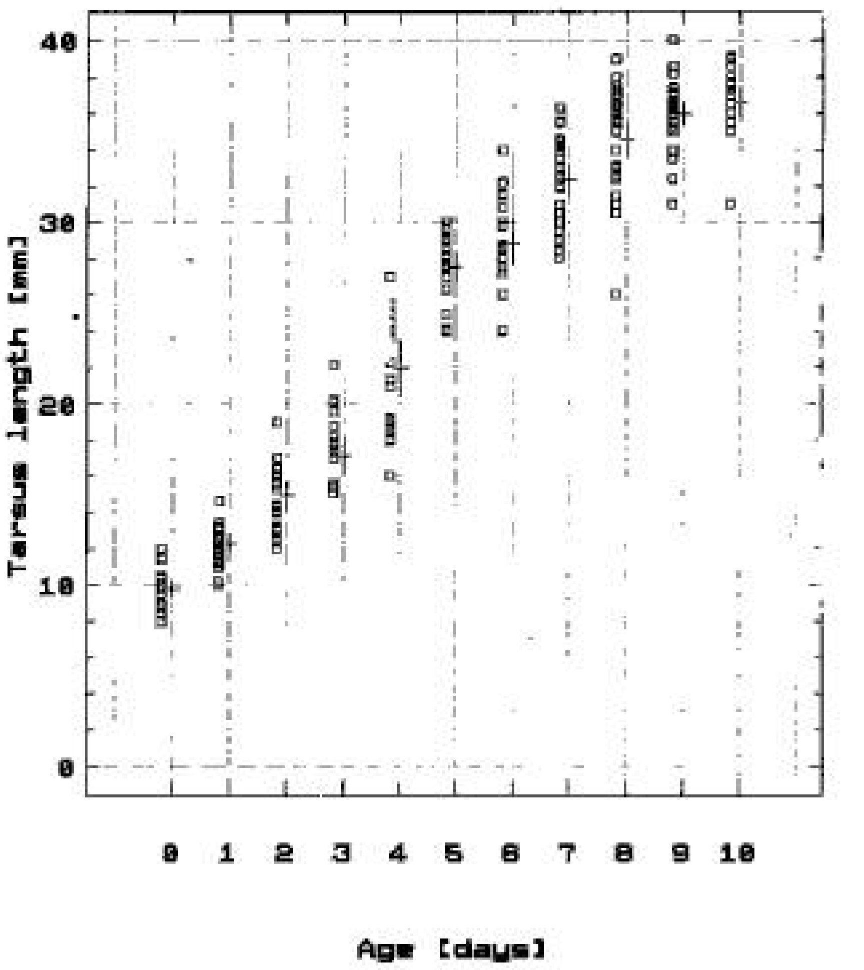

Fig. 3. Relationship between age increase in the tarsus length of Rin Ouzel. See Fig. 2 for details.

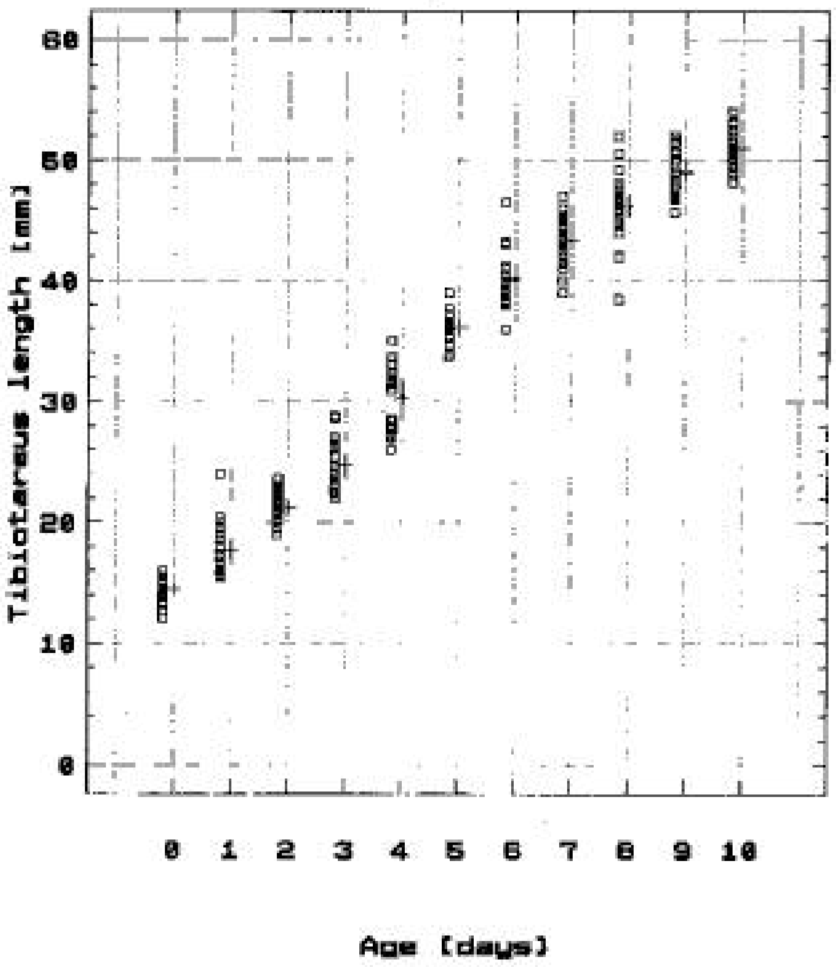

Fig. 4 Relationsip between age and increase in the tibiotarsus length. Fo details see Fig. 2.

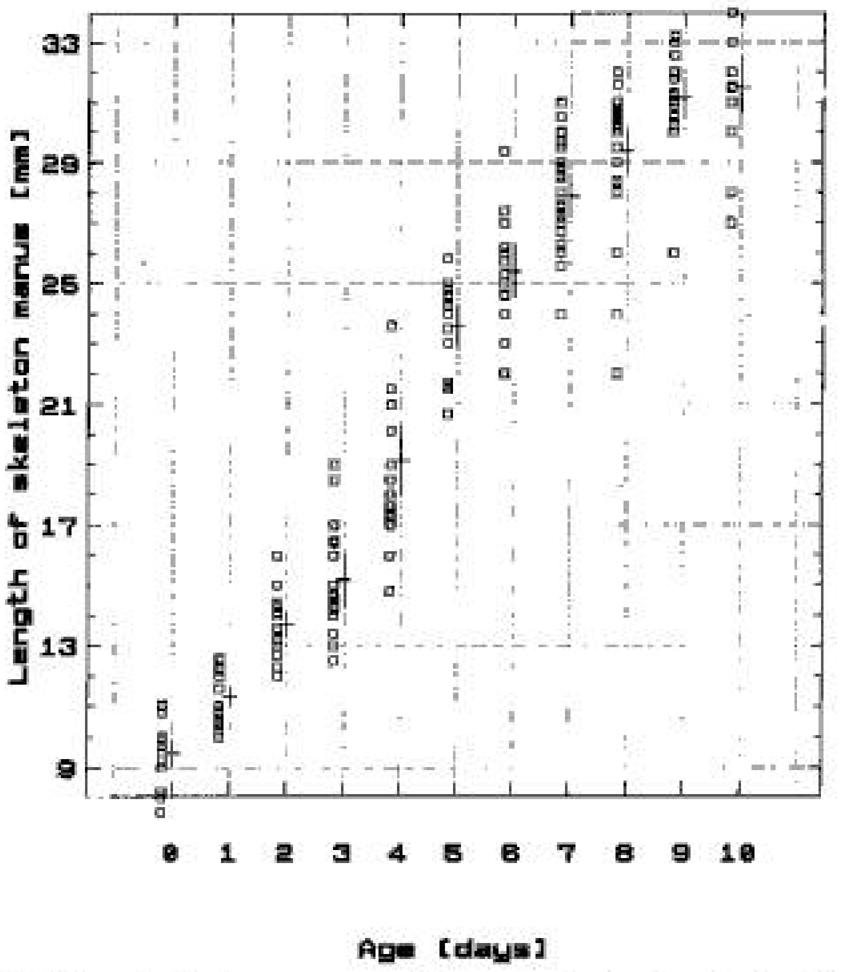

Fig. 5. Relationship between age and increase in the length of skeleto manus. For details see Fig. 2.

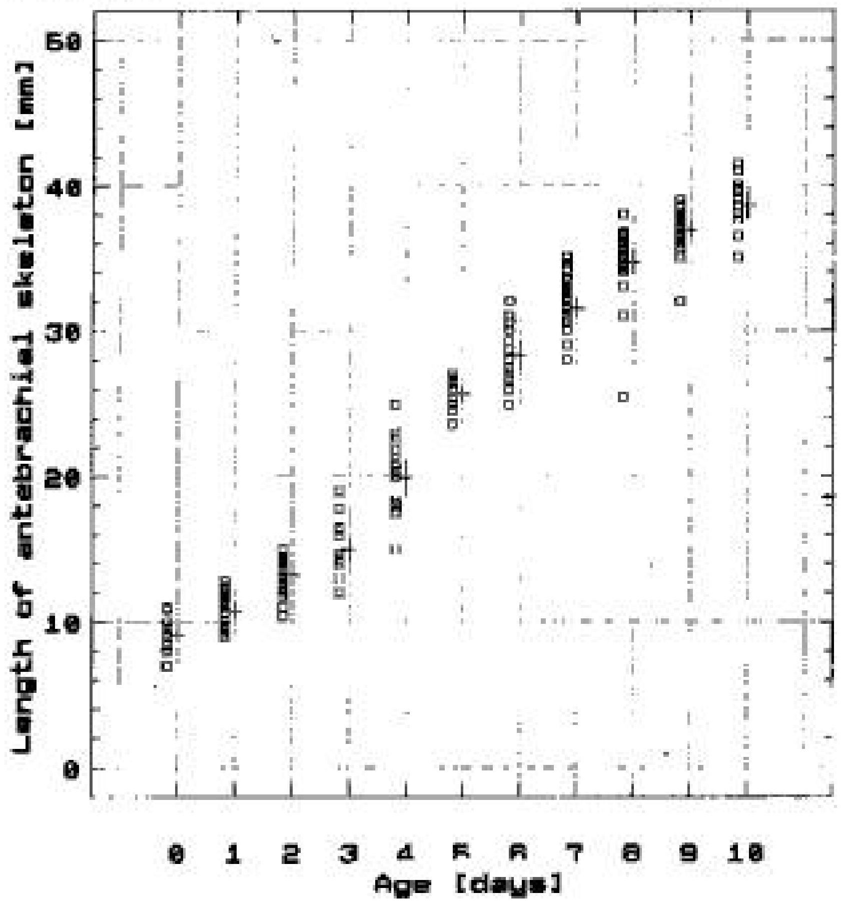

Fig. 6. Relationship between age and increase in the legth of antebrachial skeleton. For. detailes see Fig. 2.

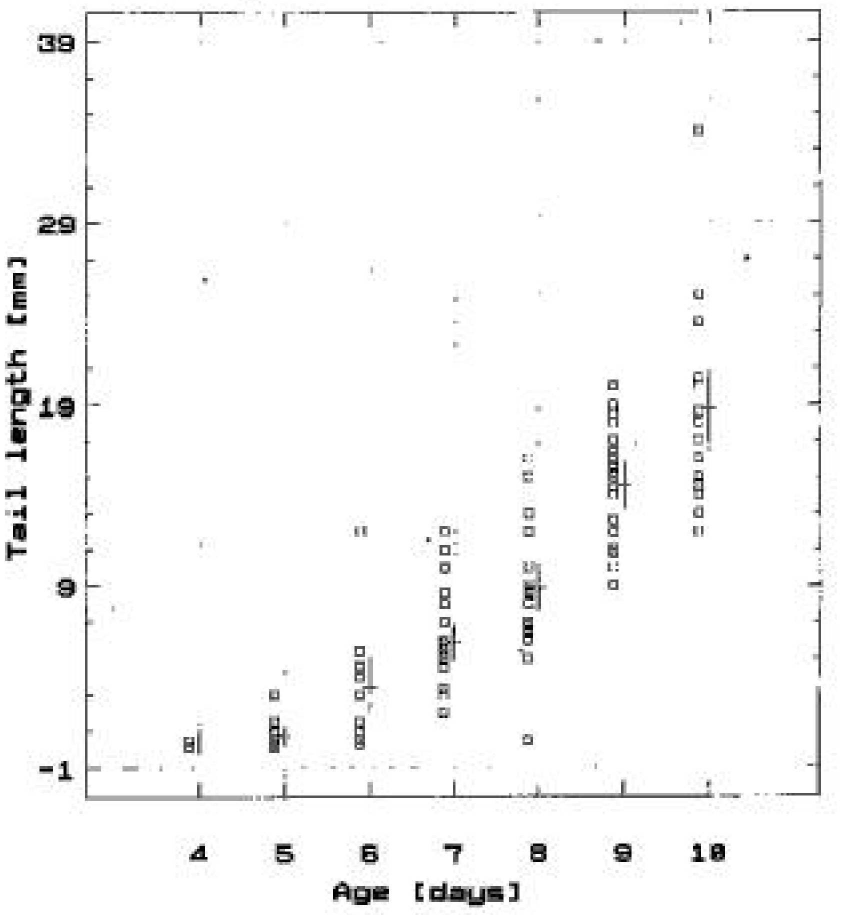

Fig. 7. Relationship between age and increase in the tail length. For details see Fig. 2.

7, 8 and 9. These show that feather development proceeded somewhat faster in alar than in abdominal feather tracts. Shafts of the remiges appear by day two or three (Fig. 11b). The growth rate of primaries and rectrices is greatest between days eight and ten (Figs. 11e, 11f). On day six (Fig. 11c) or seven, the vanes of primaries are emerged (Fig. 9). The mean growth curve for body weight of Ring Ouzel follows a typical sigmoidal pattern (Fig. 10). Following hatching (Fig. 11a), at which time they weigh from 3 to 8g, nestlings at Low Tatras, grow fastly. A sudden increase in weight is mainly seen from the third to fifth day. From the ages of three to nine days, weight increases almost linearly with the time, the peak in the body weight is attained at the age of nine or ten days.

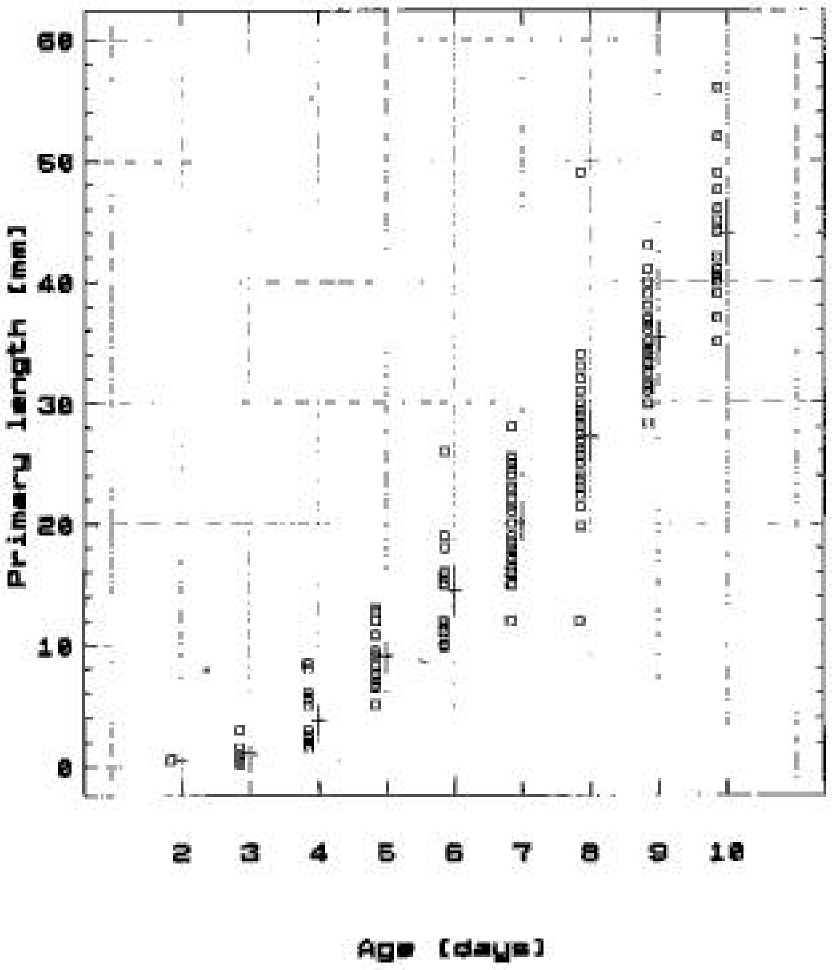

Fig. 8. Relationship between age and increase in the primary length. For details see Fig. 2.

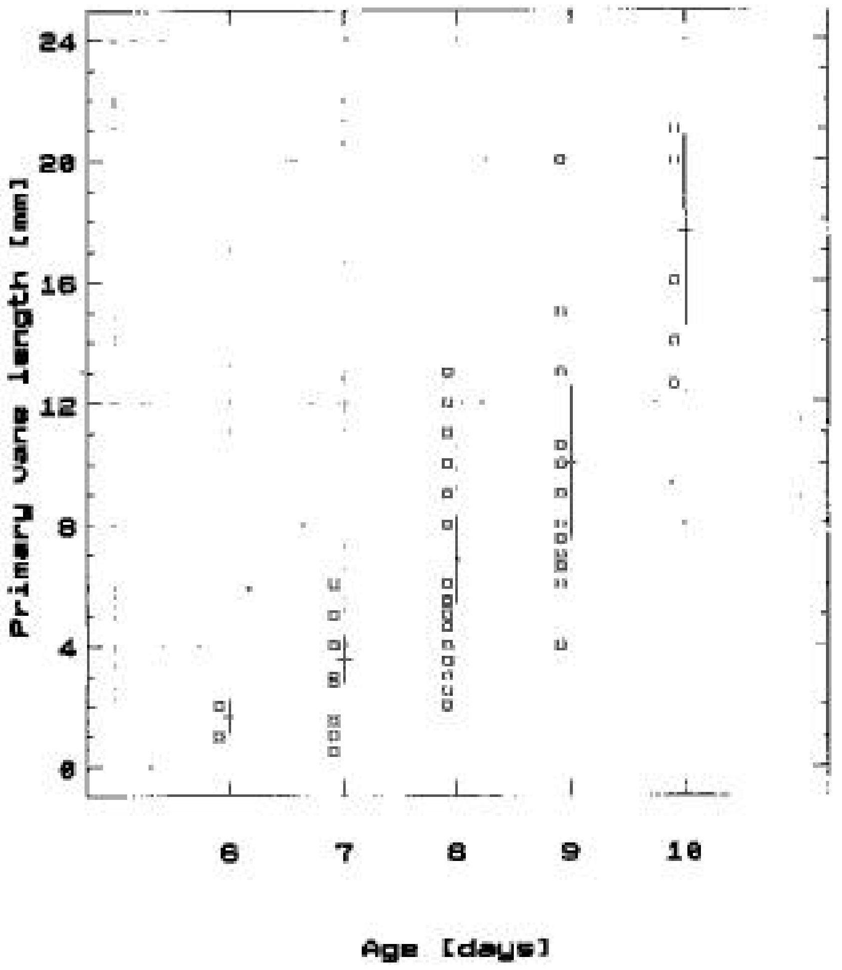

Fig. 9. Relationship between age and increase in the primary vane length. For details see Fig. 2.

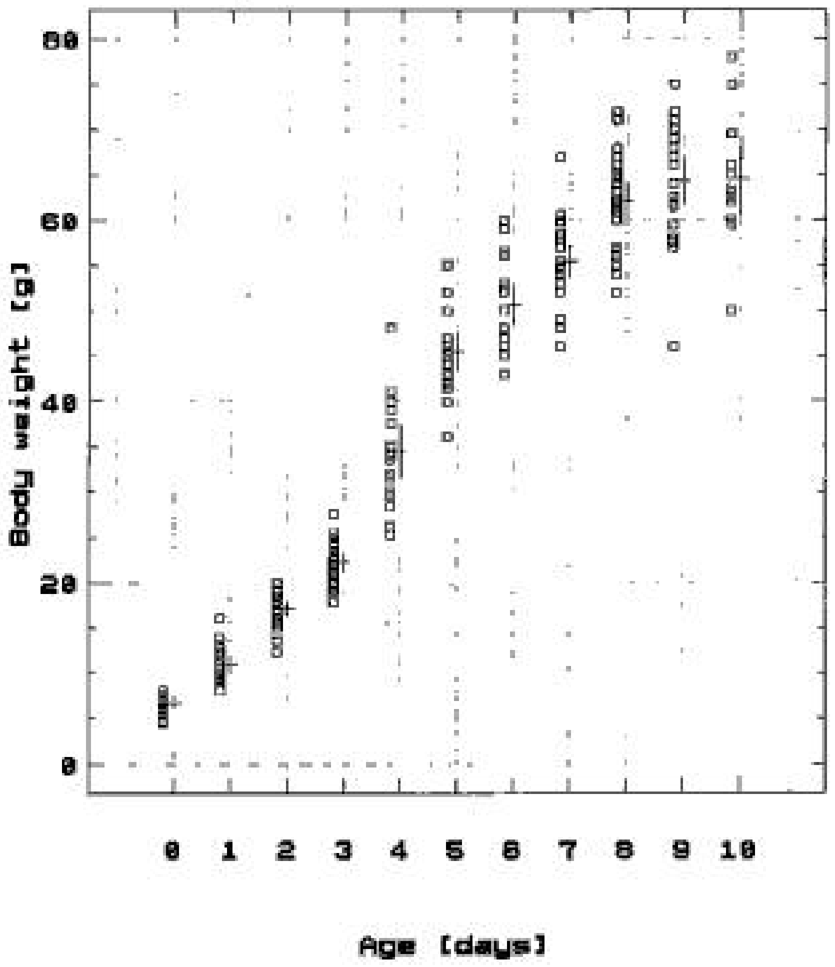

Fig. 10. Relationship between age and icrease in the body weight. For details see Fig. 2.

For a study of bird population dynamics (ringing, nature protection) we often need to estimate age of nestlings as accurately as possible. By measuring and observing the growth of nestlings in the Low Tatras I constructed the following age chart (Table 2). I have used it and find it to be quite workable, enabling one to reliably age a nestling to within 2 days. Metric variables are used to develop the age key.

Allometric comparison of growth pattern of siblings

The initial difference in body size between the earlier and later hatched chicks is almost entirely the result of hatching asynchrony, with a hatching interval of one day (Fig. 12). I examined the effect of hatch order on growth rate by comparing the component weights and component scores of older versus younger siblings from all broods in which at least two young hatched asynchronously. Analysis of variance-covariance matrices shows that the three characters (Table 3) are not equally weighted on the first components. The body weight is highly negatively allometric, growing much more slowly than the primary length. Patterns of growth differ between the earlier and later hatched nestlings.

Younger nestlings tend to be underweight for theirs primaries. The first hatchlings tend to have higher increments in the growth of body weight for the same (F = 0.0001, P = 0.9998, ns.) level of the size skeletal index (PC1$_S$). Because a nestling on the lower curve can be chracterized as underweight for its primary or also as well-feathered for its weight, we may suggest that the earlier hatched young grow better than later hatched nestlings. The structures of the second principal component for both groups agree well with this conclusion (Table 3). The second components computed here also share with the above results the feature of increased variance in the case of later hatched nestlings (1.12> 0.77).

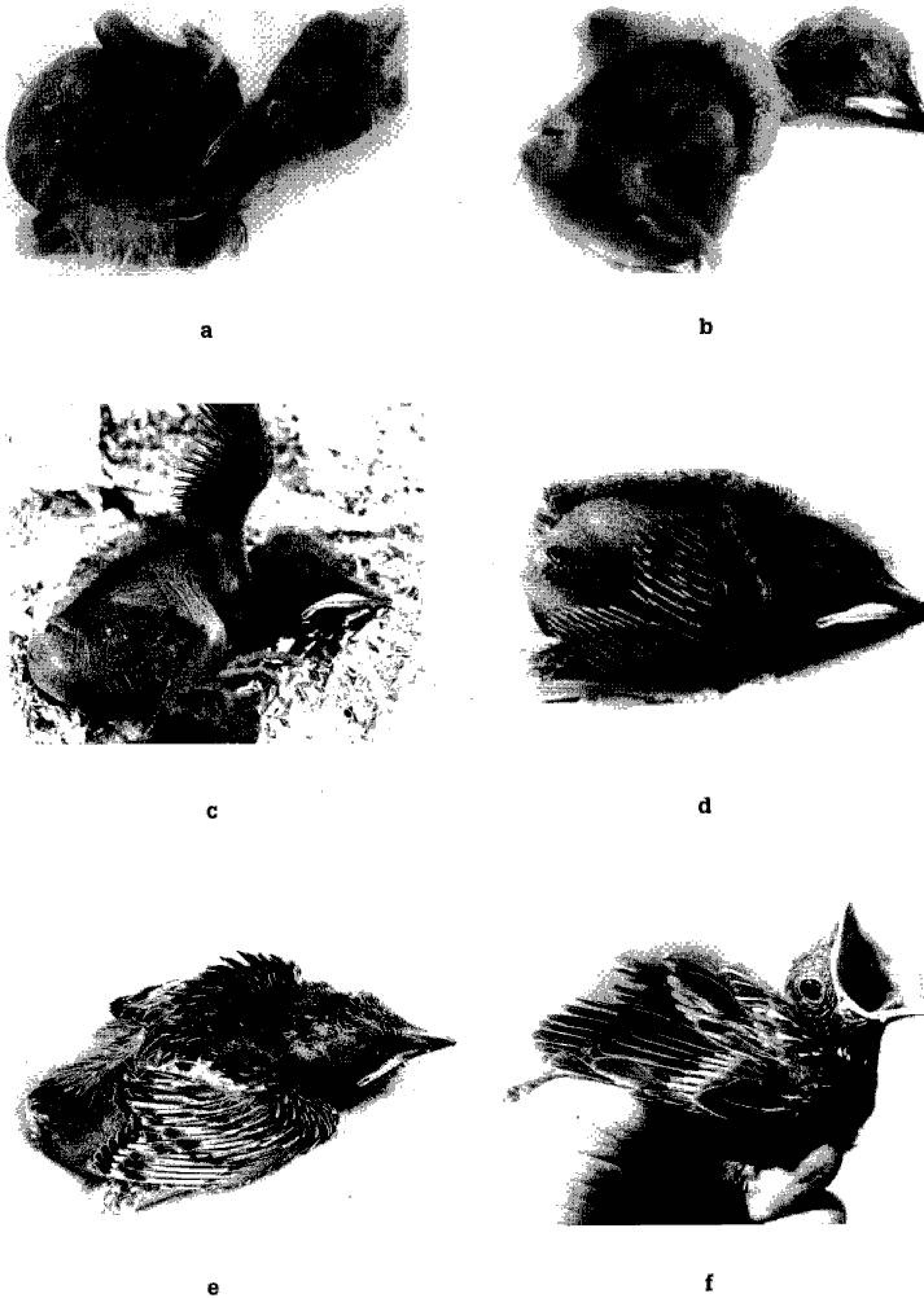

Fig. 11. Growth and development of nestling Ring Ouzels. Age: (a) 0 day = less than 24 hours after hatching, (b) 2 days, (c) 4 day
(d) 6 days, (e) 8 days, (f) 10 days.

a. Head width less than 12mm, tibiotarsus length less than 17mm, length of skeleton manus less than 11.5mm, body weight less than 10g, primaries not emerged (Fig. 11a) ...... 0 day (less than 24 hours after hatching).
a'. Head width greater than 12mm, tibiotarsus length greater than 17mm, length of skeleton manus greater than 11.5mm, body weight greater than 10g, primaries may be emerged ...... b.
b. Tibiotarsus length less than 25mm, longest primary quill less than 1mm, weight less than 22g (Fig.11b) ...... 2 days.
b'.Tibiotarsus length greater than 25mm, longest primary quill greater than 1mm, weight greater than 22g, quills of rectrices may be emerged ...... c.
c. Tibiotarsus length less than 36mm, longest primary length less than 9mm, undeveloped primary vanes (Fig.11c) ...... 4 days.
c'.Tibiotarsus length greater than 36mm, longest primary gratest than 9mm ...... d.
d. Primary vanes undeveloped or less than 2mm (Fig. 11d) ...... 6 days.
d'. Primary vanes greater than or equal to 2mm long ...... e.
e. Longest primary less than 35mm (Fig. 11e) ...... 8 days.
e'. Longest primary greater than or equal to 35mm and less than 58mm (Fig. 11f) ...... 10 days.

Table 2. Key for estimating age of nestling Ring Ouzels.

Variable	PC1		PC2	
	Siblings hatched		Siblings hatched	
	earlier* (121)	later* (52)	earlier (121)	later (52)
Skeletal size index ($PC1_S$)	0.383	0.326	0.660	0.882
Body weight	0.242	0.220	0.603	0.278
Primary length	0.891	0.919	-0.448	-0.380
% variance	98.97	98.38	0.77	1.12

* One-way ANOVA between two PC1-scores: F= 3.68 at P= 0.057.

Table 3. Relative growth of asynchronously hatched nestlings. Eigenvectors for the first two principal components extracted from covariance matrix of external measurements with percentages of total variance explained by each axis. Sample sizes of $\log_{10}$ transformed data are in parentheses.

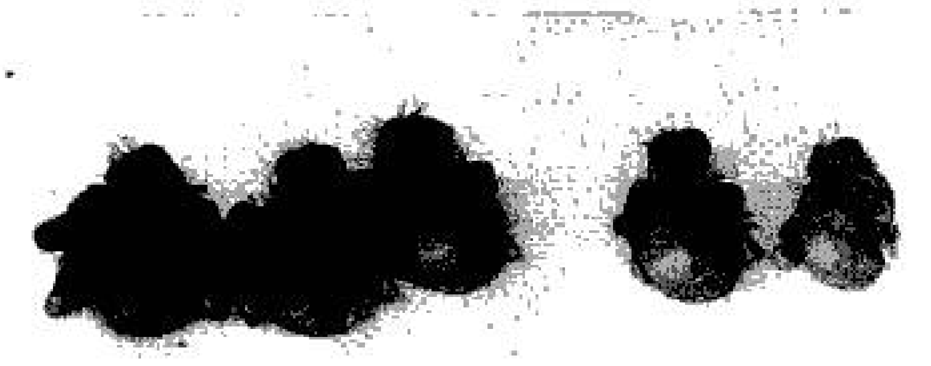

Fig. 12. Initial difference in body size between earlier and later hatched nestlings is almost entirely the result of hatching asynchrony. Siblings at the age of one (right) and two (left) days.

Brood size and growth pattern

Component elements for PC1 and PC2 are listed for each group in Table 4. In nestlings from broods of four or five, body mass has a lower growth rate with respect to the skeletal index than in nestlings from broods of one, two or three. The level of $PC1_S$ is not significantly different between the two groups (F = 3.254, P = 0.073, ns.). The results show a tendency for more young in a nest to be lighter for their skeletal size than young from broods of one, two or three. Less young in a nest tend to develop better.

Variable	PC1		PC2	
	Brood size (No. of young in a nest			
	1 - 3* (34)	4 - 5* (144)	1 - 3 (34)	4 - 5 (144)
Skeletal size index ($PC1_S$)	0.377	0.361	0.823	0.743
Body weight	0.252	0.235	0.349	0.512
Primary length	0.891	0.902	-0.447	-0.430
% variance	99.37	98.50	0.51	1.06

* One-way ANOVA between two PC1-scores: F= 1.04 at P= 0.309.

Table 4. Relative growth of nestlings of different broods. Eigenvectors for the first two principal components extracted from covariance matrix of external measurements with percentages of total variance explained by each axis. Sample sizes of $\log_{10}$ transformed data are in parentheses.

Clutch size and growth pattern

In nestlings from clutches of three or four eggs, body mass has a lower growth rate with respect to the skeletal index ($PC1_S$) than in nestlings from clutches of five or six eggs. There are no significant differences in the size skeletal index ($PC1_S$) between the two groups (F = 0.148, P = 0.705). Analysis of variance matrices shows that primary lengths are equally weighted on the first components in both groups (Table 5,level = 0.9). The observed differences in ontogenic allometry of body weight (PC1 in Table 5) are probably a consequence of a seasonal impact on breeding of Ring Ouzels (see below). The second principal components account for 1.9% and 2.3% of the character variances. This variances appear as independent of general growth vector (development) and thus most easily accounted for as fat deposition. This variability in fat deposition presumably reflects the environmental impact on the growth pattern.

Variable	PC1		PC2	
	Clutch size (No. of eggs in a clutch)			
	3 - 4* (75)	5 - 6* (77)	3 - 4 (75)	5 - 6 (77)
Skeletal size index (PC1s)	0.378	0.349	0.697	0.800
Body weight	0.217	0.261	0.573	0.418
Primary length	0.900	0.900	-0.431	-0.431
% variance	97.39	96.22	1.93	2.30

* One-way ANOVA between two PC1-scores: F= 0.046 at P= 0.832.

Table 5. Relative growth of neslings from different clutches. Eigenvectors for the first two principal components extracted from covariance matrix of external measurements with percentages of total variance explained by each axis. Sample sizes of $\log_{10}$ transformed data are in parentheses.

Comparison of effects

For all compared groups of young, the general growth vectors (PC1) account for large fractions of the total measured variance. Comparison of PC1 - scores (one-way ANOVAs in Tables 3, 4, 5 and in Fig. 13) shows that the allometric magnitude of developmental slowing is greatest among younger nestlings within a brood (Fig. 13). The effect of brood reduction on the growth pattern is almost identical to this (compare signs and numerical values of component weights in Tables 3 and 4) but the effect is probably less important than the effect of asynchronous hatching. The examination of the effect of clutch adjustment on the growth pattern shows that the growth described in the form of body weight versus size skeletal index reflects the influence of exogenous factors, most likely because of the seasonal change in food. As laying date is shown in many studies to influence growth of chicks, it is analysed here with to yearly differences, clutch size and brood size. PCA of correlation matrix (Table 6) produced three components which accout for 87.5% of the variance in the raw data. The first PC is negatively correlated with the year of laying, clutch size and brood size and positively correlated with the day of laying. Thus PC1 mainly describes that clutch and brood size declined with clutch initiation date (n = 30 nests used for this study) . The second PC shows strong positive correlation with the years of the study and partially explains that clutch size increased in the later years of the study. The third PC again shows that clutch size declined with clutch initiation date. PC2 and PC3 clearly reveal that clutch size tends to be more influenced by seasonal factors than brood size. Moreover, the fourth PC has as its main feature the contrast of brood size with clutch size. This component accounts for 12.5% of the data variance . The results confirm my assumption tha growth pattern of young from adjusted clutches is mor influenced by environmental factors than by clutch ad justment.

Variable	Eigenvectors			
	PC1	PC2	PC3	PC4
Clutch initiation date	0.514	0.121	-0.802	-0.279
Year of laying	-0.311	0.931	-0.113	0.155
Clutch size	-0.530	0.334	0.573	-0.528
Brood size	-0.599	0.084	0.123	0.787
% variance	46.87	23.02	17.58	12.53

Table 6. PCA results for correlation matrix of raw data se extracted from breeding biology of Ring Ouzels (n = 30).

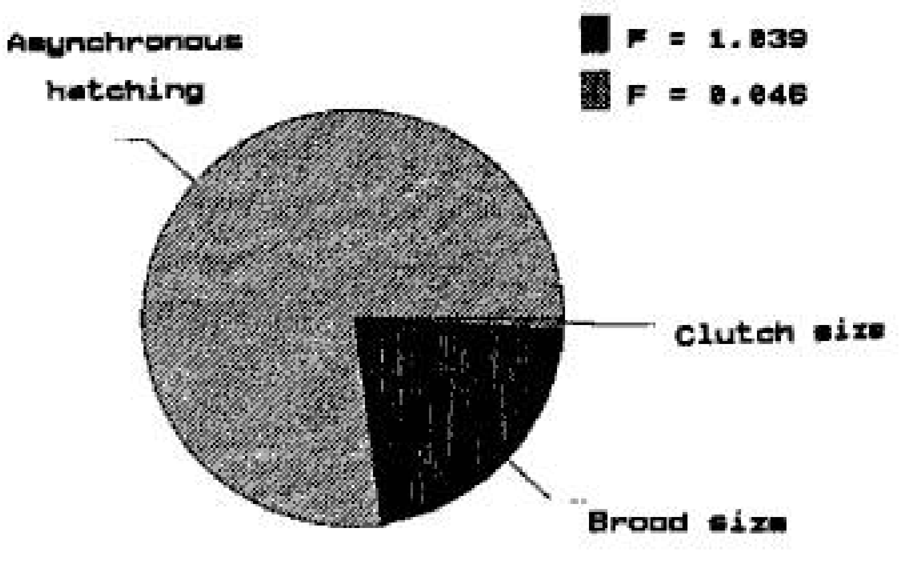

Fig. 13. Effects of asynchronous hatching, brood size and clut size on the growth pattern of Ring Ouzels. Asynchrono hatching tends to be the most important factor which influenc the growth rates of young. For F-tests of one-way ANOVAs s tables 3, 4, and 5.

Discussion

Ouzel chicks grow fast. A nestling measured in th morning and one measured in the evening of the sam day may differ in the body size, though they may be the same age, when age is measured in days. On th other hand, the young may differ in age but the featur of their development (e.g. bone lengths) may be th same. This study suggests ontogenic equivalence b tween the measured skeletal characters, but this r search is also based on the long- established knowledg (Bel'skii 1947, 1948, O'Connor 1978) that proportion differences must exist among growing organs as a resu of genetic, physiological or environmental variation. most avian species, the periods of food shortage ma lead to reduced weight gain, but physiological an morphological development continue at the species - typical rate (O'Connor 1984).

The allometric methodology used in this study is based on the observation that the mitotic activity of cells in the tissue is closely related to the instantaneous percentage growth of various organs (O'Connor 1984). Growth rates in birds are probably adjusted to the extent to which a bird's tissues are called upon to function from an early stage (Ricklefs 1973). Such internal organs as heart or liver (expressed in the variable - body weight) retain a capacity for cell proliferation and increase of cell size after cell differentiation (O'Connor 1984). Cells of feather pulps may also retain the capacity to proliferate when differentiated (O'Connor 1984). That means that the nestlings living in a more favorable environment attain their peak of body weight more rapidly than nestlings living in a poorer environment, but the feather growth of the nestlings from a poorer environment occurs earlier relative to weight (Bel'skii 1947, 1948).

Ring Ouzels show considerable variation in their growth pattern. This study suggests that the type of variation may be adapted to the overall breeding tactics of adults. The allometric differences confirm that earlier hatched young developed better than their later hatched siblings. Brood reduction also influences the growth pattern of nestlings but the effect of brood reduction on growth rate tends to be less important than the effect of asynchronous hatching. In altricial birds, the growth pattern probably reflects both the effective thermoregulation in larger broods and their higher food requirements during the later period of nestling life (Janiga 1992). In the present study the growth of Ouzels is examined between two developmental landmarks, emergence of the first quills on the alar tracts and attainment of the peak weight, i. e. in the later period of nesting care, when the effect of brood reduction on the growth pattern more reflects the food demands than social thermoregulation. In this period the reduced broods tended to develop better.

As already indicated, the brood reduction less intensively affects the growth pattern of Ouzels than hatching asynchrony. One of the most widely cited explanations of hatching asynchrony is Lack's (1954) "brood reduction hypothesis". The hypothesis states that asynchronous hatching is an adaptation for adjusting brood size to an unpredictable food supply. In contrary to the previously common approach of trying to identify the brood reduction as causal agent for asynchronous hatching, the recent papers (e. g. Clark and Wilson 1981, Bolinger *et al.* 1990) reveal an increasing awareness that hatching asynchrony may be the result of several different selection pressures, the effect of each varying between and probably also within species (Amundsen and Slagsvold 1991). Some birds begin incubation before clutch completion for reasons other than to ensure sibling competition and differential mortality within the brood. Early incubation may speed hatching or fledging, so the young can make full use of declining resources, or so the time during which the nest is vulnerable to predation is reduced (Hussel 1972). Slagsvold *et al.* (1984) argued, that in most passerines, asynchrony represents an evolutionary response to nest predation.

In the Ring Ouzels, the hatching asynchrony leads to the differences between the growth pattern of earlier and later hatched chicks. Magrath (1989) provide Blackbirds (*Turdus merula*) with additional food and compared the reproductive success of experimental synchronous and asynchronous broods in both treatments. The early mortality of Blackbird hatchlings resulted in increased growth of surviving nestlings. My results demonstrate that asynchronous hatching influences the growth pattern of Ring Ouzels but is not necessary for the process of brood reduction. I hypothesize that the ability of nestling Ring Ouzels to withstand morphological retardation represents an adaptation that enables them to reduce energy requirements over the short term, until increased food becomes avilable to complete development. If conditions improve, developmentaly retarded nestlings can recover. The "ability of worse" development may operate in combination with brood reduction. The adjustment of development rate enhances the likelihood of survival if food shortages are temporary, while brood reduction ensures the asymmetric mortality if food stress continues over the long term.

Acknowledgements

I thank Mrs. Martina Procháczková and Mrs. Katarína Marencinová for their technical assistance. They prepared the photos for this paper.

References

Amundsen, T. and Slagsvold, T. 1991: Asynchronous hatching in the Pied Flycatcher: An experiment. *Ecology*, **72:** 797-804.

Bel'skii, N.V. 1947: [Importance of food in the growth and development of birds]. *Doklady akademii nauk USSR*, **58**: 1531-1534 (in Russian).

Bel'skii, N.V. 1948: [Postembryonic growth and differentiation in altricial birds in nature.] *Doklady akademii nauk USSR*, **61:** 573-576.

Blackstone, N.W. 1987: Specific growth rates of parts in a Hermit crab *Pagurus longicarpus*: a reductionist approach to the study of allometry. *J. Zool., London*, **211**: 531-545.

Bollinger, P. B., Bollinger, E. K. and Malecki, R. A., 1990: Tests of three hypothesis of hatching asynchrony in the Common Tern. *The Auk*, **107:** 696-706.

Clark, A. B. and Wilson, D. S. 1981: Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Quarternaly Review of Biology*, **56**:253-277.

Creighton, G.K. and Strauss, R.E. 1986: Comparative patterns of growth and development in cricetine rodents and the evolution of ontogeny. *Evolution*, **40**: 94-106.

Dunn, E.H. 1976: The relationship between brood size and age of effective homeothermy in nestling House Wrens. Willson Bulletin, **88**: 478-482.

Dunn, E.H. 1979: Age of effective homeothermy in nestling Tree Swallows according to brood size. *Willson Bulletin*, **91**: 455-457.

Emlen, S.T., Wrege, P.H., Demong, N.J. and Hegner, R.E. 1991: Flexible growth rates in nestling White-fronted Bee-eaters: A possible adaptation to short-term food shortage. *The Condor*, **93:** 591-597.

Freeman, S. and Jackson, W.M. 1990: Univariate metrics are not adequate to measure avian body size. *The Auk*, **107**: 69-74.

Hussel, D. J. T. 1972: Factors affecting clutch size in arctic passerines. *Ecological Monographs*, **42:** 317 - 364.

Janiga, M. 1986: Analysis of some of the conditions of growth of young *Columba livia* f. *domestica* in an urban agglomeration. *Folia Zoologica Brno*, **35**: 257-268.

Janiga, M. 1992: Allometry of nestling growth in the Feral Pigeon *Columba livia*. *Ornis Fennica*, **69:** in press.

Jolicoeur, P. 1963: The multivariate generalization of the allometry equation. *Biometrics*, **19:** 497-499.

Kramer, G. 1959: Die funktionelle Beurteilung von Vorgängen relativen Wachstums. *Zool. Anz.* **162**: 243-255.

Lack, D. 1954: The natural regulation of animal numbers. Oxford University Press, London.

Lebeau, B., Jolicoeur, P., Pageau, G. and Crossman, E.J. 1986: Asymptotic growth, egg production and trivariate allometry in *Esox masquinongy* Mitchill. *Growth*, **50**: 185-200.

Lindstedt, S. L. and Calder, W. A. 1981: Body size, physiological time, and longevity of homeothermic animals. *Quartemaly Review of Biology*, **56:** 1 - 16.

Lougheed, S.C., Arnold, T.W. and Bailey, R.C. 1991: Measurement error of external and skeletal variables in birds and its effect on principal components. *The Auk*, **108:** 436-432.

Magrath, R. D. 1989: Hatching asynchrony and reproductive success in the Blackbird. *Nature*, **339:** 536-538.

Mosimann, J.E. and James, F.C. 1979: New statistical methods for allometry with application to Florida Red-winged Blackbirds. *Evolution*, **33**: 444-459.

Novotný, I. 1970: Breeding bionomy, growth and development of young House Sparrow (*Passer domesticus*, Linné 1758). *Acta Scientarium Naturalium Academiae Scientarum Bohemoslovacae Brno*, **4**: 1-57.

O'Connor, R.J. 1978: Structure in avian growth patterns:a multivariate study of passerine development. *J. Zool., London*, **185:** 147-172.

O'Connor, R.J. 1984: The growth and development of birds. Wiley, Chichester.

Piersma, T. and Davidson, N.C. 1991: Confusions of mass and size. *The Auk*, **108:** 441-444.

Ricklefs, R.E. 1973: Patterns of growth in birds. II. Growth rate and mode of development. *Ibis*, **115**: 177-201.

Rising, J. D. and Sommers, K. M. 1989: The measurement of overall body size in birds. *The Auk*, **106:** 666-674.

Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, Ö. and Husby, M. 1984: On the adaptive value of intraclutch egg-size variation in birds. *The Auk*, **101:** 685-697.

Sokal, R.R. and Rohlf, F.J. 1969: Biometry. Freemen & Co., San Francisco.

Somers, K.M. 1986: Multivariate allometry and removal of size with principal component analysis. *Systematic Zoology*, **35:** 359-368.

Strauss, R. E. 1985: Evolutionary allometry and variation in body form in the South American catfish genus *Corydoras* (*Calichthyidae*). *Systematic Zoology*, **34:** 381-396.

Strauss, R. E. 1987: On allometry and relative growth in evolutionary studies. *Systematic Zoology*, **36:** 72 - 75.

Strauss, R.E. and Fuiman, L.A.1985: Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (*Teleostei:Cottidae*). *Canadian Journal of Zoology*, **63**:1582-1589.

Received 24 June 1992; revised 27 July 1992; accepted 3 August 1992