

## Allometry of nestling growth in the Feral Pigeon *Columba livia*

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The body structure of nestling Feral Pigeons does not develop uniformly throughout the nestling period. By applying intraspecific ontogenetic allometry I was able to distinguish the growth patterns in reduced broods. At fledging, nestlings from broods of two had significantly lower increments in the growth of body mass with respect to the skeletal index than the nestlings from broods of one. The growth of the pigeons was most effective during the second and third nesting attempts, which was best explained by the environmental conditions. The allometric analysis performed for body weights or wing lengths showed the progressive minimization of hatching asynchrony between siblings during development. In first hatched chicks the growth increments of tarsometatarsus length tended to be greater than in second hatchlings with the same level of skeletal index. The results for tarsometatarsus length confirm that tarsometatarsus size was affected and probably reflect sexual difference.

### 1. Introduction

Pigeons typically lay two eggs and rear two chicks. This pattern of reproduction characterizes all Columbidae species. Burley (1980) demonstrated that the relatively constant clutch size is limited by food demands during the early period of nesting developments, when the young are fed cropmilk. The mortality of the young is higher when their number is increased to three or more, which is correlated with earlier feeding of plant seeds (Dorzhiev 1985). In addition, Dorzhiev (1985) found that nestlings of enlarged broods grew more slowly. In this study, three variables are examined, which may correlate to the growth pattern of nestlings: hatching asynchrony, brood size and nesting attempts.

The greater the difference in the ages of the young in a clutch the greater is the chance that

they will differ in a growth pattern (Goodwin 1954). The two life history variables which are responsible for most instances of brood reduction in Feral Pigeons are hatching asynchrony and the death of one parent. With a difference in age of two days, some 60 % of the younger siblings die, and with a difference of six days, all the younger ones die (Dabert 1987). Under these circumstances, reduction in brood size is not a life history strategy at all, and merely reflects unequal competition between siblings for food and other parental care. Pigeons can, however, evict a nestling upon becoming a single parent (Burley 1980); this halving of parental duties is obviously of great importance and clearly suggests that Feral Pigeons use a brood reduction strategy (*in sensu* O'Connor 1978a) when under maximum stress. Both, hatching asynchrony and brood size can induce growth differences in young of Feral

Pigeons (Burley 1980, Dorzhiev 1985, Kelly 1987). The main aim of this allometric study was to examine the pattern of these differences.

The most important way of Feral Pigeon to increase their reproductive output in unfavourable urban conditions (diseases, high mortality, low life expectancy — Obukhova & Kreslavskij 1985) is to breed more often in the year, to prolong the breeding season and to shorten the interclutch interval (Johnson & Johnston 1989). In this study I also examined the relationship of the first four nesting attempts in pigeons to variation in the growth pattern of the young. These variables were chosen in an attempt to understand the possible significance of growth pattern lability in the young of Feral Pigeons. I mainly suggest that a labile growth pattern may be a response to seasonal differences in food quality (peas — summer, maize — winter; Janiga 1991).

I studied the growth pattern of nestlings by the method of ontogenic allometry (Janiga 1987). For example, a nestling on a lower allometric curve is characterized as underweight for its feather length or well-feathered (longer wing) for its body mass (O'Connor 1978b). The differential development of individual organs continues throughout the nestling period (Ricklefs 1975). As both the body weight and other organs may vary independently of the wing length, I use the skeletal index (Novotný 1970, Janiga 1987) as an independent variable to characterize the development of pigeon nestlings under different conditions.

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 favourable environment attain their peak of body weight more rapidly than nestlings living in a poorer environ-

ment, but the feather growth of the nestlings from a poorer environment occurs earlier relative to weight (Belskij 1947, 1948; see also Material and methods, Data collection).

## 2. Material and methods

Data for this study were collected at three field sites in Bratislava, Slovakia (about 48°N, 17°E). The first colony (ca. 60–70 clutches in a year) was studied from January 1981 to January 1982 and from January 1984 to July 1984. The second colony had approximately 260 clutches per year. Measurements of nestlings were made from January 1984 to January 1985. The third colony was situated near the first and the young were measured from January to July 1984.

Nests were checked once or twice a week, hatched chicks were colored and older nestlings were ringed with a combination of colored plastic rings, so that each individual was identifiable. In all the data comprise 579 hatchlings. Some hatchlings were excluded from the allometric analysis because they were of unknown origin (e.g. the first or second sibling in a nest) or died. Successive clutches were monitored at individual nest sites. During night visits, I noted the plumage pattern and color of the sitting females. A proportion of breeding adults, mainly those which were similar in plumage color and patterns, was color-ringed. The pigeons laid successive clutch in the same nest or the site of the previous clutch.

### 2.1. Data collection

As all the morphometric data were collected by me, variation due to difference in technique has been largely avoided. I recorded the hatching order in siblings at my first visit after the chicks hatched. I measured the length of the following skeletal indicators: the second, third and fourth toe, tarsometatarsus, tibiotarsus, femur, ulna, antibrachial skeleton, skeleton manus and head. I also measured the width of the head, and the width and height of the beak (for details see Janiga 1986).

The variable named "skeletal index" represented the sum (Klíma 1965, Maschlanka 1972)

of all 13 skeletal features named above. Each individual was weighed to the nearest 0.1 g with a Pesola spring balance. Wing length was measured by the maximum chord method (Svensson 1975). Each individual was measured to the nearest 0.1 mm with dial calipers.

The skeletal index was largely the bones of the head and legs and also the bones of the wing. The development of body weight (and tarso-metatarsus length also) is completed earlier than that of the skeletal index and the development of wing length is completed later than that of the skeletal index (see e. g. Kramer 1959). In nestlings from better environmental conditions, body weight has a higher growth rate and wing length a lower growth rate than in young from poorer conditions with the same level of skeletal index (Belskij 1947, 1948, Kelly 1987). As the tendency for "heavier young with shorter wings" correlates with fitness in pigeons (Janiga 1987), I call this type of growth pattern "optimal". There are also two theoretical grounds on which to defend the assumption that the skeletal index was the best possible measure of "true" nestling body size (see Freeman & Jackson 1990). First, 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. Second, 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. This parameter should be a biologically sensitive predictor of "average massiveness" within populations.

## 2.2. Developmental landmarks

The data were recorded at weekly intervals and between two "discrete" developmental events: hatching 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. I recognise 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 & Strauss 1986). Each individual was measured approximately three times; hence the interdependence among data points was equal in the groups compared. The multiple pairs of the data points (e.g. mass and skeletal index) were used to construct the allometric growth curve for each group.

## 2.3. Statistical methods and physiological age

My preference for a lognormal method ( $\log_{10}$ ) in linear regression is based on the reasons given by Jolicoeur (1963) and Mosimann & James (1979). For comparisons of groups, I applied the test for differences between two regression coefficients (Sokal & Rohlf 1969), the test for differences between two regression constants (Hátle & Likeš 1972) and overall ANCOVA (Šmelko & Wolf 1977).

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 (Lebeau et al. 1986, see Discussion). I mentioned above that the measurements were done between two ontogenic landmarks. The mean and mean variance of the independent variable (skeletal index) were calculated between the two landmarks for a selected group of young (e.g. from the first nesting attempts in a year). Ontogenic equivalence was approximated by using the one-way ANOVA to test the equality ( $P > 0.05$ ) between two means of the independent variables. Before proceeding with one-way ANOVA, tests of the equality of the two variances (Sokal & Rohlf 1969) were used to evaluate the equality of group variance of the data.

## 3. Results

### 3.1. Brood size and growth pattern

In nestlings from broods of two, body mass had a statistically significantly lower growth rate with

respect to the skeletal index than in nestlings from broods of one (Table 1). The results show a tendency for two young in a nest to be lighter for their skeletal size than young from broods of one. But at hatching the body weights were lower for lone chicks than for those from broods of two. The growth pattern probably reflected both the effective thermoregulation in larger broods and their higher food requirements during the later period of nestling life. The other allometric comparisons did not show significant differences in the growth pattern.

### 3.2. Growth pattern of siblings

Pigeons lay eggs asynchronously. Data in the literature show that pigeon embryos from second egg develop faster than embryos from first eggs (see Discussion) and, at hatching, the growth differences have been minimized. The allometric analyses simply show that the growth pattern did not differ between the siblings (Table 2). I did not find any significant differences in the growth of body mass or wing length between the siblings when the variables were related to the skeletal index. But the

Table 1. Comparison of growth statistics for young reared with a sibling (2) and alone (1). Tests for differences between two regression coefficients ( $F_b$ ) and between two regression constants ( $F_a$ ), one-way ANOVA of independent variable ( $F_x$ ) and ANCOVA (F). Data transformed to  $\log_{10}$ .

Independent variable	Dependent variable	$n_2$ $n_1$	Regression		$F_b$	$F_a$	$F_x$	F
			Coefficient	Constant				
Wing length	Body weight	257	0.94	0.42	1.85	2.19	0.57	0.48
		55	1.02	0.27	ns	ns	ns	ns
Skeletal index	Body weight	209	2.49	-4.2	11.8	13.0	0.62	9.08
		38	2.89	-5.2	$P < 0.001$	$P < 0.001$	ns	$P < 0.001$
Skeletal index	Wing length	640	2.32	-4.04	0.06	0.03	0.43	1.34
		108	2.30	-4.01	ns	ns	ns	ns
Skeletal index	Tarsus length	640	1.01	-1.18	2.49	2.78	0.43	2.24
		108	1.05	-1.29	ns	ns	ns	ns

Table 2. Comparison of growth statistics for the first (1) and second (2) hatched young in a nest. Tests for differences between the two regression coefficients ( $F_b$ ) and between two regression constants ( $F_a$ ), one-way ANOVA of independent variable ( $F_x$ ) and ANCOVA (F). Data transformed to  $\log_{10}$ .

Independent variable	Dependent variable	$n_1$ $n_2$	Regression		$F_b$	$F_a$	$F_x$	F
			Coefficient	Constant				
Wing length	Body weight	398	1.13	0.13	0.69	0.34	0.88	2.49
		287	1.11	0.15	ns	ns	ns	ns
Skeletal index	Body weight	296	2.51	-4.19	0.81	0.09	0.72	0.81
		224	2.49	-4.15	ns	ns	ns	ns
Skeletal index	Wing length	356	2.29	-3.98	0.03	0.05	1.16	0.53
		264	2.28	-3.95	ns	ns	ns	ns
Skeletal index	Tarsus length	356	1.03	-1.24	5.33	5.50	1.16	0.37
		264	0.99	-1.13	$P < 0.01$	$P < 0.01$	ns	ns

siblings differed significantly when their tarsi were compared. The first hatchlings tended to have higher increments in the growth of tarsometatarsus length for the same level of the skeletal index.

### 3.3. Nesting attempts

On average, the first nesting attempts were made in May, the second in June, the third in July and

the fourth in September. The young from the second and third broods grew better than those from the first and the fourth broods (significant differences in "body weight versus wing length", Tables 3 and 4). The feather (wing length) growth in the young from the fourth nesting attempts did not covary with the growth of the skeletal index or body mass in the same way as in young from the first through the third nesting attempts.

Table 3. Regression coefficients (b) and constants (a) of allometric equations ( $\log_{10}$ ) derived from morphological variables of nestlings from different nesting attempts in a year.

Independent variable	Dependent variable	Nesting attempt	b	a	Number of measurements
Wing length	Body weight	1st	1.06	0.25	369
		2nd	1.12	0.14	304
		3rd	1.18	0.04	104
		4th	1.01	0.38	31
Skeletal index	Body weight	1st	2.46	-4.05	315
		2nd	2.54	-4.26	175
		3rd	2.50	-4.15	81
		4th	2.52	-4.20	31
Skeletal index	Wing length	1st	2.31	-4.03	380
		2nd	2.28	-3.96	203
		3rd	2.28	-3.96	100
		4th	2.41	-4.34	37

Table 4. Comparison of the growth statistics for the young from different nesting attempts in a year. Tests for differences between two regression coefficients ( $F_b$ ) and between two regression constants ( $F_a$ ), one-way ANOVA of independent variable ( $F_x$ ) and ANCOVA (F). Data transformed to  $\log_{10}$ .

Independent/Dependent variable	Nesting attempts	$F_x$	P	$F_b$	P	$F_a$	P	F	P
Wing length/ Body weight	1st / 2nd	1.19	ns	4.22	<0.05	4.48	<0.05	0.26	ns
	1st / 3rd	0.47	ns	7.96	<0.001	8.02	<0.001	0.13	ns
	1st / 4th	0.003	ns	0.38	ns	1.02	ns	3.99	<0.05
	2nd / 3rd	0.003	ns	1.78	ns	1.71	ns	0.00	ns
	2nd / 4th	0.27	ns	2.12	ns	3.48	ns	4.66	<0.05
Skeletal index/ Body weight	3rd / 4th	0.18	ns	3.66	ns	4.99	<0.05	3.10	ns
	1st / 2nd	0.02	ns	2.34	ns	2.51	ns	0.90	ns
	1st / 3rd	0.60	ns	0.39	ns	0.32	ns	1.02	ns
	1st / 4th	0.30	ns	0.32	ns	0.34	ns	0.06	ns
	2nd / 3rd	0.39	ns	0.18	ns	0.26	ns	1.63	ns
Skeletal index/ wing length	2nd / 4th	0.21	ns	0.03	ns	0.03	ns	0.03	ns
	3rd / 4th	0.001	ns	0.01	ns	0.02	ns	0.46	ns
	1st / 2nd	0.10	ns	0.30	ns	0.21	ns	2.15	ns
	1st / 3rd	1.14	ns	0.18	ns	0.12	ns	1.43	ns
	1st / 4th	0.58	ns	0.63	ns	0.99	ns	11.3	<0.001
Skeletal index/ wing length	2nd / 3rd	1.53	ns	0.00	ns	0.00	ns	0.001	ns
	2nd / 4th	0.85	ns	1.19	ns	1.56	ns	7.40	<0.001
	3rd / 4th	0.01	ns	1.33	ns	1.35	ns	6.12	<0.01

#### 4. Discussion

One important goal of biological morphometry is the quantitative comparison of organisms as ontogenic trajectories that react to short-term ecological effects (Strauss & Fuiman 1985). To attain this we need an operational basis for treating different life stages within the same mensural scheme. The concept of physiological age may often be more suitable than chronological age or physical time (Lebeau et al. 1986). Due to genetic, physical or environmental fluctuations, the degree of development may correlate poorly with physical time. 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 the 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 technique, for example PCA (Lebeau et al. 1986), may extract more variance, revealing more variation in growth than techniques using age.

Pigeon chicks grow fast. A nestling measured in the morning and one measured in the evening of the same day may differ in the body size, though they may be of the same age, when age is measured in days. On the other hand, the young may differ in age but the features of their development (e. g. bone lengths) may be the same. This study suggests ontogenic equivalence between the measured characters (independent variables), but the study is based on the long-established knowledge (Belskij 1947, 1948, O'Connor 1978b) that proportional differences must exist among growing organs as a result of genetic, physiological or environmental variation.

Feral Pigeons show considerable variation in their growth pattern. This study suggests that the type of variation is adapted to overall breeding tactics of adults (Janiga 1987). The allometric differences confirm that a single offspring in a nest developed better in the second half of nest care. Offspring mortality is greatest during the first days of life (Burley 1980), and the consequent decrease or active brood reduction should lead to more effective growth (O'Connor 1978a).

The abundance of food that young from broods of one received and the delayed fledging are factors that would make these fledglings larger and more likely to survive (Belskij 1947, Kelly 1987). A single chick may also be fed by both parents and therefore grows more quickly (Levi 1957).

At the start of nest care, the growth pattern probably reflects the advantage of social thermoregulation. If the nestlings can conserve heat more effectively by huddling together, the more favourable surface-mass effect in broods of two offspring may reduce the energy costs for maintenance (Kotov 1978, O'Connor 1978a). Young birds in broods of two may be able to produce enough heat for endothermy earlier than in broods of one (see Dunn 1976, 1979).

Feral Pigeons lay the second egg from 24 to 72 hours after the first (Kotov 1978, Dorzhiev 1985). The second egg may sometimes hatch at the same time as the first egg (Kotov 1978). Angalt (1978) observed that an interval of three days between the laying of the first and second egg corresponded to an interval of one day in hatching. At hatching, the differences in the development of young are reduced to a minimum, and I showed in this study that the siblings did not differ in their growth pattern during the nest care.

The sibling differences in the growing tarsometatarsus length versus skeletal index probably indicate sexual differences in the nestlings. The two eggs which a Feral Pigeon lays are almost always cock and hen, the cock being almost always the first (higher increment in the growing tarsometatarsus). Kotov (1978) reports that in 98 first laid eggs, the ratio of males to females was 69 to 29. The second eggs produced more hens, the ratio being 34 males to 54 females (88 hatched). His study showed that of the 29 unisexual clutches, 17 produced two males while 12 produced two females. In Bratislava, the adult males had significantly longer tarsi (mean = 34.6 mm) than the adult females (33.3 mm, Janiga 1987). The allometric analysis performed for body weights showed that the weight increments were independent of hatching order. The results for nestling wing lengths parallel this, confirming that size (tarsometatarsus) was affected and not just fat or other metabolic reserves.

Peas and wheat were the main spring-summer food items of Feral Pigeons in Bratislava (Janiga 1987). The allometric comparisons parallel this, showing that during the second and third nesting attempts were probably better conditions for the growth of nestlings than during the first or fourth attempts. In Bratislava, pigeons produced between one and eight clutches per pair in a year, the later broods dying or being proportionally unimportant for reproductive output (Janiga 1987). The growth of the birds described in the form of body weight versus wing length reflected the influence of exogenous factors, most likely because of the seasonal change in food. Independent covariance of the wing length versus the skeletal index or body weight suggests that in the fourth brood feather growth is an independent parameter, which can be separately adjusted to ecological pressures. Sunflower seeds (change from proteins to lipids) comprised the bulk of the diet in the fall (Janiga 1987).

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## Selostus: Kesykyyhkyn poikasten kasvu

Kesykyyhkyn poikasten ruumiinrakenne ei kehity tasaisesti pesäpoikasaikana. Kahden poikasen pesissä poikaset olivat luuston kokoon nähden kevyempiä kuin ainoina poikasina kasvaneet. Poikasten painon tai siiven pituuden allometrinen analyysi osoitti asynkronisesta kuoriutumisesta johtuvien kehittyneisyserojen häviävän kasvun aikana. Ensimmäisenä kuoriutuneiden poikasten jalka (tarsometatarsus) on pitempi kuin samankäisten toisena kuoriutuneiden poikasten jalka. Ero heijastanee sitä, että ensimmäiset poikaset ovat useammin koiraita kuin toisena kuoriutuneet poikaset.

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