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Environmental aspects of phenotypic plasticity in the growth and development of semi-altricial and altricial birds

Commentary on the published papers

M. JANIGA
Institute of High Mountain Biology, Tatranka Javorina 7, SK-059 56, Slovakia, e-mail: janiga@uniza.sk

Recent comparative analyses of growth in birds have shown that a large portion of variability in growth parameters is found below the level of the species, that is, growth variables often vary more within a species than between species within a genus or family.

In the present studies, I summarize the knowledge on phenotypic plasticity of young of some semi-altricial and altricial birds. The phenotypic responses of growth to differences in „environment" have been investigated in groups of birds of the same species reared under different external conditions. Measurements and allometric comparisons of growth parameters between individual chicks within group of siblings or between different broods consequently enabled me to determine the „quality of environment". The goal of this review is to summarize the concept of heterochrony and allometry in the growth studies of semi-altricial and altricial birds, and mainly to illustrate how the technique has been applied to investigate environmental processes. Throughout, I have emphasized the distinctions among methodological frameworks for both intrinsic and extrinsic time studies on bird development.

Postembryonic development and measurement of time

The 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. Two concepts, heterochrony and allometry (Klingenberg 1998) have been used extensively to study the trajectories in a variety of bird species. Both concepts deal with different aspects of ontogenic curves. Heterochrony is concerned with changes in the rates and timing of developmental processes, and therefore incorporates 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, Badayev 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). Size measures can be single measurements (Klingenberg 1998) such as body length or mass (Vízyová and Janiga 1987 - Figs. 7,8; Janiga 1986), or composite measures such as first principal component scores (cf. Janiga *et al.* 1993 - Tab.1; O'Connor 1978a, b). Angles (Paliesková, Janiga and Kocian 1990 - Figs. 2,3; Vízyová and Janiga 1987 - Fig. 6) or ratios of lengths can serve to quantify shape, and multivariate techniques offer a variety of composite shape measures (O´ Connor 1978b). The age scale is calibrated with a measure of physical time (measured usually in days). In this kind of studies, time is always the independent variable. The choice of a metric for time, however is more problematic because alternative measures of age focus on fundamentally different aspects of the passage of time for an organism (Strauss 1987). In altricial and semi-altricial birds, the age (physical time) does not increase lineary 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, Janiga and Kocian 1990 - Fig. 1, Janiga *et al.* 1993). Moreover, in many studies, especially in fossils (Klembara and Janiga 1993) or when the birds are sampled in the wild and great distances exist between nests or colonies (Janiga 1992a), the age data are not available. 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.

Concepts of intrinsic and extrinsic time

Extrinsic time, or astronomic time is independent of an organism´ s condition or environment, but the rates of biological processes measured on this time scale may fluctuate within growing birds according to conditions (cf. Janiga 1986). The time was discussed in the previous paragraph. Intrinsic time measures time with reference to processes within the individual birds. The simplest expressions of intrinsic time are stages defined by discrete events - developmental landmarks (Creighton and Strauss

1986, Rohlf and Slice 1990), such as hatching, attainment of the peak weight during the postnatal development, emergence of the first quills on the alar tracts (Janiga 1992a,b,c; Starck 1993). In my studies, I examined the modifications of the growth pattern at the most intensive increments of the parameters investigated assuming that these modifications would reflect intensively the influence of environmental or breeding constrains. I recognize that the characterization of these events as discrete is arbitrary, however they represent unambigous observable landmarks in the development (Starck *et al.* 1995). Physiological time is most commonly used to control for the influence of environmental factors in intraspecific studies (Lindstedt and Calder 1981; Strauss and Fuiman 1985; Sinervo and Doyle 1990), and the chronological time is usually substituted by size as a measure of intrinsic time (Strauss 1987). 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 the skeletal measurements and as temporaly nutrient reserve - independent size of a bird (Piersma and Davidson 1991).

Concept of skeletal size

Univariate metrics like body mass or plumage length are not adequate to measure body size because they fluctuate daily, seasonally, or even hourly in growing chicks, depending upon variables such as time since feeding, weather, nutritive value of food, effects of pollutants in the diet, etc. (O´ Connor 1984, Janiga 1985, 1991a, Janiga *et al.* 1990, Price 1991). In my studies, I used the combination of external skeletal measures which best predicts actual body size and may be commonly employed by field biologists (Nishida *et al.* 1985, Janiga 1986, 1991b, 1992a,b,c, Vízyová and Janiga 1987). A parameter composed as sum of (Kramer 1953, Novotný 1958, Klíma 1965, Maschlanka 1972, Janiga 1992a,b) or as PC1 vector (Janiga 1992c) of many bone measurements summarizes the amount of total attachment surface available for muscle and connective tissue, and also the amount of support structure for internal organs (Freeman and Jackson 1990, Smith 1998). Growth in birds provides a clear example of separate dynamics for different structures, whereas head and leg measurements reach an asymptotic value relatively early, the wing bones continue to grow longer (Kramer 1959, Novotný 1970, Boag 1984, Carrier and Leon 1990, Bogdanovych 1996). Such functional development also varies among muscle groups ((Ricklefs *et al.* 1994, Choi and Ricklefs 1997). There is also another theoretical ground on which to defend the assumption that the „skeletal index" is the useful measure of „true" nestling body size. The parameter is composed of many different skeletal characters, and it is less prone to variance caused by developmental characteristics or measurements error in a single character (Paliesková, Janiga anf Kocian 1990 - Fig. 1, Lougheed *et al.* 1991). In addition, skeletal index serves as a developmental stage which must be identified as homologous (Blackstone 1987c, Klingenberg 1998) among the groups of birds being compared, at the interval between two developmental landmarks. For this purpose, the ontogenic equivalence of the size vectors between groups was statistically tested by analysis of variance (e.g. Janiga 1992c).

Concept of „optimal growth"

One important point of my studies was to compare ontogenic trajectories of nestlings in respone to short-term environmental changes. When calibrated between two or more pooled groups of birds, the skeletal index provided a standart measure against which growth of body weight and plumage length were compared. The logarithmic transformation of the data was used, because it preserved allometries, standardized variances, and produced a scale-invariant covariance matrix (Jolicoeur 1963, Strauss 1985). Jolicoeur's (1963) concept of multivariate allometry uses the first principal component of the covariance matrix of log-transformed variables to characterize the patterns of allometric variation. The first PC is the normalized linear combination of log/transformed variables which maximizes the proportion of total variance accounted for, and can therefore be seen as a line of best fit to the data points (Pimentel 1979). The first PC score of an individual indicates its position along that line (Klingenberg & Zimmermann (1992). For most ontogenic data sets, the model of simple allometry fits well, and the model of a linear growth trajectories in the space of log-transformed characters can therefore be used to compare the growth of different groups of young (Klingenberg and Froese 1991, Smith 1998). In nidicolous birds, the development of body weight is completed earlier than that of the skeletal index and the development of wing length is completed later than that of the index (see e.g. Kramer 1959). Inclusion of body mass and feather length with a set of skeletal variables in a morphometric analysis produces indices that reflect, to a large extent, the environmental conditions (usually nutritional status) of the animal (Alisauskas and Ankey 1990, Cooke *et al.* 1990). 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 (Beľskii 1947, 1948, O´ Connor 1978b, 1984). As the tendency for „heavier young with shorter wings" correlates with positive fitnees in semi-altricial (Janiga 1991b,c, 1992b, Janiga and Žemberyová 1998) and altricial birds (Novotný 1970, Janiga *et al.* 1993), I call this type of growth pattern „optimal". Extending the concept of simple „linear" allometry (e.g. Janiga 1992b) to multiple PCA measurements is fairly straightforward. The method separates size and size-related variation in proportions of skeleton, wing length and body mass, from other, size-independent variation which mainly contrasts nestling weight with the feather length (O´ Connor 1978b, Janiga 1992c, Janiga *et al.* 1993). This is desirable if a researcher attempts to correct for growth variation when comparing two or more groups.

Static allometry and phenotypic plasticity of eggs

Allometry differs fundamentaly from heterochrony in that it does not explicitly include the dimension of time (extrinsic as well as intrinsic) in the analysis

(Blackstone 1987a, b, Rohlf and Bookstein 1987). In this context, the domain of allometry is purely morphological and concerns measures of size and shape (Jolicoeur and Mosimann 1960, Mosimann and James 1979, Klembara and Janiga 1993). For morphology, allometry implies that there is some shape associated with increase in size. The absence of size-related shape variation is isometry. Thus allometry is an association between shape and size, whereas isometry is their stochastic independence (Mosimann 1970).

Association of changes in egg size and shape, early development and life history have been reported in many species of birds (Coulson 1963, Schifferli 1973, Pikula 1976, Janiga 1986). Extending a concept of egg indices or simple linear regression and correlation coefficients (Palieskovà, Janiga and Kocian 1990) to multivariate statistics enabled to find a significant axis of egg shape that was independent of and statistically orthogonal to egg size. The variables (egg length and width) used in PCA were isometric (Janiga 1996), and they consequently provided the data (scores) for examining of influence of numerous factors on egg shape and size variation separately (Johnston and Janiga 1995, Janiga 1996, 1997).

Egg size and shape - indicators of early development

1.Size. Associations of changes in egg size and phenotypic characters of females have been reported in many semi-altricial and altricial species of birds. I found that variation in eggshell size is related to variation in age, fertility, phenotype (Janiga 1996), behavioural activity (Palieskovà, Janiga and Kocian 1990) of females. The major exogenous influence is probably to be quality of food (Janiga 1991a - Table 5), which induce size differences among local sites or at different times of the year (Janiga 1996,1997). In various species of birds an increase in eggshell size is accompanied by proportional increase in the amount of albumen in the egg; size of the yolk increases less than size of the shell. Higher proportion of protein in eggs accelerates growth of the embryo (for summary see Chapter 6 in Johnston and Janiga 1995). Too large or very small eggs are indicators of poorer quality of ovulation processes in females (Baumgartner 1990), but hatchlings from larger eggs usually grow faster and reach larger maximum weights (Schifferli 1973, Mänd 1985, Janiga 1986 - Fig. 4). Moreover, large egg size may be correlated with phenotype (size) of parent birds (Pikula 1976), and their ability to feed the young (Janiga 1991a - Table 5).

2. Shape. Egg length in semi-altricial and altricial birds tends to be a more flexible variable than the egg of width (Pikula *et al.* 1981, Palieskovà, Janiga and Kocian 1990, Janiga 1996,1997), which is perhaps a reflection of oviductal dimensions and the amount of albumen in the egg (Ricklefs and Marks 1983). I found in pigeons that the eggs from winter were as large as summer eggs, but the eggs differed in shape. Winter eggs were long and thin while summer eggs were short aand wide (for details see Johnston and Janiga 1995). The length more contributed to egg variability than width. Moreover, eggs of pigeons were significantly elongate in northern Eurasia, and fat at southerly stations. Variation in climate (temperature) is likely to cause variation in egg shape. This variation seems to occur independently of variation in food supply. The second very important variable correlated with egg shape is laying sequence. In this case, the shape of eggs is a sensitive indicator of egg physiology, and the ability of the later laid embryo to accelerate growth during incubation. A summary of the egg morphometry in the light of egg contents and physiology is discussed in chapter 6.6 in Johnston and Janiga (1995).

Morphologic plasticity of hatchlings

There exists a general correlation between the size of the egg laid and the weight of the chick hatched from it (O´ Connor 1984), but only few studies rely on differences of shape in hatchlings. As the present investigations show, allometry - „skeletal size *versus* body weight" - effectively distinguished shape variability in hatched young (Johnston and Janiga 1995 - Fig. 9.11.) I noted above that chicks reared in unfavourable conditions (e.g. in winter) usually origin from more elongated eggs. Embrya are adapted to fast growth, but the incubation periods are longer in cold than in hot periods. Greater body weight relative to skeletal size of „winter" hatchlings than the weight of hatchlings from hot laying days indicates that young from unfavourable nesting period hatch older and more well-developed than chicks from hot season.

Morphologic plasticity of nestlings

Local environmental factors (seasons, parasites, nest locations) may alter body size and shape of young of altricial and semi-altricial birds. Consequently, phenotypic plasticity in nestling size and shape may produce „new morphologies" in response to variable environmental pressures and thus create patterns of local intraspecific morphological diversity. The objective of these sumarized studies was to show that examination of „morphologies" or growth trajectories of bird nestlings may be a good way to estimate the quality of environment in which birds survive (Janiga 1992b, Morbey and Ydenberg, 1997, Johnston and Janiga 1995, 1999). Moreover, the pattern of growth is adjusted to correspond to overall breeding tactics of a species, and thus it serves as very useful method to describe the asynchronous hatching or brood reduction strategies in birds (Janiga 1986, 1992 a, c, Johnston and Janiga 1995 - page 106). Finally, the techniques measuring the growth pattern in birds enable clear comparison of developmental modes between different species of birds (Janiga *et al.* 1993).

The developmental morphometric features of eggs and nestlings of altricial and semi-altricial birds may serve as suitable parameters for the determination of the quality of surrounding environment.
Intraspecific differences in the size of eggs indicate the quality of trophic conditions while the shape of eggs is related to variation of climate, independent on food supplies. Thus, suitability of a breeding habitat for a species may be simply calibrated by egg morphometry.

Heterochronic intrinsic analysis of growth pattern of nidicolous birds seems to be another poverful tool for determination of the quality of environment. This, in turn, allows to differentiate colonies, habitats, intensities of infestation by parasites, and of course, species. Moreover, the model of optimal growth (body weight increases more rapidly and feather growth less rapidly relative to skeletal size) proves to be useful method in distinguishing developmental strategies such as clutch adjustment or brood reduction.

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