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PORTMANN'S RULE OF PRECEDENCE AND THE EVOLUTION OF ENCEPHALIZATION IN BIRDS (AVES)

J. MLÍKOVSKÝ

Department of Evolutionary Biology, Czechoslovak Academy of Sciences,
Na Folimance 5, CS-120 00 Praha 2, Czechoslovakia

According to the so-called Portmann's rule of precedence, an evolutionary change in ontogenetic type is a prerequisite for evolution of high encephalization in birds and mammals. This rule is studied in birds, corroborated at the phenomenological level, but rejected as a causal explanation of the observed pattern.

Key words: encephalization, Portmann's rule of precedence, Aves, ontogeny and evolution

During 1920/1930s, a few of the prominent evolutionary biologists of that time started to study the relations between ontogeny and phylogeny (e.g., Garstang 1922, Franz 1927, Severcov 1927, 1935, Schindewolf 1929, Šmal'gauzen 1938). Although they did not reach any generally acceptable results, they opened by their investigations a new field of research and created the basis for all future investigations of this important problem, which has still not been satisfactorily solved (see Mirzojan 1963 and Gould 1977 for critical historical reviews), and which now attracts much attention (cf. Siewing 1979, Bonner 1982, Goodwin et al. 1983, Mlíkovský and Novák 1985).

The famous Swiss zoologist Adolf Portmann envisaged already in 1930s, probably without any knowledge of theoretical papers written by the above mentioned evolutionists, that evolution and ontogeny are interrelated, when he studied on the one hand the comparative ontogeny of birds, and on the other one the brain size and encephalization in them. He noticed (1) that birds of different groups are born at very different stages of ontogeny, from mature state in "nidifugous" birds to immature state in "nidicolous" ones, (2) that between individual groups of birds there are great differences in the level of their encephalization, and (3) that all birds with high levels of encephalization belong to the nidicolous ontogenetic type. Since he considered the nidifugous state to be ancestral in birds, he concluded that a change in ontogenetic type is a prerequisite for an evolutionary increase of encephalization (Portmann 1935, 1942, 1948, 1950, 1951, 1952, 1962). In 1952 he called this hypothesis *rule of evolutionary precedence of ontogeny* ["Regel der evolutiven Präzedenz der Ontogenese"], what Gould (1977) abbreviated as Portmann's rule of precedence.

I tested this rule of precedence in birds using my own data on avian encephalization (Mlíkovský 1984) and Nice's (1962) and Ricklef's (1983)

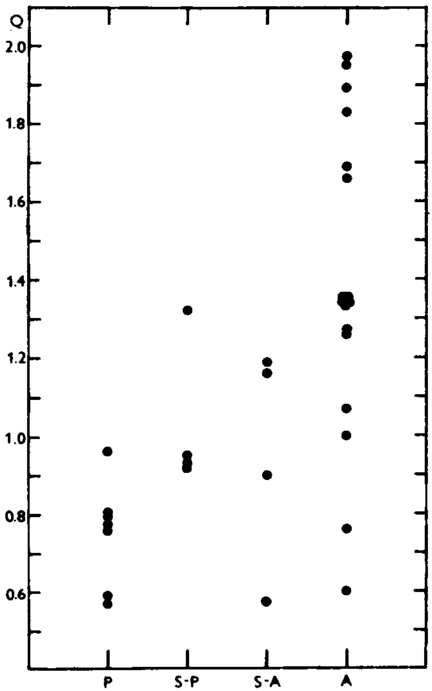

Fig. 1. Relation between the ontogenetic type and the level of encephalization (Q) in birds. See Table 1 for explanation and exact data.

TABLE 1

Level of encephalization (after Mlíkovský 1984) and ontogenetic types (after Nice 1962 and Ricklefs 1983) in 34 families of birds. P = precocial, S-P = semi-precocial, S-A = semi-altricial, A = altricial ontogenetic type. Sequence of families follows Storer (1971).

Family	Level of encephalization	Ontogenetic type
Podicipedidae	0.588	P
Spheniscidae	1.321	S-P
Procellariidae	0.949	S-P
Anseridae	0.805	P
Ardeidae	0.904	S-A
Ciconiidae	0.566	S-A
Cathartidae	0.757	S-A
Accipitridae	1.162	S-A
Falconidae	1.192	S-A
Phasianidae	0.569	P
Rallidae	0.793	P
Gruidae	0.489	P
Otididae	0.773	P
Charadriidae	0.958	P
Scolopacidae	0.758	P
Laridae	0.920	S-P
Alcidae	0.932	S-P
Columbidae	0.598	A
Psittacidae	1.952	A
Cuculidae	1.003	A
Strigidae	1.661	S-A
Alcedinidae	1.071	A
Bucerotidae	1.339	A
Picidae	1.975	A
Turdidae	1.350	A
Sylviidae	1.340	A
Paridae	1.264	A
Nectariniidae	0.720	A
Corvidae	1.892	A
Ploceidae	1.354	A
Estrildidae	1.270	A
Fringillidae	1.827	A
Parulidae	1.686	A
Emberizidae	1.340	A

classification of avian ontogenetic types into precocial (= nidifugous), semi-precocial, semi-altricial, and altricial (= nidicolous) ones (see Tab. 1, Fig. 1). Figure 1 shows convincingly that Portmann's rule of precedence is sound in birds. Exactly as predicted, low levels of encephalization were found in all four ontogenetic types, and only true altritial birds reached also higher levels of encephalization during evolution. Of interest is to note here that the two semi-precocials with the highest encephalization, Spheniscidae and Procellariidae, were classified as semi-altricials by Nice (1962) and only recently transferred to semi-precocials (Carey et al. 1980, Ricklefs et al. 1980; but see Williams et al. 1982).

Having thus confirmed Portmann's rule of precedence in birds at a phenomenological level, we have to start a search for its explanation. In birds, the relative brain size is determined in ontogeny by (1) the relative size of brain anlage, (2) the relative brain growth rate, and (3) the relative duration of brain growth; all related to the whole body size, expressed as weight in our case (Mlíkovský 1985). In spite of the fact that there is practically nothing known about the size of the brain anlage in birds, it is difficult to imagine how it could be influenced by different levels of maturation at birth.

The relative brain growth rate does not seem to be influenced by ontogenetic types as well. This rate may be calculated as a slope of a regression line between brain size and body size in neonatal birds (Mlíkovský 1985). Thus, Figure 2 testifies clearly against the role of the relative brain growth rate in evolution of higher encephalization in altricial birds. This agrees with the fact that altricial birds spend (allometrically analysed) similar time in egg as precocial ones (Rahn and Ar 1974, Ar and Rahn 1978), and that brain growth rate is heavily influenced by various environmental factors, especially during postnatal growth (see Mlíkovský 1982 for review).

However, this only ontogenetic mechanism which can hypothetically account for Portmann's rule of precedence is the different relative duration of brain growth. However, this still does not mean that this difference is caused by the evolution of the altricial ontogenetic type in birds. Certainly, do not see any possibility how these two things could be causally related. The point is that this might be the situation that Koller (1963)

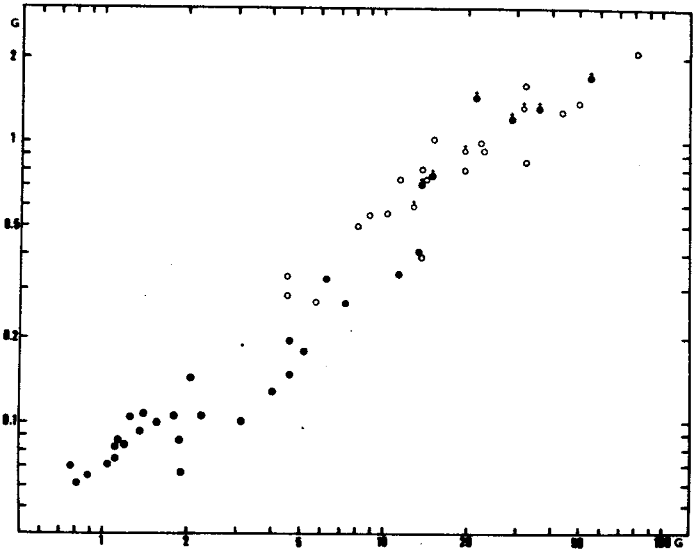

Fig. 2. Relation between brain weight (y-axis) and body weight (x-axis) in neonatal birds. Log-log scale. Data from Portmann (1947), Pegel'man and Lysov (1971) and Sazikova (1975). Full list of the data is given in Mlíkovský (1984). ● = altricial birds, ⁺● = semi-altricial birds, ⁺○ = semi-precocial birds, ○ = precocial birds.

calls community correlation ["Gemeinsamkeitskorrelation"], i.e. a case whan there is a certain observable relation between two things which is caused by a causal dependence of the two on a third thing.

I believe that the latter is the most probable explanation of the Portmann's rule of precedence. The common third thing could be the moment in which, by chance, altricial ontogenetic type and high encephalization appeared during evolution. This may be indirectly envidenced as follows: (1) It is commonly accepted that ancestral birds were precocial (e.g., Portmann 1938, 1950, 1955, Nice 1962, Ar and Yom-Tov 1978, Ricklefs 1983), similarly as it is evident that ancestral birds had relatively low encephalization (cf. Mlíkovský 1984). (2) It seems obvious that the evolution of ontogenetic types is related to various ecological factors (Nice 1962, Ricklefs 1983) and the same is true for the evolutionary increase of encephalization (Mlíkovský 1982, 1984), although the ecological factors involved are mostly different. In any case, however, it seems probable (Mlíkovský 1982, 1984) that encephalization increases in evolution only during evolutionary transitions between adaptive zones (see Mlíkovský 1983 for an analysis of this notion). The same may be true for the evolution of the derived (i.e. altricial) ontogenetic type. Then it is a matter of chance when such transitions coincide which cause both the change in the ontogenetic type (from the ancestral = precocial to the derived = altricial one), and the increase in encephalization. Although this null hypothesis is not expressible in exact mathematical terms so far, and hence cannot be tested statistically, I believe that no data indicate at present any deviation from it; this all despite of the fact that the Portmann's rule of precedence seemed at the first glance to have an excellent support in the data presented in the Table 1 and the Figure 1.

We may then conclude that a change in the ontogenetic type is not a necessary preadaptation for the evolution of high encephalization, as believed by Portmann in his rule of precedence. A similar conclusion (though on other grounds) has been achieved also by mammaliologists studying this problem (see Müller 1969, 1972 for review).

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