===== **ZOOLOGY** =====

Allometry of Reproduction in Poikilotherm and Homoiotherm Vertebrates

V. R. Dol'nik

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia
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Abstract—A comparison of 26 allometric empiric equations relating animal body weight and progeny weight, size and weight of the clutch, as well as the accompanying processes in various classes of vertebrates has revealed a principle of large-scale transformation specific for poikilotherms and two others specific for homoiotherm birds and mammals. The appearance of huge terrestrial eggs in reptiles and the transition from R-strategy to k-strategy was not accompanied by a rearrangement of the poikilotherm principle of reproduction pattern. Such rearrangement was required after the appearance of homoiotherm embryo and obligate parental care.

INTRODUCTION

Most animals without parental care put almost all reproductive energy (RE) reserved by natural selection into eggs, i.e., their production (P). Establishing production in various animal groups under different ecological conditions has considerable theoretical and practical value, and, accordingly, the data published on it are tremendous. The "Productive" problem can be solved from the weight of complete clutch and specific calorific value of the eggs (Vinberg, 1976), and, hence, allometric structure of production usually is not further analyzed in detail. One of its components—the progeny volume—is analyzed in terms of demography (fertility and death rates, etc.) while another component—the starting weight of a progeny—is a subject of growth theory.

Long ago, ornithologists realized that there is no equality between RE and P for their subjects: a portion of RE is spent to create the clutch (it can be easily determined) while another unknown portion is spent on various activities related to parental care and dissipated as heat. A development of assays on energy expenditure for protecting nesting area, nest building, clutch incubation, fledgling, and brood driving was the most interesting and instructive stage in ornithology of recent decades (reviewed in King, 1973; Ricklefs, 1974, 1983; Rahn *et al.*, 1975; Kendeigh *et al.*, 1977; Drent and Daan, 1980; Walsberg, 1983; Dol'nik, 1971, 1992, 1995a). The energy put into eggs ranges from 5 to 25% the total energy expenditure for reproduction in a pair of various avian species. Allometric generalizations of the relationships between various reproductive indices and the parents body the weight, egg weight, and weight of a nestling (starting or completed growth) revealed a ravelment of *a priori* unpredictable relationships, mostly due to the hypometric weight relationship between the egg and parents (Weathers, 1992;

Drent *et al.*, 1992; Dol'nik, 1992, 1995b; Dol'nik and Dol'nik, 1994).

One way to get out of this problem is to use the allometry of a "sister" homoiotherm class of mammals and ancestor classes of vertebrates, primarily, reptiles. Analysis of the equations for all vertebrate classes has revealed a pronounced allometric relationships never discussed before, which became the subject of this publication.

MATERIALS AND METHODS

Reliable empirical allometric equations were to be used as the material. Due to the "productive" approach, the allometry of the egg weight, the number of eggs in the clutch, and the weight of complete clutch were virtually not analyzed separately, despite being the most informative. Fortunately, Blueweiss *et al.* (1978), with quite another aim in mind (to clarify different lifespans), calculated the equations of concern.

Equations of Blueweiss are quite representative and not outdated for fish and mammals, since they are based on comprehensive reports covering the whole range of size and many species. In particular, the allometry of a newborn mammal weight was calculated later by Rahn (1982) from considerably more material, and the resulting equation did not reliably differ from that of Blueweiss. In the case of birds, Blueweiss' report was quite reliable (Heinroht, 1922); however, more modern equations covering 809 species can be presented as well (Rahn *et al.*, 1975; Rahn, 1982; Dol'nik and Dol'nik, 1982).

In the case specifically concerning reptiles, Blueweiss' equations were calculated for 37 species covering all size ranges of the class. We found data on an additional 30 species within the same size range. The equations calculated from these data do not reliably differ from Blueweiss' equations; the equations based on

the joint data were not reliably different as well. Hence, we use Blueweiss' equations for reptiles; however, they are now based on 67 species.

The situation is different for amphibians: the data are scarce and the size range is so short that the equation cannot be calculated with a reliable exponential factor. In the Blueweiss' report, all five data on amphibians are close to the fish regression curves. We found seven more published data appearing in the same range. In such a situation we can only accept the fish exponential factors for amphibians. One should keep in mind that the regression curves of these equations are empirical by the level and specified by the slope.

Allometry

Scale conversion = scaling = allometry of a particular character of the organism (y) as a function of the animal body weight (m) within the size range of a high rank taxon (from type to order) is usually adequately described by exponential equations:

$$y = am^b, \tag{1}$$

where a is a value of the character at $m = 1$, and exponential factor b is a slope of regression curve of the equation plotted in logarithmic scale. Coefficients a and b are determined empirically by the least square calculation from the data on the character value in species with different body weight. On the basis of geometrical transformations, the empirical value of b is called similometric, hyper-, or hypometric if it is similar, higher, or lower than the expected value, respectively (Stahl, 1962; Wilkie, 1977; Shmidt-Nielsen, 1987). These terms can also be applied when the character is compared to some physical law or other characters defining the "slope" of the tested character (e.g., the relationship between body weight and standard metabolism) rather than the specimen geometry.

Metabolic processes in animal organisms are hypometric to their mass (usually in various classes with b ranging from 0.67 to 0.83); hence, it is not easy for them to provide energy and nutrients for processes such as growth and reproduction, which upon completion should restore similometry between the parent body weight and the definitive offspring weight (Peters, 1977). The specific (per body weight unit) power of metabolism (with dimensions of speed) features an exponential factor b ranging from –0.33 to –0.17 in animals of various classes. Hence, the time it takes the animal metabolism to do the work proportional to their own weight ("biological" or "metabolic" time) is proportional to their weight raised to the power ranging from 0.33 to 0.17; i.e., it depends on the size of the animal (Calder, 1974; Stahl, 1962; Shmidt-Nielsen, 1987).

Allometry of Single Progeny

It seems quite easy to preserve complete similarity between species with different body sizes. For instance, the size proportion between a newborn progeny (or its egg) and a parent should be similar in both large and small animals, i.e., the exponential factor of the relationship between newborn (m_n) and adult body weights (m_{ad}) should equal 1.0. Moreover, it is true in the class where we belong that there is direct relationship between the weights of a newborn and its mother (Blueweiss et al., 1978):

$$m_n, \mathrm{g} = 0.097 m_{ad}^{0.92} \tag{2}$$

(0.92 the exponential factor does not reliably differ from 1.0). However, such occasions are rare in nature. In all other studied animal classes there is hypometric relationship between the weights of a progeny and female, i.e., b is below unity.

Aquatic Egg of Poikilotherms

In poikilotherms that lay eggs in the water (crustaceans, fish, amphibians, etc.), the relationship between the egg and female weights has the exponential factor in the 0.24–0.70 range, being 0.5 on the average (Blueweiss et al., 1978).

The hypometry of the aquatic egg was never specifically considered; however, one possible explanation is quite simple and results from the interaction between two counter pressures of natural selection. On one hand, the egg is a cell, and cell size in animals does not depend on their size (i.e., they are proportional to m_{ad} raised to zero power); on the other hand, it is a primordial organism and it is desirable to compose the same size fraction of adult size (i.e., it should be proportional to m_{ad} raised to unity power). Counter selective pressures lead to a compromise, and the exponential factor appears somewhere between zero and unity; when both pressures are equally strong it holds an intermediate position around 0.5.

Fish. In fish weight, the proportion between the egg (m_e) and female body (m_{ad}) has an exponential factor of around 0.5 (Blueweiss et al., 1978):

$$m_e, \mathrm{g} = 0.00059 m_{ad}^{0.43}. \tag{3}$$

Amphibians. Apparently, amphibians preserved the same relationship (3).

Terrestrial Egg of Poikilotherms

The transition to terrestrial reproduction in both insects and reptiles was accompanied by a sharp increase in the egg size, since it should be protected by envelopes and completely supplied by nutrients, salts, and water accounting its loss by evaporation.

Reptiles. Despite a weight increase of hundreds times relative to amphibians of a similar size, the reptil-

ian egg preserved the same poikilotherm relationship pattern as the female weight (Blueweiss *et al.*, 1978):

$$m_e, \text{g} = 0.41 m_{ad}^{0.42}. \tag{4}$$

Hypometry of the reptilian egg is particularly pronounced compared to avian eggs: in small reptiles the eggs are slightly larger or similar to those of birds of a similar size, while in large reptilians, the egg weights are tens of grams compared to ~1 kg in birds of a similar size (Fig. 1). In reptiles, this is compensated by the absolute independence of the progeny: embryonal development occurs at the temperature of the environment where the eggs were laid; it is quite long (from one month to over a year) and depends on the environmental temperature; the progeny hatches out independently and can independently feed and take care of itself.

Terrestrial Egg of Homoiotherms

Homoiotherms and poikilotherms differ at the levels of both organism and cell (Porter and Martin, 1995): all metabolic processes including embryonal development, in homoiotherms are 10 times faster and can only go at high temperature. No development proceeds without heat flow from parents in either platypus and avian eggs, marsupium of poached, or placental uterus. The necessity of incubation (as well as subsequent nursing of the progeny) in homoiotherms affected the allometry of progeny size via additional factors of selective pressure: the duration of embryonal and postembryonal development and energy expenditures for parental care.

Significant hypometry of the egg weight specific for reptilians will be unfavorable for large homoiotherms in conditions of parental care: the lower the starting weight of the progeny relative to its definitive weight, the longer it will need to be taken care of until it reaches this weight. Note that such care should be distributed between each progeny in the clutch, and its volume is limited. Ideally, the exponential factor of the progeny weight relationship becomes unity (as in placental mammals, who abandon the terrestrial egg and transited to intrauterine development (2)).

Birds. Indeed, the relationship of the avian egg weight acquired a higher exponential factor (Rahn *et al.*, 1975):

$$m_e, \text{g} = 0.258 m_{ad}^{0.73}, \tag{5}$$

however, it remained below unity. According to the common notion, birds measure the power of egg synthesis by their dependence on the basic metabolism with the same exponential factor 0.72 (Rahn *et al.*, 1975; Dol'nik and Dol'nik, 1981, 1982; Walsberg, 1983).

Reptiles slowly synthesize the clutch, all eggs increase almost simultaneously and are laid at once after synthesis.
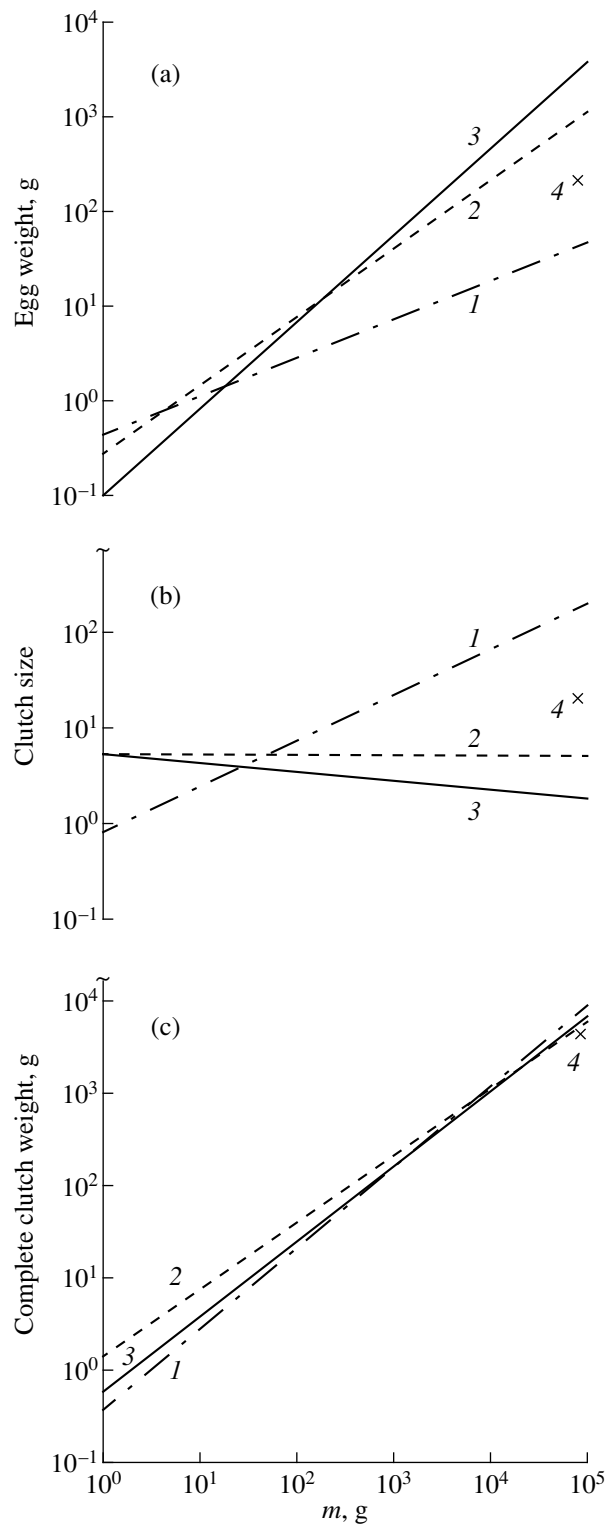
Fig. 1. Regression lines of relationships between species-specific body weight and main reproductive properties of modern reptiles (*1*), birds (*2*), mammals (*3*), and extinct reptile protoceratops (*4*); logarithmic scale; (a) weight of single reptilian or avian egg or mammalian newborn; (b) size of complete reptilian or avian clutch or mammalian newborn brood; (c) weight of complete reptilian or avian clutch or mammalian newborn brood; abscissa: body weight (*m*), g.

Birds essentially rearranged the strategy of synthesis: this process is impetuous, the eggs are synthesized sequentially, and the finished eggs are laid at a typical interval of one day (King, 1973; Dol'nik and Dol'nik, 1982). Since the egg hypometry was measured by the metabolic power of the female, the duration of either an egg (Walsberg, 1983) or the whole clutch synthesis (Dol'nik and Dol'nik, 1982) does not depend on the female weight. Generally, the period of rapid synthesis in birds is 8.7 days, with a weight exponential factor of 0.07, which does not reliably differ from zero (Dol'nik, 1995a).

There was another reason for the egg hypometry: the duration of the incubation (t_i), which increases with the egg size (Rahn and Ar, 1974):

$$t_i, \text{days} = 12.0 m_e^{0.217}. \qquad (6)$$

An egg weighing 1000 g should be incubated for 54 days, while an egg weighing 10000 g should be incubated 88 days. However, the incubation is only possible during a limited favorable season. Moderate hypometry of the egg size allowed birds to have a more reasonable relationship between the duration of the incubation and the female weight (Dol'nik, 1995b):

$$t_i, \text{days} = 9.1 m_{ad}^{0.167}. \qquad (7)$$

Two other generalized equations based on independent data produce similar exponential factors: 0.16 (Blueweiss et al., 1978) and 0.19 (Westmoreland et al., 1986). The fact that the egg is much larger than in reptiles is due to the nutritional demands of the embryo for its own heat production required for stable development. By the end of embryonal development, it is often high enough to maintain the clutch temperature, providing up to 40% their heat demands during the whole incubation (Kashkin, 1961; King, 1973).

The starting weight of a nestling remains hypometric to the parental weight (Rehn, 1982):

$$m_n, \text{g} = 0.289 m_{ad}^{0.703}. \qquad (8)$$

On the one hand, it is compensated by the duration of postembryonal growth (t_g), which is longer in nestlings of large birds (Weathers, 1992):

$$t_g, \text{days} = 7.97 m_{ad}^{0.259}, \qquad (9)$$

and, on the other hand, it is compensated by the hyperthermic relationship between a nestling's nutritional demands (TME) and its starting body weight (Dol'nik, 1995b):

$$\text{TME, kJ} = 142 m_n^{1.37}. \qquad (10)$$

Complete expenditure of the reproductive energy (RE_{rep}) per single reproduction cycle in a pair of birds is described by equation (Dol'nik, 1992):

$$\text{PE}_{rep}, \text{kJ} = 218 m_{ad}^{0.673}, \qquad (11)$$

where only 10% of the energy is used for the clutch synthesis on the average, while all the resting energy is used for reproductive behavior—the territory protection, nest building, clutch incubation, and fledgling. Most of these items of energy expenditure are hypometrically related to the parent's body weight; while energy expenditures on fledgling (RE_r) feature a hypometric relationship, which maintains the hypermetric nutritional demands of the nestlings (Dol'nik, 1995b):

$$\text{PE}_r, \text{kJ} = 7.0 m_{ad}^{1.121}. \qquad (12)$$

Placental mammals. Having abandoned the terrestrial egg and transferred embryonic development into a maternal body, placental mammals came to an allometry different than that of birds. The duration of the pregnancy (t_d) depends less on the limiting environmental effect; hence, it managed to acquire a more "steep" dependence on the female body weight as compared to birds (Blueweiss et al., 1978):

$$t_d, \text{days} = 11 m_{ad}^{0.26}. \qquad (13)$$

In large mammals, pregnancy can last over a year. The exponential factor 0.26 is not accidental (Millar, 1977); it precisely compensates the difference between the metabolic properties of the female proportional to its basic metabolism (which is proportional to the weight raised to the 0.75th power in mammals) (Kleiber, 1961) and a newborn progeny weight, which is proportional to the female weight raised to the power of about unity (2).

Milk-nursing is necessary for mammals. The daily production of milk is strictly related to the basic metabolic power of the female and features the same exponential factor 0.75 (Millar, 1977; Millar and Hickling, 1991). This necessarily defines the rate of sucklings growth with exponential factor of 0.75 relative to parent weight (Millar, 1977) and seemingly increases the lactation period with the female weight raised to 0.25 power so that total milk production acquires an exponential factor of 1.0—similometric to body weight production of growing cubs. However, mammals solved this problem in a different way: the ablactation age does not depend on the female weight (with exponential factor 0.05; Millar, 1977), while a cub weight at the moment of ablactation (m_f) is hypometric to the female weight and definitive weight (Millar, 1977):

$$m_f, \text{g} = 1.03 m_{ad}^{0.73}. \qquad (14)$$

Having successfully born a similometric progeny (2), mammals had to put it on independent nutrition in the hypometric condition due to the limitations specific for the mechanism of productive energy transmission from the female to cub via lactation.

Birds feeding their nestlings with food collected and brought are less restricted by the metabolic limitations. A hypometric nestling after hatching (8) receives the energy within the time compensating the starting hypometry (9) and the feeding is stopped when a nest-

ling weight equals or even exceeds the parent weight (Ricklefs, 1968, 1983). Nutrition energy hypometric to its starting weight (10) fed to a nestling forces it to grow similometrically to its weight (with exponential factor 1.0; Dol'nik, 1995b). A nestling can assimilate the necessary amount of energy to increase its weight due to the particular allometry of metabolic properties different from adults: its basic metabolism and daily energy consumption are related to the body weight, with an exponential factor around unity (Dol'nik, 1995b, 1995c).

Dinosaur eggs. The huge difference of egg allometry between poikilotherm reptiles and homoiotherm birds allows us, in the case of large and very large animals, to predict if it is a homoiotherm or poikilotherm from weights of the female and its egg. If dinosaurs and pterosaurs were poikilotherms and did not incubate their eggs, there is no reason for them to follow the allometry of modern reptiles, i.e., the data on them should fit extended regression line (4). If these animals were endotherms or even homoiotherms and incubated their eggs with heat production as was proposed recently (Bakker, 1971, 1972; Bakker and Galton, 1974; Paladino *et al.*, 1990; Paul, 1994; Nesov, 1997), their egg should primarily acquire the properties essential for a homoiotherm egg. First, it should be supplied with sufficient resources of water (to compensate huge drying) and nutrients to provide the proper high heat production of the embryo. This alone should increase the egg size. In addition, the relationship between the egg and female weights should become more steep, similar to avians. This will be easily revealed on the plot, since weight data on the female and its egg should not fit the regression line of modern reptiles but rather should approach the avian regression line.

As direct ancestors of birds, dinosaur eggs are the key subject for understanding the avian egg. Dinosaurs were the first to have calcium carbonate envelope of the egg, which imparts firmness to a liquid egg and a pore system controlling the egg drying and providing for the embryo gas exchange (Seymour, 1980). Birds improved this system only by an order of values corresponding to their specific metabolic power (Ar *et al.*, 1974). The evolutionary process of dinosaurs creating an egg with a huge mass—up to 5.5 or even 10 kg (Horner and Currie, 1994). In modern birds (with many times lower parent weight) the egg reaches 1 or 9 kg in the extinct epiornis (Rahn *et al.*, 1975).

Brilliant allometric compromises relating to the eggshell firmness and external load, as well as the metabolic capacity of the nestling to destroy it from inside (Ar *et al.*, 1979), was also settled by the evolutionary process of dinosaurs.

Note that the apparent advantage of a large egg with a firm eggshell over other reptiles could be used without the appearance of endothermy.

Allometry of Complete Clutch or Brood

By contrast to the size of a single egg, similometry between the female weight and the complete reproductive weight (weight of eggs in ovaries, complete clutch, newborns in the brood, etc.) is preserved in all studied animal classes except birds. In aquatic invertebrates, the weight of a complete spawn directly increases with the female weight raised to the 0.8–1.1 power, which does not reliably differ from 1.0 (Blueweiss *et al.*, 1978).

Fish. The weight of a complete spawn virtually directly increases with the female weight in fish (Blueweiss *et al.*, 1978):

$$Nm_e, \mathrm{g} = 0.27 m_{ad}^{0.92}. \tag{15}$$

Amphibians. As already mentioned, the relationship in amphibians is, apparently, similar to that of fish.

Reptiles. In reptiles, the weight relationship between a complete clutch and female also has an exponential factor not reliably differing from unity (Blueweiss *et al.*, 1978):

$$Nm_e, \mathrm{g} = 0.31 m_{ad}^{0.90}. \tag{16}$$

The metabolic allometry of reptiles favors the energy supply of a similometric clutch. The power of the standard metabolism responsible for the rate of egg biosynthesis increases with the body weight, raised to the 0.8th power in reptiles (Andrews and Pough, 1985). Energy consumption with food and its expenditure under natural conditions (providing nutrients for the synthesis) also has exponential factors, 0.82 and 0.80, respectively (Farlow, 1976; Bennett and Nagy, 1977). Hence, the metabolic time (duration of clutch synthesis) implicitly depends on the body weight (with an exponential factor of 0.1).

Mammals. In homoiotherm viviparous mammals, the relationship between the complete weight of a newborn brood and the female weight is close to similometry (Blueweiss *et al.*, 1978):

$$Nm_n, \mathrm{g} = 0.55 m_{ad}^{0.82}. \tag{17}$$

Birds. Only birds feature a hypometric relationship between the weight of a complete clutch and the female weight, differing between orders with an exponential factor from 0.30 to 0.76 (and Dol'nik, 1982). It is hypometric in the equation most convenient for comparison, combining all birds as a whole (Blueweiss *et al.*, 1978):

$$Nm_e, \mathrm{r} = 1.24 m_{ad}^{0.74}. \tag{18}$$

The initial cause of the hypometric clutch in birds—in the possibility of creating a similometric egg—has already been discussed. Birds could not compensate egg hypometry by increasing the number of eggs in the clutch in the dimensional series similar to poikilotherms without parental care because there is feedback in homoiotherms with parental care between the progeny volume and the capacity of parents to bring them up, which limits the progeny volume at a level independent of parents weight.

Allometry of Progeny Volume

Poikilotherms without parental care. In poikilotherms with aquatic eggs, the volume of the progeny (N, number of eggs in ovaries or spawn) is positively related to female body weight, with an exponential factor around 0.5, which usually compensates the exponential factor 0.5 of the egg weight to an exponential factor of 1 of the complete spawn).

Fish and amphibians. Apparently, the relationship between N and the body weight is described by the same equations in these poikilotherm vertebrates with aquatic egg (Blueweiss *et al.*, 1978):

$$N = 347 m_{ad}^{0.47}. \qquad (19)$$

Hypometry of the egg weight (3) is compensated by the high number of eggs in large animals (19), which preserves the direct relationship between the female body weight and the total spawn weight (15). The principle is simple: large species produce smaller eggs compared to small species, but in a proportionately higher number. A lower starting weight and longer growth to the definitive size in the progeny of large species is compensated by their high starting abundance. In the absence of parental care specific for these animal classes, they can produce any volume of the progeny required by selection since there is no metabolic feedback between them.

Reptiles. Poikilotherm reptiles also have no parental care and, hence, preserve (with huge terrestrial egg) the same relationship pattern between complete the clutch volume and female weight (Blueweiss *et al.*, 1978):

$$N = 0.77 m_{ad}^{0.48}. \qquad (20)$$

Reptiles provided virtually no change in the material contribution in the complete clutch relative to fish and amphibians (compare (15) and (16)) and increased the egg weight over 600 times ((3) and (4)), but reduced the number of eggs in the clutch 450 times—to a level comparable to that of birds and mammals. These cardinal transformations shifted them from the *R*-strategy (i.e., production of high progeny volume) to the *k*-strategy (i.e., production of low progeny volume); however, they preserved the ancestral poikilotherm allometry: hypometry of their egg weight (4) is compensated by a high number of eggs in the clutch (20). Hence, there is a direct relationship between the female body weight and clutch weight (16). The larger the reptile, the smaller progeny (relative to the definitive one) it produces and the longer it will take them to grow to the definite size; however, it produces a higher progeny volume compared to a smaller reptile.

Homoiotherms

In the course of evolution, birds and mammals independently increased the power of metabolic processes almost tenfold. Accordingly energy consumption is increased from food and its expenditures of various

activity forms—from maximum activity to the rest (Bennett and Nagy, 1977; Bennett, 1982). The possible energy expenditure for reproduction also increased 10–20 times; however, it was used in a particular way. For instance, putting all productive energy into egg production could increase the total progeny weight tenfold; instead, only an increase of 1.5 and 2 times is observed in mammals and small birds, respectively; while in large birds it is slightly lower than in reptiles of a similar size (Fig. 1). The resting energy was used for accelerated productive synthesis (small fraction) and for parental care of the embryos and growing youngsters. Birds are most illustrative in this respect: huge part of their productive energy is dissipated during various forms of parental care—from additional heat production for the incubation to food search and transport to the nestlings. In mammals, a significant portion of the energy is also dissipated for parental behavior; however, most of it is transmitted via complex physiological pathways directly to the progeny: embryos during pregnancy and youngsters during lactation.

Progeny of homoiotherms require parental care and investment of parental reproductive energy both at embryonal and postembryonal stages of development. That is why the number of youngsters in the brood or nestlings in the clutch is limited by the capacity of the parents to take care of them. Since the number of parents is one or two in all species and their number does not depend on the species weight, there was and is significant selective pressure obviating the poikilotherm relationship between the progeny volume and female weight, i.e., towards the relationship with a zero exponential factor. This was soundly demonstrated by separate allometric analysis of various mammalian groups with different brood volumes: the more the brood volume, the smaller the newborn weight and the lower the growth rate and body weight at the moment of ablactation (Millar, 1977).

In most mammalian orders, the brood volume does not depend on the female weight or even is implicitly negatively related. The general mammalian equation acquires the form (Blueweiss *et al.*, 1978):

$$N = 5.7 m_{ad}^{-0.1}. \qquad (21)$$

In some avian orders, the number of eggs in the clutch does not depend on the female weight, while others have an implicitly negative relationship. The following exponential factors were calculated for the class as a whole: –0.03 (Blueweiss *et al.*, 1978), –0.015 (Dol'nik and Dol'nik, 1981), and –0.067 (Dol'nik, 1995a). A calculation based on equations (5) and (18) produces:

$$N = 4.8 m_{ad}^{0.01}. \qquad (22)$$

Hence, homoiothermy inevitably leads to the independence between progeny volume in the complete clutch of brood and the parent body size (Fig. 1). Having abandoned reproduction with terrestrial eggs, placental mammals reached a new type of reproductive allome-

try: the parental organism potential for reproduction directly related to their weight (17) is completely realized through the birth of a weight-independent volume of progeny (21), while weight of each of them is directly related to the weight of parents (2). Birds solved the problem of reproductive allometry rearrangement in a different way: the volume of their progeny also does not depend on the parents' weight (22); however, the weight of each single newborn progeny is hypometric to their weight (5) and (8). Hence, their potential to reproduce progeny with the starting weight directly related to the parents weight is not used completely by large birds (18). Large birds compensate the hypometry of the nestlings by hypermetric parental care (12), which is due to limitations specific for a huge egg: too much instant energy expended for its synthesis and an impermissibly long incubation (6).

Milk-nursing of youngsters also has inevitable limitations. It is a current belief that this "invention" of mammals is the epitome of perfection. Now that we know all essential quantitative properties of a different strategy—nourishing with brought food in birds—they can be objectively compared.

The top limit of energy consumption with food in adult birds and mammals is uniform when expressed in basic metabolism units (BM) and equals 4 BM (Drent and Daan, 1980; Kirkwood, 1983). Energy consumption for life support is also similar: 2.3 BM in birds (Walsberg, 1983; Dol'nik, 1995a) and 2.6 BM in mammals (King, 1974; Farlow, 1976). Hence, the top energy that both of them can put in reproduction is also quite similar, around 1.5 BM.

A lactating female should independently consume the corresponding amount of food (RE_r), synthesize milk from it (with 0.77 efficiency; Kleiber, 1961), and give it to youngsters. In their turn, they should assimilate milk (with 0.8 utilization index; Millar, 1977) and produce their own brood-metabolized energy (TME_{br}) used for life support and growth. Hence, during lactation, mammalian TME_{br} is always less than the female RE_r, i.e., direct investment of the female productive energy in the progeny is always accompanied by a certain loss, and essentially cannot exceed the 1 : 1 ratio.

A bird fledging its nestlings has reproductive energy similar to a mammalian female and also receives it through additional nutrition. However, this energy is not transmitted directly to the nestlings, rather it is reinvested in the collection and transport of food. Since the proportion between energy expenditures for getting food and energy of this food is always much lower than 1 : 1 (Dol'nik, 1995b), the female first reinvests its productive energy and then transmits this reinvested energy to the nestlings.

Total energy expenditures during avian nestlings fledging are described by equation (12), while the total expenditures of the brood (TME_{br}) are described by equation (Dol'nik, 1995b):

$$TME_{br}, kJ = 149m_{ad}^{0.938}. \qquad (23)$$

Equation (23) divided by equation (12) produces the efficiency of productive energy reinvestment in birds:

$$TME_{br}/PE_r, kJ/kJ = 21.9m_{ad}^{-0.219}. \qquad (24)$$

The strategy of nourishing with brought food increases the investment in the next generation by one order of magnitude. The nestlings feature short-term and active growth (Drent and Daan, 1980):

$$G, g/day = 0.202m_{ad}^{0.74}. \qquad (25)$$

Growth of mammals at the stage of suckling is five times slower (Millar, 1977):

$$G, g/day = 0.04m_{ad}^{0.70}. \qquad (26)$$

Now it is clear why mammals hurry to finish the milk-nursing stage (14) and transit to nourishing with brought food in some species or to independent feeding in other ones.

Dinosaurs. The range between weight-independent size of the clutch (with zero exponential factor) in homoiotherm birds and growing clutch size with exponential factor 0.84 in poikilotherm reptiles is not large but extends with weight. At 100 kg weight, avian and reptilian clutches consist of 5 and 195 eggs, respectively. If dinosaurs and pterosaurs were homoiotherms and their progeny was independent starting from hatching similar to modern reptiles, they would have no reasons to affect the class-specific allometry and their clutch would contain tens and hundreds eggs. If they were endotherms, incubated the clutch with their own heat, and nursed the progeny as proposed by certain paleobotanists, not only should the egg size increase (as was already mentioned) but also the number of eggs in the clutch should, first, become independent of the body size and, second, should decrease to the number suitable for efficient parental care. This is easily visualized when the data on the extinct reptiles clutch relative to weight of the females that laid them is added to the plot of avian and reptilian clutch size.

Now when the pathway is outlined, all essential work for selecting reliable data on a dinosaur clutch can be only done by paleontologists. In order to prime, we included widely cited data on *Protoceratops andrewsi* inhabiting the territory of modern Magnolia during the Cretaceous in the figure. The weight of an adult specimen is estimated in various publications from 100 to 200 kg (Weishampel and Horner, 1994). A more precise estimate is 80 kg (Thulborn, 1991; Paul, 1994). The first estimate of the clutch size by the American pioneers (30 eggs) was definitely erroneous, and now American paleontologists believe that the complete clutch contains 18 eggs (Thulborn, 1991; Weishampel and Horner, 1994; Paul, 1994). The most ample and

reliable data were collected during many years work in Magnolia after Andrews' expedition (Mikhailov *et al.*, 1994). According to these data, the complete clutch contains 19–22 eggs, with 20 being the average. In the first communication, the egg size was 6 × 4 in. which gives 490 ml volume. Adherents of homoiotherm dinosaurs considered this egg too small for their theory and they called to increase it (Bakker, 1971). As a result, the published estimate of its weight reached 1 kg (Weishampel and Horner, 1994). At the same time, according to the real paleontology data (Mikhailov *et al.*, 1994), the average weight of the egg was 220 g. Properties of the protoceratops clutch correspond to neither avian nor modern reptilian allometry, although by body weight (80 kg) it fitted the dimensional series where the equations were calculated (ostriches, crocodiles, and marine turtles). So far this says nothing about homoiothermy of the dinosaurs but suggests a careful rechecking of the paleontology data (primarily, if the clutch really belongs to the assigned species).

Nevertheless, it is clear that after developing a calcium carbonate envelope for egg protection which allowed a big egg, dinosaurs gained the advantages offered by it such as large body dimensions, and dictated from the allometry of other reptiles to find their own (yet unclear) allometry.

Birds—evolutionary successors of dinosaurs—improved their egg and could build their allometry on the basis of a dinosaurian one. Hence, if complete clutch weight will appear hypometric to the female weight in dinosaurs, this will become another reason explaining the hypometric reproduction in birds.

CONCLUSION

A review of the empirical allometric equations describing the pattern of relationships between certain reproduction properties and species-specific body weight within each class of vertebrates reveals several relationships specific for all poikilotherm vertebrates and a different pattern of these relationships in homoiotherm birds and mammals.

(1) There is a simple relationship for the total female production (weight of complete clutch or newborn brood in mammals): production increases with the female weight (i.e., the exponential factor of the relationship is close to 1.0).

(2) Division of the total production between the components (i.e., weight of a single egg and number of eggs in the clutch) is "equal" in all poikilotherms: the exponential factor of the relationship between the egg and female weights is about 0.5 and the exponential factor of the relationship between the number of eggs and weight is about 0.5.

(3) We propose a simple explanation of this relationship: aquatic egg of fish and amphibians are subjected to two counter selective pressures. One preserves the independence of the egg size from species-specific dimensions of the animal, since the egg is a cell and cell size does not depend on animal dimensions. This pressure requires that the exponential factor of the relationship between the egg and animal weight equals zero. Another selective pressure requires a direct relationship between the egg and female weights, since its size defines the duration of progeny growth to definitive size. This pressure requires that the exponential factor of the relationship between the egg and animal weight equals 1.0. As a result, a compromise is found: the exponential factor of the relationship between the egg and female weight is about 0.5 (in the middle between 0 and 1.0) but the exponential factor of the relationship between number of eggs and female weight also equals 0.5.

(4) Reptiles reproduce with huge terrestrial eggs compared to fish and amphibians; however, the same relationship is specific for them: the exponential factor of the relationship between the egg weight or number of eggs and the female weight is about 0.5. We believe that reptiles inherited allometric relationships from their ancestors since there was no selective factor changing this relationship. Parental care is not specific for reptiles and youngsters hatch out completely independently.

(5) All poikilotherms without parental care have no metabolic feedback with them and, hence, are not pressed by the number of produced progeny.

(6) The progeny of homoiotherms requires interaction with the parents during the whole embryonal and postembryonal development at an individual level, i.e., each progeny needs a parent. Since the number of parents (one or two) does not depend on the weight of homoiotherms, selective pressure forces them, first, to limit the number of progeny in the brood and, second, to make their number independent from the species-specific body weight of parents (i.e., to a zero exponential factor). This pressure is so hard and efficient that we found no reliable relationship between either the clutch volume in birds or the brood volume in mammals and body weight.

(7) Placental mammals abandon terrestrial eggs and completely rearrange the total production of the female: the exponential factor of its dependence on the weight is unity, the exponential factor of the relationship between the progeny volume and weight is zero, while the exponential factor of the relationship between weight of each progeny and parent the weight is unity.

(8) Birds solved similar problems on the basis of reproduction with eggs. The egg was improved relative to reptiles and became a huge homoiotherm egg. The number of eggs in the clutch became independent of the female size. One could expect that the exponential factor of the relationship between the egg and female weight should become unity. However, this was not completed: birds drew out from the reptile relationship with an exponential factor of 0.5 and stopped at a 0.73 factor corresponding to the relationship between their metabolic power and body weight. Thus, they

became a single class with a disturbed direct relationship between the female body the weight and weight of its total production.

(9) Due to the significant difference (increasing with body size) between regression lines describing the relationship between egg weight and the complete clutch volume in reptilians and birds, it is possible to assign giant extinct reptiles to either poikilotherms or homoiotherms with parental care from their egg weight, number of eggs in the clutch, and body weight.

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