

Ecological, Functional, and Thermodynamic Prerequisites and Consequences of the Origin and Development of Homoiothermy: A Case Study of Avian Energetics

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Abstract—The study is based on the results of the integrated measurement of the energy expenditure at rest and common activity in birds belonging to various systematic groups that display considerable variation in their phylogenesis, specific features of ecology and feeding, locomotor methods, and body sizes. We believe that the emergence of homoiothermy was directly associated with the development of high activity due to the aerobic metabolism. The standard metabolism of the extant birds and mammals is over one order of magnitude higher than poikilotherms of equal size. This high level of heat production, in combination with low heat conductance, is the basis for homoiothermy. Heat conductance is a result of the interactions between vasomotor and pilomotor responses. The differences in the level of heat production by one order of magnitude are present, even when the body temperature of poikilotherms reaches the same values as in homoiotherms. The maintenance of homoiothermy is energetically expensive and requires considerably higher level of food consumption as compared with poikilotherms. It is rather unlikely that such an increase in metabolism developed in phylogenesis only for the sake of thermoregulation, especially at the earliest stages in the evolution of homoiothermy, when it was inefficient to maintain thermal stability. This is also highly improbable, since homoiotherms developed in the early Mesozoic era, which was the warmest and most thermostable period in the history of the Earth. Thermoregulation is a side effect of the increase in aerobic capacity. We believe that an increase in the aerobic capacity, which leads to an increase in activity, was the major selective factor that formed the background for the development of homoiothermy. The selective advantage of elevated activity may be considered to be a major condition for the survival and reproduction of homoiotherms. An advantage of birds and their ancestors with higher energetics can easily be explained in terms of selection; they are able to maintain higher flying speed and cover larger distances when searching for food and, in defensive behavior, will better protect their area and occupy new sites, as well as succeed in courting and reproduction. Despite an increase in the energetic cost for existence, these advantages are also important, since increased minimal capacity makes it possible to correspondingly elevate the energy input for meeting new energetic demands.

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The energetic cost for homoiothermy in birds and mammals is high, and establishment of homoiothermy had required the considerable remodeling of many vertebrate body systems. Birds and mammals evolved at different rates. Nonetheless, the homoiothermy of birds and mammals developed concurrently in various groups of their reptilian ancestors, and its main parameters (body temperature and metabolism) are similar. The selective factors that influence its evolution should have been essential and highly specific to induce such pronounced changes in the energetics, physiology, and behavior of these two groups of higher vertebrates. The questions on the selective factors that caused the development of homoiothermy and the sequence of events in its establishment, yet have no commonly accepted answers. The author attempted to provide answers by studying the levels of energy expenditure and consumption in passerine and non-passe-

rine birds. This paper is based on our own studies of bird energetics, as well as on the published data on the energetics of various homoiotherms (Brodkorb, 1971; Peters, 1983; Calder, 1984; Dol'nik, 1995; McNab, 1997, 2008, 2009; Darveau et al., 2002; Brown et al., 2004; Glazier, 2005; White et al., 2006) and poikilotherms (Hemmingsen, 1950, 1960; Bennett, 1976; Bennett and Ruben, 1979; Peters, 1983; Bennett and Lenski, 1999; Bennett et al., 1999, 2000; Feder et al., 2000). The bird energetics and general issues in the maintenance of the heat balance by homoiotherms have been discussed in earlier papers (Gavrilov, 1994a–d, 1995a–c, 1996a, 1996b, 1998, 2000a, 2000b, 2004, 2011; Gavrilov, 1994, 1997, 1999a, 1999b, 2001; Gavrilov and Dolnik, 1985). Only some of the most important facts will be considered in this paper.

The goal of this work was to propose a possible evolutionary and ecological scenario for the causes and conditions underlying the establishment of homoiothermy and the colonization of major ecological niches by homoiotherms. The paper is based on a set of experimental data on the energetics of the extant vertebrates, its theoretical substantiation, and an analysis of the relevant literature on the major events in the Mesozoic era.

This study utilizes the results of an integrated measurement of the energy expenditure at rest (assessed according to oxygen consumption) and common activity, i.e., the so-called existence metabolism (assessed according to food consumption), as well as the energy expenditures in flight and at a maximal loading in birds belonging to various systematic groups that display considerable variations in their body sizes. The main attention was focused on clarifying the balance between the minimal metabolic capacity (basal metabolic rate, *BMR*) and other levels of energy expenditures, such as the standard (resting) metabolic rate and energy expenditures for the existence at different ambient temperatures (T_A). To estimate the maximal potential of birds in dissipating excess heat, we had to estimate the maximal and productive metabolic rates, as well as the energy expenditures for activity in various passerine and non-passerine species. Thus, this paper is an attempt to understand the scenario of homoiothermy origination from the standpoint of ecological energetics.

BIOSPHERIC CONDITIONS AND PREREQUISITES FOR ORIGINATION OF HOMOIOOTHERMY AND HOMOIOOTHERMS

The specifics of the boundary between the Permian and Triassic periods saw significant changes in terrestrial vertebrate fauna. The prevalent reptile groups in the Permian period were theriomorphic reptiles and cotylosaurs, whereas the groups with diapsid skulls (lepidosaurs and archosaurs), united under the name "sauropsids," remained rather few in number. This balance had drastically changed by the beginning of the Mesozoic period. Of all the cotylosaurs, only procolophons (disappeared by the end of the Triassic) succeeded in passing to the Triassic period and, of the theriomorphic reptiles, only a few groups of dicynodonts and higher theriodonts carried over. However, the abundance and diversity of diapsid reptilians constantly increased, and they became dominant in the second half of the Triassic period (Iordanskii, 2001).

Robinson (cited according to Iordanskii, 2001) proposed a hypothesis that related the changes in reptilian fauna of the Triassic period to the specific physiological features of sauropsids and theriomorphic reptiles, which, to a certain degree of probability, can be estimated according to the corresponding characteristics of the extant descendants of both groups. The set of adaptations to the life under the conditions of a

hot arid climate is characteristic of the currently existing sauropsids (in a broad sense, this term is used to unite all extant groups that belong to the class of reptiles and birds). Sauropsids are able to withstand considerably higher temperatures compared to the descendants of theriomorphic reptiles, mammals. The end product of the protein metabolism in sauropsids is uric acid, versus urea in mammals. Uric acid can form oversaturated solutions; correspondingly, its excretion from the body requires an approximately tenfold smaller amount of water compared to urea. Evidently, the excretory system of sauropsids saves water for the body considerably more efficiently than in mammals. The Permian glaciation and the subsequent global warming led to a considerable change in the general appearance of the flora. The ancient club mosses, which is typical of the forests of the second half of the Paleozoic period, disappeared along with pteridosperms and cordaites. These mosses were replaced by various representatives of other gymnosperms, such as cycads, ginkgoes, and conifers. These species mainly formed the general appearance of the forests in the first half of the Mesozoic period.

The origin of homoiotherms dates back to the Mesozoic period. The Mesozoic was the era of tectonic, climatic, and evolutionary activities. The major outlines of modern continents were formed at that time, as well as the mountains at the peripheries of the Pacific, Atlantic, and Indian Oceans. The separation of the terrestrial part of the globe enhanced the speciation and other most important evolutionary events. During this entire period, the climate was exclusively warm; the first half of this period was drier, while the second half was more humid. Furthermore, some chilling periods took place in the late Jurassic and the first half of the Cretaceous, and pronounced warming took place in the mid-Cretaceous (the so-called Cretaceous temperature maximum); at approximately the same time, the equatorial climatic belt was formed (Budyko, 1982; Krasilov, 1985). The specific climatic features of the Mesozoic period played an important part in the evolution and emergence of new animal species. By the end of this era, the majority of biological diversity had approached its current state. Zherikhin (1984) described the situation as follows: "Over several millions of years, i.e., during the first half of the Cretaceous, angiosperms replaced the majority of characteristic mesophytic plants in paleontological deposits. At the same time, the mesophytic groups that escaped extinction, ferns and conifers, change in order to acquire an appearance similar to the modern one. Animals also undergo changes concurrently with plants. By the end of the early Cretaceous, the most ancient known eutherians were found and resembled the extant tenrecs of Madagascar (a kind of hedgehog). Birds became numerous and the first snakes emerged in the mid-Cretaceous, while the composition of insects changed drastically. In particular, ants appeared, and termites and butterflies became

numerous. Multitudes of bony fish emerged in the sea. Since that time, all of these animal groups, together with angiosperms, belong to the most important species that determine the face of nature."

Mammals have been known since the Triassic period and birds have been since the Jurassic period; some of the Triassic and Jurassic findings can be ascribed to mammals and birds (Ivakhnenko et al., 1997; Lopatin, 1997; Falkowski et al., 2005; Wible et al., 2007). Consequently, we must consider them to be homoiotherms, presumably with imperfect homoiothermy. Under Triassic and Jurassic conditions with a prevalence of mesophytic vegetation and low productivity of communities, the homoiothermy of birds and mammals could not provide them with ecological niches with the necessary energy flow, to say nothing of the possibility to increase their diversity. Small primitive forms of the most ancient mammals were approximately rat-sized and could not seriously compete with the flourishing reptilian fauna, which rich was rich in large, even giant forms. Having appeared at a relatively late stage of life, in a manner, mammals and birds occupied places that had been empty; moreover, their considerably higher energy demands required corresponding food potential. The emergence of homoiothermy (first and foremost, increase in the aerobic metabolism for the sake of increase in activity) dates back to the early and mid-Mesozoic; however, the biospheric conditions prevented the advantages of homoiothermy from being efficiently utilized until the late Cretaceous because of the absence of sufficient food potential. The energy channel necessary for development of homoiotherms only appeared with the emergence of angiosperms and the associated fauna in the mid-Cretaceous.

The progress of reptiles at that time was connected with the solution of two physiological problems, i.e., the establishment of true lung respiration and the emergence of an amniotic egg. The advantages of lung respiration require no comments. As for the amniotic egg, on the one hand, it has serious advantages over amphibian spawn, which allowed them to leave aquatic habitats. However, on the other hand, the egg is a factor that determined the size of the offspring, since the size of a youngster is limited by the maximal size of the egg; if the egg is too large, the shell will be crushed by the pressure of the liquid, whereas if the thickness of the shell is increased, the embryo will suffocate. In addition, a low metabolism and correspondingly limited food demand allowed for the rapid adaptive radiation of reptiles. At that time, reptiles entered the class of large animals (some dinosaurs with a mass to 60 t are known). As for the egg, it remains (due to purely physical reasons) approximately the same size as that of the extant African ostrich (which has a body mass of about 100 kg and egg mass of about 2 kg). Thus, it was difficult for the giant reptiles to nurse their offspring due to the difference in size between adults and youngsters. It is known that mainly large reptiles

died off in the late Cretaceous; as for the fauna of, e.g., lizards, it changed earlier concurrently with insects and was less drastically affected by the late Cretaceous extinction (Zherikhin, 1978; Rasnitsyn, 1988). For almost 130 million years, birds and mammals lived concurrently with the tremendous diversity of reptiles and, for a long time, could not utilize the opportunities of their homoiothermy and the advantages provided by the high activity and survivability because of the high energy consumption it entails and the impossibility to channel the necessary food sources.

Birds and mammals only started to occupy an appropriate position in biocenoses in the mid-Cretaceous. By the end of the Cretaceous, birds had lost their teeth and mammals were represented by both marsupials and eutherians. This is associated with the general evolution of the organic world, which, in the Mesozoic period, led to the emergence of flowering plants, which is considered to be the golden age of the associated invertebrate fauna, and a large diversity of flying insects. The emergence of angiosperms dates back to the early Cretaceous, while that of modern insects dates back to the mid-Cretaceous (Zherikhin, 1978; Rasnitsyn, 1988). The emergence of flowering plants or angiosperms that were initially entomophilic, i.e., attracting insects for pollination, induced evolutionary changes in insects and the development of contemporary entomofauna, or the "angiospermization of the world" according to Ponomarenko (1993). This process involved all of the remaining components of the continental ecosystems and determined the fast spread of birds and therian mammals, as well as of bony fish in freshwater aquatic bodies. In the second half of the Cretaceous period, angiosperms colonized vast areas on land and represented an almost inexhaustible source of food (Krasilov, 1989). The diversity of flowering plants stimulated the evolution of insects as their pollinators. The insects (especially flying ones) display a considerably higher activity compared to the reptiles that coexisted with them.

Biocenoses changed with the emergence of angiosperms. The biomass of angiosperms increased, as well as the biomass of the associated invertebrates. The degree of mosaicism in biocenoses increased as well. The natural succession of gymnosperm biocenoses was destroyed, leading to significant changes in the faunas (Zherikhin and Rautian, 2000; Zherikhin, 2003). Angiosperms more intensively take up many macro- and trace elements. The corresponding result is a more advanced biological turnover, which allows for the more successful resistance to mineral starvation. The role of the ability to take up calcium, which appeared in these plants, was of special importance, since this element started to accumulate in soils after plant death and neutralize the acid medium, thereby interfering with leaching. Since that time, it has become possible for highly fertile soils to be established and large amounts of biogeochemical

energy to be accumulated (Gorshkov, 1985; Perfilova and Makhlaev, 2009).

The Mesozoic vegetation was poorly adapted to consumption by large terrestrial vertebrates (Ponomarenko, 1998) and prevented the emergence of herbivorous animals with high energy demands. In the Cretaceous period, the productivity of communities first decreased, then considerably increased with the colonization of new areas by angiosperms; moreover, both the plant entity and invertebrates contributed to this increase (Plotnikov, 1979). The angiosperms, presumably, grasses, produced a significant biomass that was rich in protein and fairly stable in its production level. The grasses provided for a considerable biomass of herbivorous organisms, which led to a drastic increase in the abundance of predators. After the spread of angiosperms in the mid-Cretaceous, leaf consumers, mainly miners (the insects living inside plants and “mining” tunnels there), emerged almost immediately. However, the actually massive consumption of green plant parts only commenced with the spread of cereal biomes. This gave rise to the ecosystems with a large volume of biomass comprising most diverse herbivorous forms, their predators and parasites, coprophages, and necrophages (Ponomarenko, 1998).

One more reason why the poikilothermic vertebrates could not consume the manifold increased amount of biomass is that they were adapted to feeding on other plants and that there were many predators among them, although some characteristics of their dentition suggest that certain dinosaurs attempted to adapt to eating angiosperms (Es'kov, 1999; Es'kov and Iordanskii, 2001).

The mean daily energy expenditures for life-supporting activities measured under natural conditions at optimal ambient temperatures in extant animals by the doubly labeled water technique, the so-called “field” metabolic rate (*FMR*, *W*), suggest the following allometric dependences on the body mass (*m*, kg):

$$\text{Reptilian } FMR = 1.07m^{0.89} \text{ (Nagy, 2005);}$$

$$\text{Avian } FMR = 3.36m^{0.68} \text{ (Nagy, 2005); and}$$

$$\text{Mammalian } FMR = 8.91m^{0.734} \text{ (Nagy, 2005).}$$

These equations demonstrate that the amount of energy spent by birds and mammals for their life-supporting activities is larger by one order of magnitude and, correspondingly, they consume more energy. We would like to emphasize that, of the overall reptiles, only ambush predators and a few herbivorous forms (mainly of the small size cohort) succeeded in surviving to present day, and almost all of them are confined to warm habitats. On the other hand, homoiotherms have almost colonized the overall part of the biosphere appropriate for living, channeled new energy flows, and forced reptiles away from major niches. Thus, an increase in the amount of energy spent for common life activities gives a serious selective advantage.

On the other hand, an increase in the energy expenditures cannot be subject to the positive control of natural selection, since an increase in the energy expenditures per se is disadvantageous for an organism. How, then, does natural selection control an increase in the capacity of energy metabolism? What are the ecological advantages gained by the animals with a high metabolism? What is the cost of possessing a high metabolism? And why did homoiothermy not emerge with lower body temperature? Researchers studying the ecological energetics of modern vertebrate groups face all of these questions and, in their answers, will give deeper insight into the origin of homoiothermy.

HOMOIOTHERMY

The evolution of homoiothermy is usually discussed in the literature in the context of the advantages conferred by a stable body temperature (diurnal activity, enzyme functions, and tolerance to freezing) and thermoregulation (Hemmingsen, 1960; Peters, 1983; Dol'nik, 1995; Darveau et al., 2002; Else et al., 2004). Only some researchers pay attention to the increase in activity and fatigue resistance in homoiotherms (Bennett and Ruben, 1979; Bennett et al., 2000; Dol'nik, 2003). The author also believes that thermoregulation is not the only selective advantage in the evolution of homoiothermy. Most likely, thermoregulation was not even the initial factor for the emergence of homoiothermy. Large extant reptiles are completely able to maintain a constant body temperature over 30°C under the conditions of an equable warm (subtropical) climate with small diurnal temperature variations (Bennett, 1976; Dol'nik, 2002). This phenomenon is referred to as “inertial homoiothermy.” Several biophysical models have been constructed to assess the possible body temperature of large dinosaurs (O'Connor and Dodson, 1999; Gillooly et al., 2006); their estimates are 30–47°C. Advances in radioisotope research methods have allowed us to assess the body temperature in discovered extinct dinosaurs with various degrees of accuracy (Barrick and Showers, 1994; Fricke and Rogers, 2000; Seebacher, 2003; Amiot et al., 2006; Eagle et al., 2010, 2011). All of the isotope-based estimates for the body temperature of dinosaurs mainly fall into the range predicted by biophysical models. Nonetheless, the question on the true endothermy of dinosaurs remains open (Seebacher, 2003; McNab, 2009b; Eagle et al., 2010, 2011). Most frequently, they are compared to contemporary crocodiles, which display certain attempts at endothermy. However, there is no final evidence that the metabolism of dinosaurs differed from the metabolism of extant reptiles (Seebacher, 2003; Pierson, 2009; McNab, 2009b; Eagle et al., 2010, 2011). Correspondingly, it is quite adequate to assume that the metabolism of extinct reptiles had no serious differences from the metabolisms of recent forms (Bennett

and Ruben, 1979; Bennett, 1994; Bennett and Lenski, 1999; Bennett et al., 2000; Hicks et al., 2000; Dol'nik, 1998, 1999a, 1999b, 2002, 2003), despite the publications that imply such a difference (for example, Seymour et al., 2011) that constantly appear in prestigious journals.

Differences in metabolism are naturally reflected in the food consumption, which remains in the reptiles by over one order of magnitude lower compared to mammals and birds. The establishment of homoiothermy was directly connected with the development of high activity, which is enabled by aerobic metabolism. This high aerobic metabolism made the evolution of complex behavioral patterns feasible in birds and mammals. This evolution had to be based on the preceding evolution of metabolic systems capable of providing high activity. This resulted in an increased standard (resting) metabolic rate (*SMR*), which became the minimal capacity level. The *SMR* increased in order to enable even higher levels of work intensity in homoiotherms (Bennett and Ruben, 1979; Gavrilov, 1995a, 1995b, 1996a, 1996b, 2000a, 2000b, 2006; Dol'nik, 2003). These tremendous ecological consequences failed to properly manifest for over 130 million years. The destruction of the bottom tiers of the ecological pyramid (the prime of angiosperms) was required for homoiotherms to colonize the new major niches formed at that time. The development of homoiothermy and homoiotherms is quite adequately described by models that simulate the development of crises in biological evolution by Zherikhin and Rautian (Zherikhin, 1984; Rautian and Zherikhin, 1997; Zherikhin and Rautian, 2000).

EXPERIMENTAL EQUATIONS FOR DEPENDENCE OF ENERGETIC PARAMETERS ON AMBIENT TEMPERATURE (T_A) IN HOMOIOOTHERMS

The general patterns of the effect of ambient temperature on the energetics of a homoiotherm have been discussed in various aspects in several publications by the author (Gavrilov, 1994a, 2001, 2004). While working on this paper, all of the available published energetic models for birds and mammals have been critically revisited. An analysis of the experimental and published data enabled a generalized model to be constructed for the energetics of homoiotherms, which specifies the general dependence of the major energetic parameters for any studied species on the ambient temperature (Fig. 1). Here, $DEE = h_{\min}(1 - \alpha\alpha)(T_B - T_A) + aBMR$; *DEE* is the daily energy expenditure at any level of activity (*a*); $h_{\min}$ is the minimal degree of nonevaporative heat loss (heat conductance) at rest ($h_{\min} = \tan \angle \beta h_{\max}$); $h_{\max}$ is the maximal degree of changes in nonevaporative heat loss (heat conductance) at rest ($h_{\max} = \tan \angle \beta_1 = 4 \tan \beta$); α is the efficiency of the conversion of the metabolic capacity into mechanical (external) work ($\alpha = 0.25$); T_B is the body

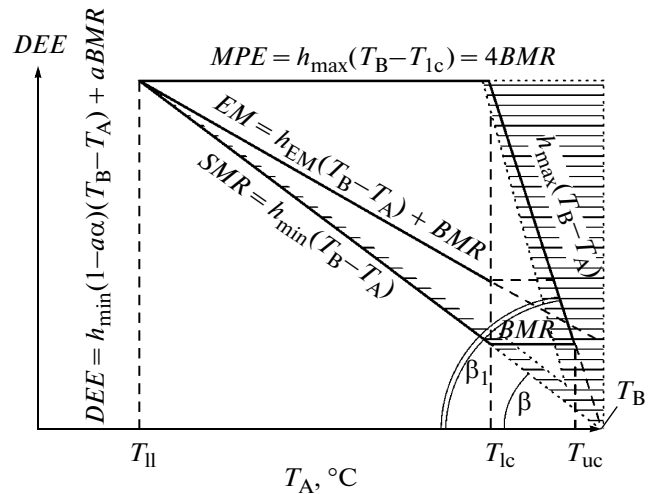


Fig. 1. Experimentally determined dependences of energetic parameters on ambient temperature (T_A , °C). See text for explanations.

temperature, which amounts to 40°C for birds and 37°C for mammals; T_A is the ambient temperature; *BMR* is the basal metabolic rate; T_{lc} is the lower critical temperature; T_{II} is the lower limit of specific temperature tolerance; T_{uc} is the upper critical temperature; $Q_{\min} = SMR = h_{\min}(T_B - T_A)$ is the minimal heat loss or standard metabolic rate; $Q_{\max} = h_{\max}(T_B - T_A)$ is the maximal heat loss; $EM = h_{EM}(T_B - T_A) + BMR$ is the existence metabolism; *a* is the activity level (at $a = 0$, $DEE = SMR$ and, at $a = 1$, $DEE = EM$); and $MPE = h_{\max}(T_B - T_{lc}) = 4BMR$ is the maximal potential existence metabolism. The hatched area corresponds to evaporative heat loss. The generalized mode for the energetics of homoiotherms demonstrates that two major characteristics, i.e., minimal and maximal heat losses, depend equally on the ambient temperature and theoretically reach zero (where they cross the abscissa at the same point) at an ambient temperature equal to body temperature (Fig. 1). Thus, both the minimal ($Q_{\min} = SMR$) and maximal ($Q_{\max} = MPE$) heat losses precisely follow the Newton's law in the interpretation by Scholander. It is essential that the maximal heat loss without any considerable increase in the evaporation, which we introduce here and has been determined for a large number of species for the first time, also precisely corresponds to the Scholander model. Thus, the Scholander model is supplemented with the dependence of the maximal heat loss on the ambient temperature, so that it acquires finished form (Fig. 1). Birds are able to dissipate any available amount of energy between two events of heat loss that converge at an ambient temperature equal to body temperature. As a result, a temperature–energy space is formed in which animals are able to function for an infinitely long time. The evaporative heat loss expands this space towards higher ambient temperatures (hatched area in Fig. 1). Existence at a tempera-

ture that exceeds the upper critical temperature is only possible at a high level of water evaporation and, consequently, requires its continuous replacement. The evaporative heat loss between the minimal and maximal values of heat loss (hatched area under the *SMR* line) shows the level of adaptive evaporative heat loss.

Homoiotherms always have a certain minimal level of heat production that results from the generation of heat during basic physiological processes, which can be never arrested. This minimal heat production level is referred to as the basal metabolic rate (*BMR*) and represents the major minimal capacity of a homoiotherm.

The experimentally determined correlations between energetic parameters allow them to be represented in strict mathematical form, that is, as models.

For the mean daily energy expenditure *EM* at a certain activity level, we take the following equation as a unit:

$$EM = h_{EM}(T_B - T_A) + BMR, \quad (1)$$

where h_{EM} is the temperature coefficient of an increase in *EM* with a decrease in ambient temperature (T_A) by 1°C, T_B is the body temperature, and *BMR* is the basal metabolic rate.

For the daily energy expenditure (*DEE*) at any activity level (*a*),

$$DEE = h_x(T_B - T_A) + aBMR, \quad (2)$$

where h_x is heat conductance at a given activity level.

For the level of daily work output (*DWO*),

$$DWO = \alpha DEE \quad \text{or} \quad (3)$$

$$DWO = h_l(1 - \alpha)(T_B - T_A) + \alpha a BMR,$$

where h_l is the minimal heat loss at rest (at a zero activity) and α is the efficiency of the conversion of metabolic capacity into mechanical capacity (work output).

For the main sample of species (26 passerine and 16 non-passerine species), such equations have been obtained for two seasons, winter and summer, and for over 60 passerine and 24 non-passerine species, only for one of the seasons. These results make it possible to objectively determine ecologically important zones of ambient temperatures, including optimal, upper and lower lethal, sublethal, and so on, according to the cross points of several energetic parameters.

ABILITY TO CHANGE HEAT LOSS AS A PREREQUISITE FOR EMERGENCE OF HOMOIOOTHERMS

During animal activity, large amounts of heat are generated and the body temperature rapidly increases, which is detrimental, since proteins are denatured at a high temperature. Correspondingly, perfect systems for dissipating heat are necessary to ensure the balance between heat generation and loss. *The major thermodynamic in the activity of poikilotherms is dissipation of*

the heat generated during activity and work in general. For this purpose, efficient mechanisms for heat dissipation are required, namely, a developed circulatory system and the ability to control the heat-insulating properties of body covers. This suggests the following prerequisite for homoiothermy. All of the ordered biochemical processes in an animal body convert into heat, which, in the steady-state case of a constant body temperature, should be dissipated beyond the body into environment. The amount of energy generated in biochemical processes in the body with a constant mass is determined according to caloric characteristics of the consumed food and the coefficient of food assimilation, which varies insignificantly in homoiotherms around 0.8 (Kendeigh et al., 1977). The generated heat is mainly dissipated via thermodiffusion and is proportional to the difference in the body and ambient temperatures. It also takes place via heat absorption during water evaporation by the body. The coefficient that relates the heat flow to the temperature difference provided by the thermoinsulating layer in physics is referred to as the coefficient of heat conductance. The homoiotherms are able to control the heat conductance of the effective surface that thermoinsulates later by changing the characteristics of their feather (hair) cover, blood circulation in the surface body layers, etc., thereby changing the coefficient of heat conductance. An animal can either change its heat generation at the same ambient temperature or retain the heat generation at a constant level in the case of considerable changes in the ambient temperature (McNab, 1997; Wright et al., 2004; White et al., 2006). The former option allows the animal to utilize the surplus energy, which exceeds the necessary expenditures for maintaining its life, productive processes, and any type of locomotor activity. The latter option explains the existence of a so-called thermoneutral zone, i.e., the range of ambient temperatures where the minimal metabolism *BMR* can be maintained at a constant level.

BMR is the minimal level of energy expenditure; it maintains the major physiological functions vital for the life. The energy required by the systems responsible for blood circulation and respiration, as well as the other systems that never cease working (excretory, nervous, etc.), is the factor that determines the minimal energetic capacity, i.e., *BMR* capacity.

RESTING METABOLIC RATE IN DIFFERENT ANIMAL GROUPS

An all the groups of poikilothermic vertebrates (fish, amphibian, and reptiles), the metabolic levels are almost equal. The allometric dependences of the reptilian, avian, and mammalian energetic characteristics demonstrate that the *SMR* of reptilians heated to the body temperature of homoiotherms is one order of magnitude lower than the avian and mammalian *BMRs* in the level of energy expenditure. The high

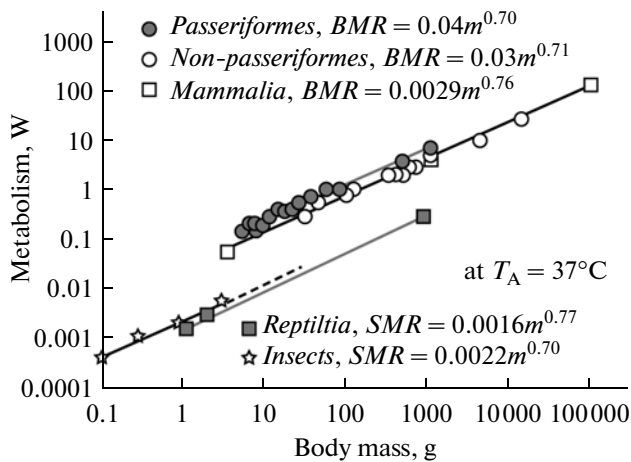


Fig. 2. Dependence of standard metabolic rate (*SMR*) on body mass in different animal groups.

level of heat production, in combination with a low heat conductance of the body covers and the ability to change heat dissipation via the vasomotor response form the foundation of homoiothermy. The difference of one order of magnitude in the heat production between homoiotherms and poikilotherms exists even in the situation when the body temperature of poikilotherms reaches that of homoiotherms (Fig. 2). However, the food consumption by reptiles in this case still remains one order of magnitude lower than in birds and mammals. The development of homoiothermy

was directly connected with the development of high activity, which is ensured for by aerobic metabolism. This particular metabolism allowed for the evolution of complex behavior patterns in birds and mammals. This evolution required the preceding evolution of metabolic systems able to provide for a high level of activity. This resulted in an increased *SMR*, which became the minimal capacity level. The *SMR* level had increased in order to enable one to achieve higher levels of work intensity in homoiotherms (Bennett and Ruben, 1979; Gavrilov, 1995a, 1995b, 1996a, 1996b, 2000a, 2000b, 2006; Dol'nik, 2003).

Birds are an advantageous model for studying the evolutionary aspects of animal energetics, although their ability to fly hinders the comparison of locomotor activity. The metabolism of non-passerine birds corresponds to that of mammals, whereas the *BMR* of the passerines is 1.3–1.5-fold higher. Figure 3 shows the *BMR* dependences on body mass for different avian orders (the regressions were constructed according to the data of Gavrilov and Dolnik (1985)) and additional data for birds belonging to 16 orders, as well as a mixed group of Struthioniformes, Rheiformes, and Casuariformes, referred to as “ostriches.” A total of 687 species have been analyzed, including 352 Passeriformes, six Caprimulgiformes, five ostriches, and ten or more of the remaining orders; the regression lines are drawn from the minimal to maximal body masses of the species measured within an order.) A comprehensive integrated study of the energetics of passerine and non-passerine birds and its comparison

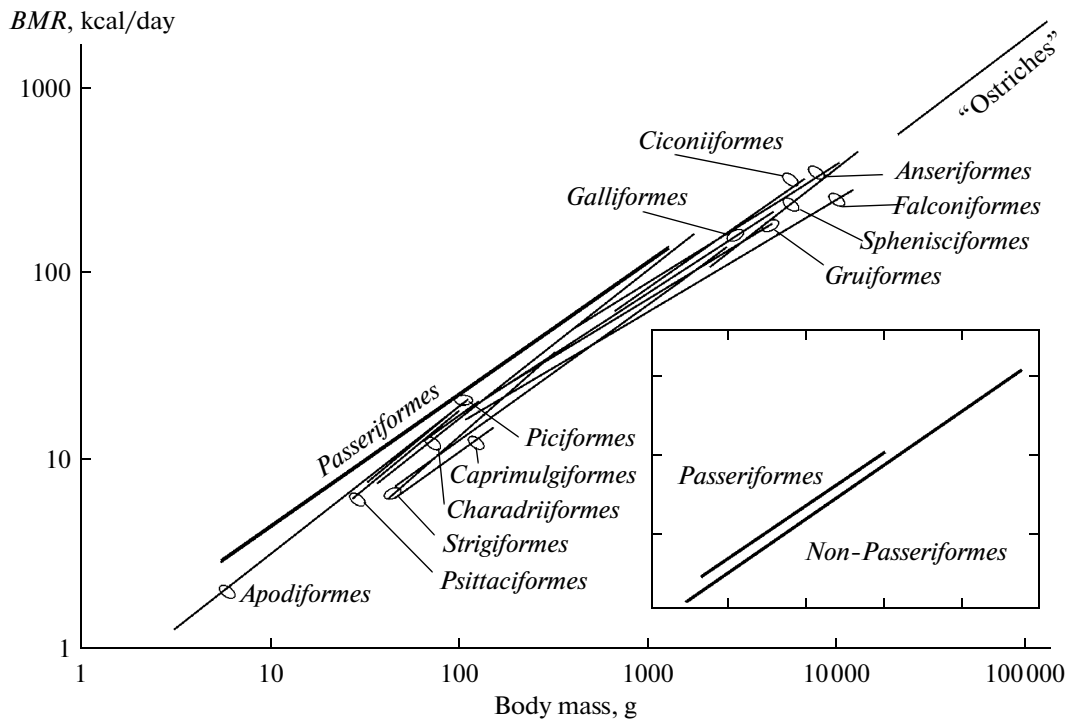


Fig. 3. Dependence of *BMR* on body mass in different avian orders.

with the energetics of mammals provides insight into the evolutionary, taxonomic, and ecological consequences of homoiothermy.

FORMATION OF BASAL METABOLIC RATE

As is evident from the scheme in Fig. 1, once the ability to change heat dissipation appears, the minimal metabolic capacity, or *BMR*, should inevitably emerge. Without *BMR*, the heat dissipation would merely decrease (or increase) at a certain rate, and switching to another activity mode would require a certain period of time, which is actually observed in poikilotherms, which must change their activity to a resting period rather rapidly. Thus, the *BMR* level is the factor that determines the transition from one degree of heat conductance change to another, which, naturally, is important for the thermoregulation at rest, but has even greater significance in locomotor activity. This is why the periods of locomotor activity in homoiotherms may be very extended (just recollect that birds during their migrations are able to fly for up to several days without any rest) and easily alternate with rest periods, when the minimal metabolic activity is maintained and the transition to locomotor activity is instant.

A certain damper device that would quench the fluctuations in ambient temperature and provide an instant transition from rest to activity becomes necessary to stabilize the body temperature and ensure constant preparedness for activity.

In order to rapidly perform this transition, animals should have a certain component independent of the ambient temperature. *BMR* is the component that plays this role, being an integral characteristic of physiological organization. Birds always display a certain minimal level of heat generation, which results from heat production in basic physiological processes that can be never arrested. This level of heat generation allows the body temperature to be maintained within a certain range, i.e., the so-called thermoneutral zone.

What is the range of ambient temperatures where the *BMR* level is sufficient to maintain a constant body temperature? It is natural that this level should damp certain average temperatures on Earth. The average temperature on the earth surface is approximately 14°C and, for a relatively long period, the mean maximal temperature continued to be about 33–35°C. Therefore, it is reasonable to assume that the *BMR* level should support animal existence in the range of 14 to 33–35°C without any additional expenditure for thermoregulation. The thermoneutral zone of the non-passerine birds with a mass of 1 kg falls into the range of 14–35°C, that is, their *BMR* is able to damp the fluctuations of ambient temperatures from the mean T_A of the earth surface to the mean maximal temperature continuing for a relatively long period. This is indirect evidence for the fact that the first birds were of this particular size, as has been confirmed by

paleontological and morphological data (Brodcorb, 1971). It is important to emphasize that, although this reasoning is based on a certain global approach, both at that time and now, the range of 14 to 33–35°C is the most optimal for homoiotherms. Moreover, there are no precise data in the area of the Earth where the first homoiotherms appeared; however, it is more or less clear that this took place not at high latitudes and that the mean maximal temperature, which continued for a relatively long period of time in the area where homoiotherms originated and lived, did not exceed 33–35°C, which is very important for the establishment of a constant body temperature.

ACTIVITY IS ENERGY EXPENDITURE

With an increase in physical activity, the energy demands are satisfied by an increase in aerobic metabolism. After a lag phase, the oxygen consumption by the body increases in proportion to the demand (Bennett, 1976; Bennett and Ruben, 1979; Savina, 1992; Suarez, 1996; Palese et al., 2003; Makarieva et al., 2006). The difference between the maximal and minimal aerobic capacities in poikilothermic vertebrates has a direct effect on the level and duration of activity that these animals can withstand. The aerobic metabolism of four-footed animals increases during walking or running and linearly increases with speed. After reaching the maximal level of oxygen consumption, it remains constant at higher speeds. Anaerobic metabolism supplies additional energy in the case when the speed exceeds the value when the oxygen consumption becomes maximal. The speed when the anaerobic metabolism is activated is referred to as the “anaerobic threshold.” This can be achieved at a speed slower than that of the maximal oxygen consumption. Compared to the aerobic potential, the cost for locomotion in the poikilothermic vertebrates is high and even a moderate activity level rapidly surpasses the aerobic limit for reptiles. Any activity of terrestrial poikilotherms above a slow walk requires the switching of the anaerobic metabolism and lactic acid production or the pure catabolism of energy-rich phosphate compounds. The metabolic capacity that can be achieved in an anaerobic manner supplements the aerobic capacity of lower vertebrates; in these animals, both moderate and high activity levels can only be attained via the activation of anaerobiosis. Although the anaerobic metabolism of reptilians and amphibians is much more developed than birds and mammals, these anaerobic processes are able to maintain muscle contractions for only relatively short periods, i.e., 2–5 min (Bennett, 1976; Bennett and Ruben, 1979; Hoppeler and Weibel, 2005). Correspondingly, the lower vertebrates lack sufficient tolerance even for moderate activity, and they rapidly run themselves out. Rehabilitation requires a long period; sometimes, complete restoration to an active state takes several hours.

Active flapping flight requires a certain minimal level of energy input, which significantly exceeds the aerobic capacity of the extant reptiles. In particular, the minimal theoretical and empirical levels of energy input for a horizontal flight of the *Melospittacus undulatus* with a mass of 35 g is 3.5 W. The maximal aerobic capacity of a desert iguana (*Dipsosaurus*) of the same size is only 0.4 W (Bennett, 1976; Bennett and Ruben, 1979). A long flight with this energy input will require incredibly large, thin wings. Anaerobic metabolism is unable to safely provide the power necessary for flight, since the fatigue would be fatal. Consequently, the evolution of the flight behavior characteristic of modern birds required the fundamental strengthening of aerobic metabolic systems.

Behavior is the relationship between the animal and environment and, first and foremost, comprises activity, and any complex task-oriented behavior in which long-term activity is only possible with the help of an aerobic metabolism. The emergence of homoiothermy immediately causes the metabolic intensities and, correspondingly, oxygen consumption rates in the vertebrates both at rest and in activity become 10–12-fold higher compared to the poikilotherms of the corresponding mass. This allows for the possibility to multiply increase the activity by elevating the aerobic capacity, which is the most significant result of homoiothermy. However, the homoiotherm exists in the environment, and its energetics follows the strict laws of physics, the most important of which is the law of the conservation of energy. Therefore, the maintenance of a constant body temperature and a satisfactory heat balance with the environment when the ambient temperature changes in a wide range are provided for in the homoiotherms by the preservation of the balance between heat generation and heat dissipation.

With an increase in physical activity, the energetic demands are satisfied by an increase in aerobic metabolism. If the energetic demands exceed the capacity of aerobic system, then anaerobic metabolism adds to energy supply. The oxygen consumption can increase more than 16-fold in both various passerine and non-passerine birds and mammals (Fig. 4; Gavrilov, 1994a, 1995a, 1995b; Suarez, 1996; Gavrilov, 1997). Correspondingly, the energy expenditures for the highest activity reaches the same level of 16 metabolic capacities in various avian and mammalian species (Brody, 1945; Hemmingsen, 1960; Dol'nik, 1969, 1995; Bennett, 1976; Kirkwood, 1983; Suarez, 1996; Gavrilov, 1997), which is illustrated in Fig. 4. An increase in *BMR* leads to an adequate increase in all other levels of energy expenditure (*ME*), namely, maximal potential existence metabolism $MPE = 4BMR$ and maximal aerobic metabolism $MAM = 16BMR$. This expands the range of ambient temperatures appropriate for life, which is conditionally determined as the difference between T_B and T_{II} , and allows the animals to withstand lower ambient temperatures, attain higher activ-

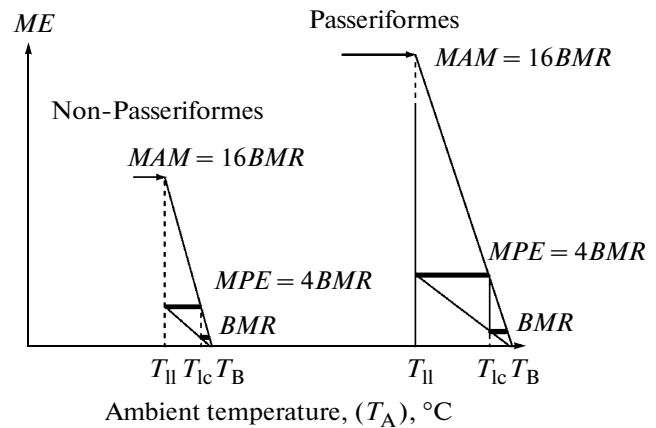


Fig. 4. Scheme demonstrating the energetic effect of the differences in the basal metabolic rates (*BMRs*) between non-passerine (left) and passerine (right) birds with equal body masses. See text for explanations.

ity, and increase their work output (Fig. 4). At $MAM = 16BMR$, the organism could not provide oxygen consumption for an infinitely long period of such high activity. In homoiotherms, an increase in the capacity when passing to each of the standard activities always exceeds the minimal metabolic capacity severalfold (*BMR* capacity), that is, the minimal energy expenditure when of the same “engine” is “idling” that is responsible for activity (Brody, 1945; Dolnik and Gavrilov, 1971; Berger and Hart, 1974; Kendeigh et al., 1977; Gavrilov and Dol'nik, 1983; Calder, 1984). Reptilian lungs are also able to increase oxygen consumption by approximately 16-fold. The oxygen can be consumed at this level for only a very short period, e.g., when escaping from a predator or chasing prey (Bennett, 1976; Bennett and Ruben, 1979; Hoppeler and Weibel, 2005). This limitation in oxygen consumption is absent in, e.g., insects with their tracheal system of oxygen transport. Some insects are able to increase their oxygen consumption 50–200-fold compared to the level at rest (Bennett and Ruben, 1979; Suarez, 1996). Consequently, insects have a considerably wider zone of activity supported by an increase in the aerobic metabolism. Insect hunters should display even higher activity supported by aerobic metabolism.

However, this maximal oxygen consumption is unattainable at a low body temperature and should be preceded by an increase in the tissue temperature to high levels. Although the tracheal system for oxygen transport provides the ability to considerably elevate oxygen consumption, it nonetheless does make it possible to increase the animal's size for purely physical reasons. This size is limited to a mass of approximately 3 g (West et al., 1997; Darveau et al., 2002; Sapoval et al., 2002; Kozłowski and Konarzewski, 2004; Makarieva et al., 2005; Chaui-Berlinck, 2006; Etienne et al., 2006).

In connection with elevated metabolism, due to both activity and heat stress, the heat dissipation capacities of homoiotherms correspond to the balance between the nonevaporative heat dissipations at different temperatures, namely, at the beginning and end of the thermoneutral zone.

Compared to the reptiles, *BMR* had established in the homoiotherms; *BMR*, together with heat conductance, enables the existence of thermoneutral zone, where the heat dissipation changes from minimal (when the animal minimizes its heat losses, minimal heat conductance) to maximal (when the animal maximizes its heat losses, maximal heat conductance). Thus, in away, the ancestors of homoiotherms fixed the maximal level of the reptilian working metabolism and made it their own *BMR*. The *BMR* of homoiotherms is a certain fee for the opportunity to instantly switch to an active state. *BMR* comprises the energy expenditures for the functioning of the systems that never cease working, such as the nervous, circulatory, respiratory, and excretory systems. In addition, the establishment of *BMR* also provides the opportunity to change the heat conductance within the thermoneutral zone. In reptiles, the body temperature decreases with the ambient temperature, and all of these systems function with a capacity of only 3–4% (John-Alder and Bennett, 1987; Hicks et al., 2000; Bennett et al., 2000). To restore a normal operation rate and capacity of these systems, reptiles require time for heating; the larger the animal, the longer the necessary time.

The *BMR* and heat conductance together represent the basic characteristics of the energetics of homoiotherms and determine their level of physiological organization. Both characteristics include architectonics of the circulatory and respiratory systems, as well as the structure of body covers. The circulatory architectonics and the capacities of vasomotor responses are reflected to a greater degree in heat conductance.

The minimal and maximal nonevaporative heat conductances in birds and mammals change with the body mass in a similar manner, and the inclinations of regression lines are equal (Gavrilov, 2011). On the other hand, the maximal heat conductance ($h_{\max}$) is approximately fourfold higher than the minimal heat conductance ($h_{\min}$). The equation $h_{\max} = 4h_{\min}$ suggests that, compared with the minimal capacity, the maximal daily energy consumption from food may reach fourfold values (the level of $4BMR$), but still not exceed this value, since the heat balance preservation requires that the amount of energy consumed from food does not exceed the amount of dissipated heat without an increase in evaporation. An excess amount of consumed energy can be stored in energy depots spent to increase body mass or used to generate certain products (eggs, feathers, etc.), but cannot exceed the level of $4BMR$ for a long periods of time. An empirical model gives the following limit values: $Q_{\max} = MPE = h_{\max}(T_B - T_A)$ at $T_A = T_{lc}$ (T_{lc} is the lower critical temperature and, at the same time, optimal), where it

reaches the value of $4BMR$ (Fig. 1). Consequently, the maximal potential daily metabolism should not exceed $4BMR$ without an increase in the evaporation or the disturbance of the heat balance. For homoiotherms, the maximal *ME* for long periods is $4BMR$, and an animal can spend this amount of energy for an infinitely long time, as long as food is provided. This conclusion in no way contradicts the facts that, when measured, the energy expenditure over one or several days may considerably exceed $4BMR$, since in these cases, either the accumulated reserves are utilized or body mass is spent. Both events later require time and resources for their restoration.

A fourfold increase in the potential *ME* relative to *BMR* has been experimentally confirmed (Calder, 1974, 1984; Calder and King, 1974; Kendeigh et al., 1977; Drent and Daan, 1980; Kirkwood, 1983; Saarela et al., 1989; Bryant and Tatner, 1991; Ricklefs et al., 1996; Gavrilov, 1997; Godfrey, 2003). Thus, both heat conductance and *BMR* are integrated characteristics for the functioning of systems associated with oxygen assimilation and maintaining a constant body temperature.

Reptiles lack such systems; they have no heat insulation covers, and their vasomotor responses are rather poorly developed compared to homoiotherms due to the absence of the separation of the venous and arterial bloods.

The maximal daily average distance covered by reptiles and homoiotherms can be estimated based on the total energy expenditures for activity (E_{act} , W). Numerous studies have demonstrated that the amount of energy spent by homoiotherms for all types of locomotor activity in a common life is 15–20% of the energy for existence (Kendeigh et al., 1977; Dol'nik, 1995; Gavrilov, 2000a). The energy expenditures of the extant reptiles (usually measured in their most active representatives, Lacertidae) is considerably lower, amounting to 3–4% of the *FMR* at an ambient temperature of about 30°C (Nagy, 2005). Correspondingly, E_{act} (W), which depends on the body mass (m , kg) in reptiles, is $0.04m^{0.89}$ (Bennett, 1994; Nagy, 2005, recalculated); in birds, it is $1.41m^{0.68}$ (Gavrilov, 2000a); and, in mammals, it is $1.12m^{0.75}$ (Sthal, 1967, recalculated).

The expenditures for locomotion depend on the locomotion type (flying, swimming, walking, or running) but within each type can be expressed in a general form as the distance covered by the animal's center of mass over one day (S) multiplied by the body mass (m); hereinafter, this is referred to moving on the ground). The energy possessed by vertebrates may be converted into units of work to determine the maximal distance that animal can cover over one day. The energy and work unit in the MKGSS system (kgf m) is the work (*DWO*) performed by a force of 1 kgf by moving the point of application a distance of 1 m in the direction of this force (1 kgf m/s = 9.80665 W; 1 kgf m = 9.80665 J). Applying this procedure to representatives

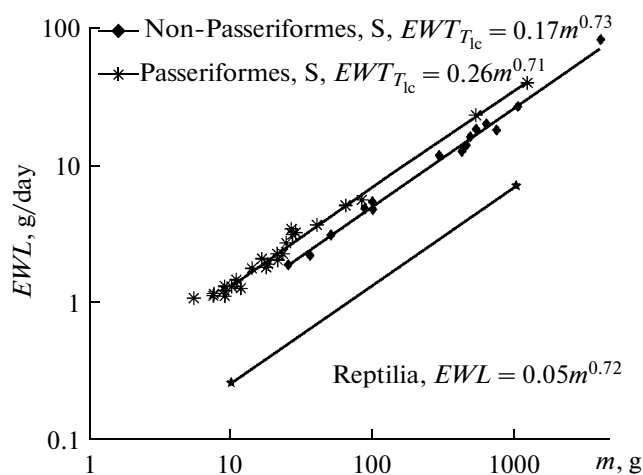


Fig. 6. Dependences of evaporation water losses (EWL) at an optimal ambient temperature (T_{lc}) in different groups of poikilotherms and homoiotherms.

40°C. Because of an apparently small difference in body temperature associated with different temperatures of protein denaturation, the group of mammals with elevated BMR could not have emerged, since the upper critical temperature (T_{uc}) and T_B would be too close to the high temperatures that frequently occur on Earth. Despite significant ecological and energetic advantages associated with a high BMR , the route of increase in BMR did not spread among other homoiotherms, except for passerines. The price paid by passerines for the increase in BMR and the elevated energetic capabilities compared to other orders of homoiotherms is high water expenditures for evaporation (Fig. 6).

OXYGEN SUPPLY TO CELLS AND ORGANS

Although the energy expenditures of poikilothermic vertebrates at rest are considerably lower, part of the cost for this energetic economy is paid by their inability to maintain a high level of aerobic energy supply. In all vertebrates, the levels of oxygen consumption at rest and its maximal consumption display a constant correlation. As is shown above, the oxygen consumption can increase no more than 16-fold on average in both poikilotherms and homoiotherms (Peters, 1983; Kirkwood, 1983; Calder, 1984; Dol'nik, 1995; Gavrilov, 1997). This general conclusion is true, not only for animals active at an optimal body temperature, but also for poikilotherms in a wide range of changing body temperatures; low levels of oxygen consumption at rest are associated with a low level of the maximal oxygen consumption. The mammals in hibernation or torpor are unable to reach normothermic levels of maximal oxygen consumption until they restore the normal body temperature. This low factorial increase is likely to be a standard specific feature of vertebrate physiology and can present a major limitation for the capacities of systems involved in oxygen

supply or utilization (most likely, both). Which particular system limits the oxygen transport in mammals is still being discussed, and the available information for the other vertebrate classes is scarce.

The rate of oxygen transport (heart rhythm, minute volume, and blood oxygen capacity) of the homoiotherms is several times higher compared to poikilotherms. However, these differences remain in tissue sections or isolated cells, when the restrictions connected with oxygen availability are removed. Certain data now suggest that cell membranes in homoiothermic and poikilothermic vertebrates have different molecular structures (Savina, 1992; Palese et al., 2003). The cell membranes of homoiothermic vertebrates contain more channels compared to poikilotherms, which allow the latter to preserve ion gradients with considerably lower energy expenditures. However, drastic differences in the levels of the respiratory chain and molecular architectonics of cell membranes between these two animal groups disappear when analyzing the number and quality of mitochondria in their tissues. The tissues of many poikilotherms contain a tremendous number of mitochondria, even relative to the homoiotherms; these mitochondria display no differences in the content of cytochromes and the other carriers of the inner mitochondrial membrane, as well as in the enzyme activities of the Krebs cycle from the mitochondria of warm-blooded vertebrates (Savina, 1992; Palese et al., 2003). Despite the difference in the body temperature from the remaining homoiotherms, the number of mitochondria in Monotremata, as well as the enzyme activities of the Krebs cycle, is identical to those of marsupials and eutherians (Brice, 2009; Hamilton et al., 2010). Approximately 20–40% of the energy is spent for the proton leak through the inner mitochondrial membrane. The remaining 60–80% are coupled with ATP synthesis, which is necessary to maintain protein synthesis (20–30%); the transmembrane gradients of ions, including Na^+ , K^+ (20–28%) and Ca^{2+} (4–8%); various ATPase activities; and other energy-dependent processes (15–20%). There are certain differences between the vertebrate classes in the proton leak; however, their effect on energetics is rather vague (Brand, 1990; Brand et al., 1991, 2003, 2005; Porter and Brand, 1993; Rolfe and Brand, 1996; Porter et al., 1996; Brookes et al., 1998; Hulbert et al., 2002).

In mammals, erythrocytes are enucleate biconcave cells versus larger nucleated cells in birds. These differences in the shape and volume also influence the ability of hemoglobin to bind and release oxygen. The efficiency of oxygen transfer by erythrocytes depends on the general state of an organism and is accompanied by the changes in cell morphology and volume, as well as the viscosity and permeability of the erythrocyte plasma membrane (Maksimov et al., 1996, 2001; Rodnichenkov et al., 2005; Luneva et al., 2007). Currently, only a few papers deal with the assessment of the changes in hemoglobin state in avian erythrocytes and

the effect of changes in cell shape and volume on hemoglobin state and, consequently, the efficiency of oxygen transfer in the body. However, it is impossible to ignore this issue, since erythrocytes are the main oxygen carrier to the tissues and a mediator in the carbon dioxide removal. Any changes in erythrocyte characteristics can have a significant effect, not only on the rate and efficiency of hemoglobin delivery to the tissues, but also on the characteristics of hemoglobin itself. Thus, the studies that directly address the dependence of hemoglobin conformation on the shape of avian erythrocytes are evidently sparse. The problem here lies in clarifying the precise correspondence between the cell shape and volume on one hand, and the conformation of the oxygen-binding region in hemoglobin on the other (Maksimov et al., 2001).

INCREASE IN AEROBIC CAPACITIES

How could the increase in aerobic capacity have evolved? Considering the diversity of extant reptiles, it is possible to detect potential adaptations in the reptilian metabolic system. It is known that the oxygen transfer potential in the most active species is activated. The lizards of the *Varanus* genus are an illustrative example of these adaptations. Presumably, the higher level of their metabolism results from a considerably increased lung surface area, highly efficient blood buffers, and the high myoglobin content in skeletal muscles (Bennett and Lenski, 1999).

Presumably, a further increase in oxygen processing capacity requires the energy contribution to the structures associated with oxygen assimilation and transfer, e.g., to the development of more capacious lungs and ventilation system or heart compartmentalization, as well as to a considerable increase in blood flow, blood pressure, and blood oxygen capacity. Homoiothermy is implemented based on the muscle metabolism, and involves the metabolisms of many organs. The mitochondrial enzyme activities of crude liver and skeletal muscle homogenates of lizards and mammals match the difference in the levels of aerobic metabolism of the corresponding animals. If the catalytic activity of mitochondrial enzymes is a major limiting factor for the oxygen-processing ability of the animals that had developed a higher metabolic level, then the ability in question could be elevated with the help of minimal genetic transformations via an increase in the volume of mitochondria or the overall chondriome (Bennett, 1976; Bennett and Ruben, 1979; Savina, 1992; Hicks et al., 2000; Palese et al., 2003).

Figure 7 and 8 show the allometric dependences of the heart and lung masses in vertebrates constructed using published data (Peters, 1983; Calder, 1984) and own measurements. It is evident that the lung mass is almost equal in birds and mammals but is considerably higher in reptiles, thereby reflecting their more primi-

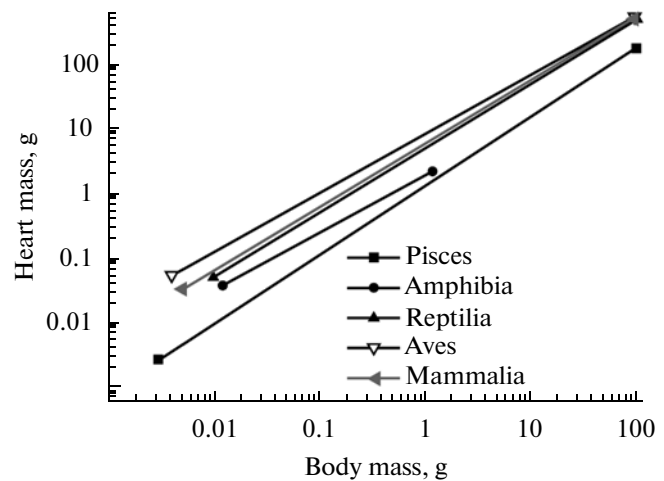


Fig. 7. Allometric dependences of heart mass in vertebrates.

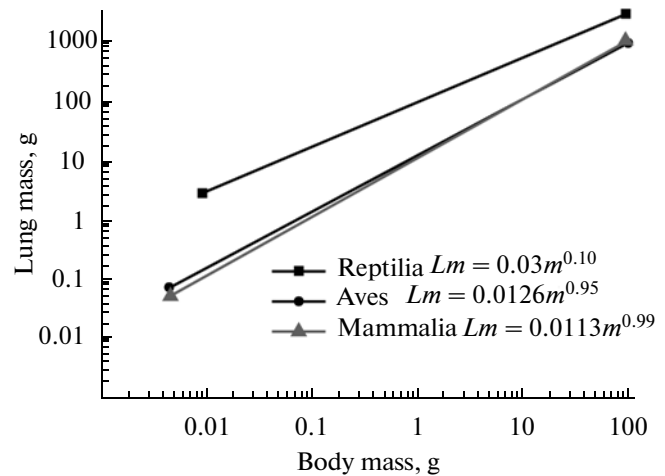


Fig. 8. Allometric dependences of lung mass in vertebrates.

tive structure. As for the heart mass, it is higher in birds but almost equal in mammals and reptiles.

The metabolic intensities and, correspondingly, the oxygen consumption rates in birds and mammals both at rest and in activity are 10–12 times higher than in poikilotherms of the corresponding masses (Fig. 2), but are likely to be attained in birds and mammals in different ways. Mammals, which had developed an aerobic metabolism, emerged in the Triassic, when the oxygen content in the atmosphere was by approximately 50% lower than the current level and even lower than in the Jurassic period (Yanshin, 1997; Ivanov, 2000). A drastic decrease in the total content and percentage of oxygen in the Triassic was connected with the prevalence of arid conditions on the continents (Yanshin, 1997). Under these conditions, mammals got rid of the nuclei in erythrocytes (having obtained enucleate and biconcave cells, where the sur-

face area of the contained hemoglobin was larger), which led to thinner capillaries, while the biconcave shape provided a larger exchange area. Birds, which originated from more advanced reptiles, had established powerful respiratory and circulatory systems and, since they emerged at the time when the oxygen content in the Earth atmosphere approached the present level, had no need to eliminate the nuclei from their erythrocytes.

AEROBIC SUPPLY OF ACTIVITY AND SENSORY SYSTEMS

Intensive blood aeration and high body temperature created the necessary conditions for rapid neural responses and formed a prerequisite for the expansion of the behavioral repertoire. The high activity and, as a consequence, fast and distant migration in space should be provided by the development of the ability to orient in space, which is essential for mobile animals.

Orientation requires the enhanced development of various sensory systems, first and foremost, auditory and visual ones. The maturation of these sensors, the level of their development, the their state, and the functional characteristics in bird ontogenesis strictly correlate with the establishment of homoiothermy. An efficient thermoregulation, with a sufficient oxygen supply to the developing sensors, allows a juvenile to adequately analyze the ambient parameters (Golubeva, 1991).

Experimental data suggest that the functional significance of the increase in *BMR*, both during the evolution (which took place in passerines) and at the level of the individual, should appear as an increase in the work output; lead to an increase in the maximal *ME* and potential productive energy; and, as a consequence, to an increase in the productivity (see Fig. 4).

Thus, natural selection stimulates an increase in the rate of energy metabolism via the control of productive energy balance, that is, an increase in the energy balance towards the energy spent for productive processes and behavior (growth, reproduction, molting, migrations, etc.), as well as for the basic physiological processes underlying the existence of the organism and the possibility of productive activity. An increase in the productive energy balance is attained via the progressive complication of organization, which, on one hand, elevates the energy expenditures for basic physiological processes and, on the other hand, increases the productive energy.

Another important fact is the establishment of the minimal metabolic capacity, which, on one hand, determines other characteristics of the energetic capacity and the level of work output in homoiotherms (this follows from experimental equation (3)) as follows: $DWO = h_f(1 - a\alpha)(T_B - T_A) + a\alpha.BMR$ and, on the other hand, allows an instant transition from rest to activity.

It is impossible to describe all consequences of the emergence of homoiothermy. However, it is important to clearly understand that everything that we have in higher vertebrates is its result. Homoiothermy and, as a consequence, a high aerobic metabolism, had enhanced accelerated development of the sensory systems and brain (Figs. 9, 10). The development of sensory systems and brains allowed behavior to reach a new level and become more complex. Note that the brain mass in the bony fish, which have no problem with oxygen supply due to their bronchial respiration, is even higher than in reptiles (Fig. 9).

An increase in the aerobic capacity and the need of stable temperature conditions in order for the nervous system to function in complex behavior patterns were major selective factors in the establishment of homoiothermy; this is what provided for the metabolic and sensory support of the elevated activity. Birds (and mammals) display a higher level of aerobic metabolism, which is sufficient to provide for complex behavioral patterns that are unfeasible for lower vertebrates. In addition, their homoiothermic state, as well as high and stable body temperature, allows them to avoid the decelerating effect of cold temperatures on both the metabolic support of their behavior and the metabolic level. Independently of definition, behavior is the interaction between an animal and the ambience, that is, first and foremost, its locomotor activity. In this interaction, both the basic and intermediate metabolic rates are changed, as well as the neurosecretory, humoral, and emotional statuses and the work intensity of the sensory systems. All of these processes require an adequate oxygen supply. Correspondingly, any complex goal-oriented behavior is only feasible in the presence of aerobic metabolism.

The emergence of homoiothermy with its aerobic provision for long-term activity and opportunities to regulate metabolic and heat-dissipation levels created many new prospects for birds. The achieved high level of long-term energy utilization provided for longer activity, while its sensory support complicated and diversified the avian (and mammalian as well) behavioral repertoire, allowing them to colonize almost the entire part of the biosphere suitable for life (except for completely exotic habitats, e.g., abyssal).

HOMIOOTHERMY, MINIMAL SIZE, AND PARENTAL CARE

The next most important consequence of homoiothermy is that it led to an increase in the minimal size of birds and mammals. There can be no homoiotherms with weights smaller than 3 g, whereas the body mass of the smallest gecko lizards, *Sphaerodactylus parthenopion* and *S. ariasae*, is 1.5 g. These geckoes, as well as some frogs, are the smallest terrestrial vertebrates on Earth. The size difference between the adults and newborns (or just hatched individuals) is also considerably smaller in homoiotherms. Calculations show

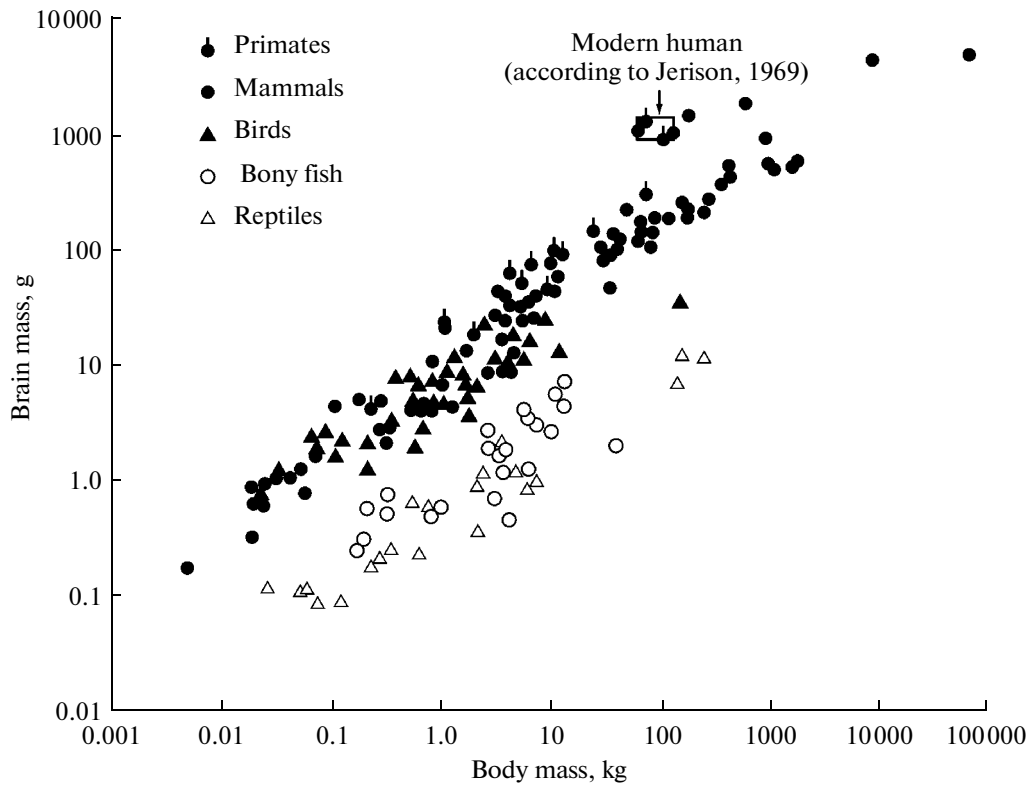


Fig. 9. Dependences of brain mass on body weight in different animal groups.

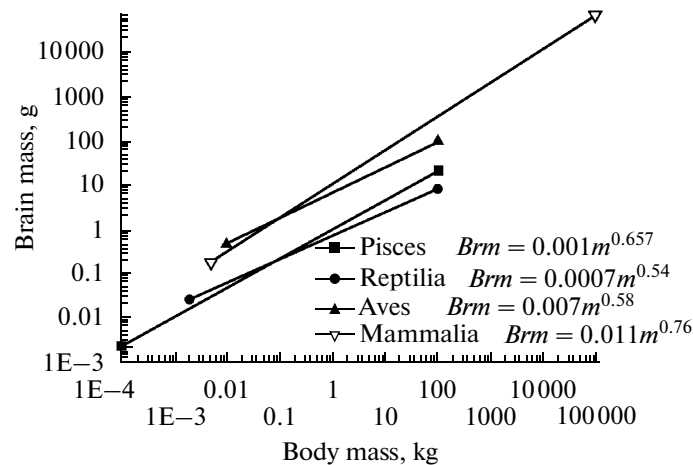


Fig. 10. Allometric dependences of brain mass in vertebrates.

that the mass of bird hatchlings cannot be smaller than the adult weight divided by 32; this result of homoiothermy follows from the equations $h_{\max} = 4h_{\min}$ and $MPE = 4BMR$. The same correspondence (except for the marsupials and some large predators) is also true for the mammals. This is an important result of homoiothermy, which allows birds and mammals to include parental care in their development.

Consider the ontogenesis of birds. As is known, a wide range of ontogenetic patterns with two polar variants, precocial and altricial, is characteristic of birds. The brain of the adult precocial birds is smaller in a statistically significant manner compared to altricial birds; on the other hand, the newly hatched altricial birds have smaller brains than precocial birds. During the postnatal ontogenesis, altricial birds, in many

respects via training, not only catch up with precocial birds in the brain mass, but even considerably exceed them (Stark and Riklefs, 1998). The brain mass of the adult altricial birds exceeds that of the precocial birds in a statistically significant manner.

Parental care allows for information accumulated during life to be transferred to the offspring. Parental care and pronounced homoiothermy were the factors that allowed for the emergence of humans with their ability to hand down the cultural heritage from generation to generation (by the way, this is why the period of childhood in humans is considerably longer as than in any other animals of a similar size). As for large reptiles, the extended care for their offspring was impossible for them due to the significant difference in size between adults and newborns; presumably, this was one of the causes of their rapid extinction.

CONCLUSIONS

Thus, the emergence of homoiothermy and homoiotherms, with the primary intensification of their aerobic metabolism for the sake of increasing their activity, are dated back to the early and mid-Mesozoic period; however, the biospheric conditions prevented them from fully taking advantage of homoiothermy until the mid-Cretaceous period because of insufficient food resources. Only the advent of angiosperms and the associated invertebrate fauna provided the necessary energy channel for the development of homoiotherms. The so-called “mammalization” of theriodonts took place in the Mesozoic period (Tatarinov, 1976). Note here that the higher theriodonts displayed a number of progressive characters absent in sauropsids (for example, they were able to chew their food, which considerably increased the degree of its assimilation by the organism, which presumably had a hair cover, and so on). The “ornithization” of theropods took place at the same time (Kurochkin, 2006). Indeed, the fossils recently found in China and Mongolia suggest that feathered and, in some cases, flying animals had been formed in several different groups of theropods (Kurochkin, 2001, 2006; Kurochkin and Bogdanovich, 2008). Certainly, these flying reptiles were not homoiotherms and their flight was a mere gliding that utilizes terrain features (Unwin, 2003; Pierson, 2009; Lü et al., 2009a, 2009b; Lü et al., 2010).

As the author sees it, plumage in different reptilian groups can be explained by attempts to regulate heat dissipation induced by overheating during activity, as well as to provide thermoregulation connected with the alternation of day and night, since these animals were relatively small.

The morphophysiological basis of homoiothermy was provided by the evolutionary development of body systems associated with the blood circulation, respiration, and development of thermal insulation of body covers. All of these systems allowed for changes in heat

dissipation without intensifying evaporation and the progress in homoiothermy with the obligatory establishment of basic metabolic capacity. The basic metabolic capacity enables homoiothermy to be maintained; however, its origin is connected with the need to maintain a high activity level, rather than the problems in thermoregulation. Thermoregulation is a side product of the increase in aerobic capacity in the establishment of homoiothermy. This episelective evolutionary mechanism is comprehensively described by A.S. Severtsov et al. (1993).

The emergence of terrestrial vertebrates and the establishment of lung respiration, on one hand, and the advent of angiosperms and insects as food resources on the other demanded the enhancement of the overall animal organization. The author believes that a metabolic way of activity support, namely, an increase in the aerobic capacity, is the most significant result and simultaneously a prerequisite for the emergence of homoiothermy. Homoiothermy, with its obligatory aerobic maintenance of long-term activity, requires a constant minimal (basal) metabolic rate. *BMR* was formed as a singular phenomenon and is historically connected with the metabolism in active behavior, rather than thermoregulation. The thermoregulatory muscle tone, which is the basis for chemical thermoregulation in birds and mammals, is lacking in reptiles. Presumably, the stepwise evolution of endothermy in the phylogenesis of birds and mammals led to a metabolic level equal to that developed by reptiles when running at a high temperature. This particular level had become the *BMR* for extant homoiotherms. For about 100 million years, birds and mammals were wallflower, rather than prevalent reptiles. Natural selection allowed animals with high-energy metabolisms to only increase their diversity and abundance when these (homoiothermic) animals could satisfy their substantially elevated demands for food resources. This took place in the mid-Cretaceous with the emergence of angiosperms and increase in the associated invertebrate fauna. The mid-Cretaceous period was a time of global crisis in the terrestrial biocenoses (Rasnitsyn, 1988). According to Zherikhin (1980), “...the late Cretaceous insects differ most drastically from the early Cretaceous insects; however, Cenomanian faunas are already quite typical of the late Cretaceous and retain only a few archaic traits. Presumably, this change, which was the most rapid and drastic in the overall history of insects, was associated with the expansion of angiosperms at the end of the early Cretaceous.” This is the approximate time when the ecological expansion of birds and mammals commenced, manifesting as adaptive radiation. The spread of angiosperms and insects as food resources able to satisfy the homoiotherms, but not the majority of reptiles, adapted to feeding on the preceding mesophytic flora and fauna, enhanced the ecological expansion of homoiotherms. Birds and mammals forced reptiles out of the major niches, colonized var-

ious habitats, and rapidly entered large size classes (mammals entered eight size classes and birds entered six). This was also assisted by a gradual decrease in the global temperature at that time. The fact that homoiothermy, which is a pronounced aromorphosis, smoldered for over 100 million years deep in the bosom of the biosphere, awaiting its time, is also worth special study. Two variants of explanation for this paradox are possible; i.e., either dinosaurs were actually homoiothermic, or the true homoiotherms (mammals and birds) only emerged in the Cretaceous. It is difficult to admit that homoiotherms, which possess a capacity that exceeds that of dinosaurs by one order of magnitude, did not manage to conquer a decent place in biocenoses. The mammals and birds of the Triassic and Jurassic periods were just trial rounds in the biosphere to create animals with developed aerobic capacity and constant (basal) metabolic rate, which enables an instant switch to activity.

The ecological advantages of animals that display a constant minimal (basal) metabolic rate are evident. *BMR* renders the animal able to attain daily work output that is one order of magnitude higher than with a poikilotherm, as well as higher productivity. In turn, the basal metabolic capacity, or *BMR*, determines all the other levels of energy spending, maximal potential existence metabolism, maximal aerobic metabolism, and level of work output (Gavrilov, 1996a, b). These particular energetic parameters determine the ecological potential of species and, correspondingly, their resistance to environmental factors.

As a result, natural selection favors an increase in the energy expenditure for life-sustaining activities, since this considerably elevates the potential of productive work. However, these animals (homoiotherms) can exist only in ecological niches with large and constant energy flow, while niches with small energy flow remain empty, which provides the possibility for species with low energetic demands to successfully exist. High *BMR* is unambiguously correlated with high productivity and high activity of an individual (Gavrilov, 1999c). Individuals that display a high minimal capacity are able to yield high work output (males display high locomotor activity and females produce more eggs). Males with high *BMR* have larger protected areas. A correlation between the work output and its result has been found; i.e., the individuals that spent more energy on reproduction yield better offspring (Gavrilov et al., 1999). There is also a correlation of reproduction success with the survival rate of the offspring and their energetics (Gavrilov et al., 1996a, b).

Thus, the homoiothermy in birds and mammals originated independently and at different geological times. However, in both cases, it was formed as a side product of the selection for upgrading the aerobic metabolism, which provides an increase in activity. The advantages of high and stable body temperature, which is necessarily connected with an increase in

metabolism, induced development of thermoregulatory adaptations, such as fur and plumage. This allowed the metabolically generated heat to be preserved and the heat absorption in hot ambience to be decreased. The capacities of the ventilation, respiratory, and enzymatic systems of extant reptiles is completely able to maintain the level of the homoiothermic metabolism at rest. The contemporary reptiles have considerably reduced aerobic limits and functional anaerobic system for the provision of a short-term activity (Bennett, 1991; Bennett and Lenski, 1999).

The emergence of homoiothermy with the aerobic maintenance of long-term activity and the possibility to regulate the levels of the metabolism and heat dissipation created new vistas for homoiotherms. Attaining this level of long-term energy utilization made it possible to extend the activity period, and its sensory support complicated and diversified the avian behavioral repertoire, as well as that of mammals, and allowed them to colonize almost the entire part of the biosphere suitable for life. This was enhanced by including parental care into their ontogenesis, as well as transmitting the information accumulated during their lives to the offspring. It is assumed that some burrowing dinosaurs made attempts to nurse their offspring (Varricchio et al., 2007). Evidently, the degree of parental care increases from amphibians and reptiles to birds and mammals.

High levels of aerobic metabolism in birds and mammals have been attained in parallel in various groups of their reptilian ancestors. The level of homoiothermy when aerobic metabolism enables fairly long activity was formed in birds and mammals in different ways; they have differently disjoined venous and arterial systems, nucleated or enucleate erythrocytes, and different lung structures that concurrently displayed equal minimal metabolic capacities and similar body temperatures, corresponding to the environmental conditions on Earth.

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