Energy assimilation, parental care and the evolution of endothermy

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The question of the selection forces which initiated the evolution of endothermy in birds and mammals is one of the most intriguing in the evolutionary physiology of vertebrates. Many students regard the aerobic capacity model as the most plausible hypothesis. This paper presents an alternative model, in which the evolution of endothermy in birds and mammals was driven by two factors: (i) a selection for intense post-hatching parental care, particularly feeding offspring, and (ii) the high cost of maintaining the increased capacity of the visceral organs necessary to support high rates of total daily energy expenditures.

Keywords: basal metabolic rate; energetics; evolutionary physiology; life history; vertebrates

1. INTRODUCTION

Birds and mammals are endothermic homeotherms, i.e. they are able to maintain a relatively constant, elevated body temperature (homeothermy) by means of a high rate of energy metabolism (endothermy). The principal characteristics of endotherms are high levels of resting or basal metabolic rate (RMR and BMR) and daily energy expenditure (DEE), which require a high rate of food acquisition. Thus, although the advantages of the ability to maintain high body temperature are easily recognized (e.g. the ability to sustain activity in the cold), it is not clear what selection forces initiated the evolution of this 'wasteful' strategy of energy use (see the reviews in Hayes & Garland (1995) and Ruben (1995)).

Of several hypotheses proposed, the 'aerobic capacity model' has been regarded as the most plausible (Bennett & Ruben 1979; Hayes & Garland 1995; Ruben 1995). According to this model, the evolution of endothermy was driven by selection favouring high sustainable loco-motor activity supported by aerobic metabolism.

A critical assumption of the model is that the capacity for aerobic metabolism and the BMR are physiologically linked, so that the selection for high aerobic capacity results in increased BMR as a correlated response. However, the maximum aerobic metabolism depends on muscular work, whereas the BMR results primarily from the metabolism of the visceral organs (Hayes & Garland 1995; Ruben 1995). A few mechanisms linking the aerobic capacity and BMR have been suggested, e.g. increased leakiness in plasma membranes, increased mitochondria density and the enhanced support function provided by the visceral organs (Else & Hulbert 1981, 1985, 1987; Ruben 1995).

Whatever the mechanism, a positive correlation between the maximum aerobic metabolic rate and BMR is expected if the assumption is correct. Numerous studies, both inter- and intraspecific, have provided only mixed support for the hypothesis (see the review in Hayes & Garland (1995)). Moreover, the ratio of maximum to resting metabolic rate, both in ecto- and endotherms, varies from at least six to more than 35 and large increases in aerobic capacity may cause only small increases in the costs of maintenance (e.g. Kamel & Gatten 1983; Koteja 1987; Hoppeler & Turner 1989).

There is also no clear evidence that genetic selection for a high aerobic capacity or endurance training results in a significantly increased BMR (e.g. Konarzewski *et al.* 1997; Wilmore *et al.* 1998). Finally, it has been suggested that theropod dinosaurs were able to achieve maximum rates of aerobic metabolism as high as that of endotherms, despite maintaining the low levels of resting and routine metabolic rates typical of ectothermic reptiles (Ruben *et al.* 1999). Such a hybrid type of physiology would be superior to both ectothermic and endothermic strategies of energy use (Wuethrich 1999), at least from an engineering point of view. If the hybrid physiology was indeed possible, the selection for high aerobic capacity alone would be unlikely to support wasteful, endothermic energetics.

In this study, an alternative model is offered in which endothermy evolved as a side-effect of two factors: (i) natural selection favouring intensive post-hatching parental care, and (ii) the high cost of maintaining the visceral organs.

2. THE ASSIMILATION CAPACITY MODEL

Suppose that, similar to the aerobic capacity model, natural selection acts in favour of increased locomotor activity (figure 1, bottom panel). It will be shown later that such increased locomotor activity may have been necessary for the evolution of enhanced parental care. Other things being equal, more active individuals should have their total DEE increased and, consequently, increased rates of food consumption and energy assimilation. A higher rate of energy processing requires an increased capacity of the alimentary tract and other visceral organs, i.e. the liver, kidneys and heart (e.g. Karasov & Diamond 1985). As the visceral organs are responsible for a greater proportion of the BMR (at least in mammals) (e.g. Wieser 1986), an increase in the BMR should occur as a correlated response to selection for a high overall rate of energy processing. A higher BMR contributes to a further increase in the DEE, with a consequent requirement for an increased rate of food gathering, which may require additional time and energy investments in locomotion and again an increased DEE. Thus, selection favouring behaviour requiring an increased DEE can initiate a self-reinforcing (cf. Szarski 1971), inflationary evolution of the
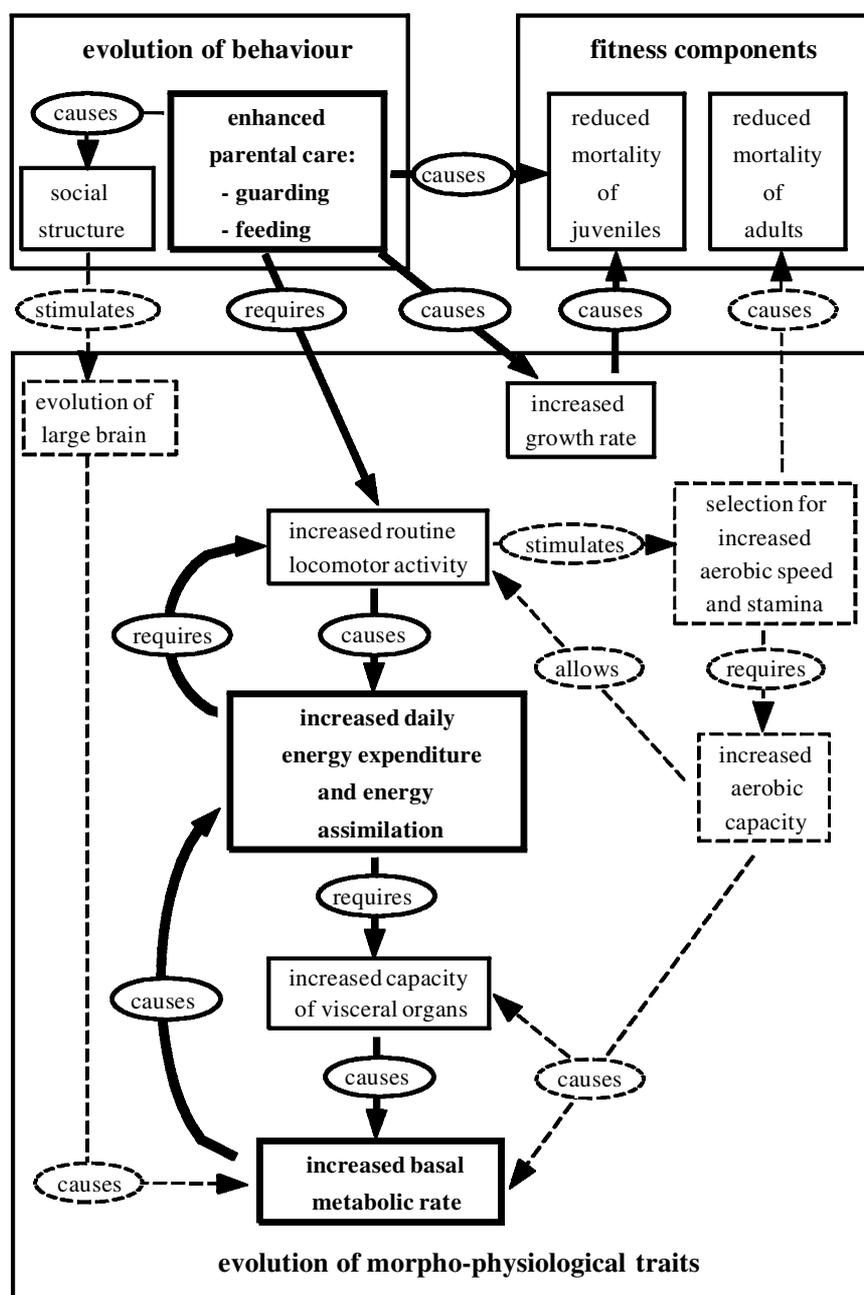
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Figure 1. Box-chart model of the hypothetical evolution of endothermy driven by the evolution of intense, post-hatching parental care. Heavy lines indicate the hypothetical main causal links leading to an increased BMR and broken lines show the additional mechanisms contributing to an increased BMR in endotherms. See §§ 2 and 3 for further explanation.

energy budget leading to high BMRs. This scenario could be described as the 'assimilation capacity model' (figure 1, bottom panel).

Although the aerobic capacity model includes expansion of the size and metabolic activity of the visceral organs as an important element, the scenario proposed here is not a simple 'reworking' of the classical model. The aerobic capacity model emphasizes a difference between short bursts of activity (a time-scale of seconds to minutes) which can be supported by anaerobic metabolism and sustainable locomotor performance requiring aerobic support (a time-scale of minutes to hours). The assimilation capacity model goes one step further and emphasizes that the total DEE must be balanced by the energy assimilated from food (a time-scale of hours to

many days). Consider two situations from the perspective of DEE. First, the upper limit to locomotor activity and maximum aerobic metabolism can be increased without increasing the total energy expenditure if the time spent resting is extended accordingly. Second, the total energy expenditure can be increased by spending more time in moderate activity, without approaching the ceiling for aerobic capacity. An evolution towards a higher RMR would occur in the first situation according to the aerobic capacity model, but in the second situation according to the assimilation capacity model proposed here.

Increases in aerobically supported locomotor performance may grant a better chance of escaping predators or capturing prey. This almost directly contributes to Darwinian fitness and can therefore be a target for

natural selection (Jayne & Bennett 1990). Although increasing routine levels of activity and extending the duration of the activity also has advantages, e.g. associated with gathering food, the potential gains are offset by the proportional increases in energy expenditure. If the evolution towards endothermy was driven by increases in routine levels of activity and DEE, as suggested here, the model must propose a mechanism linking the increases in energy expenditures with clear rewards in fitness.

3. CORRELATED EVOLUTION OF PARENTAL CARE AND ENDOTHERMY

Evolutionary ecologists agree that decreasing juvenile mortality and accelerating growth to maturity are among the most effective ways of increasing fitness (Kozłowski 1992; Sterns 1992; Kozłowski & Weiner 1997). Both of those aims can be facilitated by intensifying various forms of parental care (Clutton-Brock 1991). Although the forms of parental care differ between birds and mammals, in both groups of endotherms the highest DEEs are observed during a period of intense parental care: feeding the juveniles (Daan *et al.* 1990; Weiner 1992; Hammond & Diamond 1997). Such an intensive form of parental care is unknown in extant reptiles (Clutton-Brock 1991). Thus, selection for offspring-feeding behaviour seems to be a good candidate for the mechanism leading to parallel evolution of birds and mammals.

Large macroevolutionary events could begin with a small change in behaviour not requiring any morphological or physiological adaptations (Garland & Carter 1994). The evolution of endothermy could have begun with guarding hatchlings and, at a later stage, involved bringing food to the offspring (figure 1, upper panel). Guarding hatchlings, present in some extant reptiles, can obviously decrease mortality of the young (Clutton-Brock 1991). Supplying offspring with food is a simple extension of the behaviour. Initially, the young could have just used the leftovers of the prey captured by the parent. An immediate advantage of such behaviour is reduced mortality of the young, who do not have to search for food. Thus, natural selection could favour parents who captured more prey than they ate and those who allowed their offspring to eat whatever was left.

Up to this point, the hypothetical evolution concerned only behaviour. However, once the offspring-waits–parent-brings-food strategy is established, the morphology and physiology of juveniles could be subject to selection for optimal resource allocation enabling maximization of growth rates. An increased growth rate contributes again to decreased mortality of the young. When food available to the young is not a limiting factor, it is optimal to allocate as much energy as possible to the organs related to energy assimilation at the early stage of the growth (Konarzewski *et al.* 1990). Thus, a maximum growth rate is possible when the young minimize investments into locomotor activity. However, their parent (or parents) must be able to provide excess food and protect them, which involves increasing their locomotor activity and, consequently, their DEEs. As explained earlier, behaviour leading to an increased DEE is likely to result in an increased RMR.

The evolution of parental care creates a social structure which might stimulate evolution towards increased mental capabilities (the ability to learn from parents) and larger brain size. Although a hypothesis that selection for increased brain size was a major mechanism driving the evolution of endothermy does not seem plausible (Hayes & Garland 1995), the mechanism could contribute to an increased BMR in the model presented here (figure 1, left side of the bottom panel).

When the level of the routine locomotor activity of parents approaches the maximum aerobic speed, selection for increased aerobic capacity should also occur. This includes an increased capacity of muscle mitochondria, the development of a circulatory and ventilation system and postural changes, all of which can also contribute to an increased BMR, as proposed by the aerobic capacity model (figure 1, right side of the bottom panel). Thus, the evolution of parental care could be a driving force behind the inflation of DEEs, the capacity for energy assimilation and the maximum aerobic metabolism and BMR—the combination of characters defining the endothermic physiology of birds and mammals.

The scenario outlined in this study has an important property which makes it a plausible evolutionary hypothesis: an enhancement of any of the elements (e.g. a higher capacity to assimilate energy by young or increased rate of supplying food by parents) increases the evolutionary advantages of the changes in all the other elements of the scheme (figure 1). Such a positive feedback mechanism may be a necessary condition for a rapid macroevolutionary process to occur (Szarski 1971, 1983).

The idea that the evolution of intense parental care is related to the evolution of endothermy is not new (Hopson 1973; Case 1978). However, both Hopson (1973) and Case (1978) suggested that endothermy was a factor enabling or even forcing altricial development and intense parental care. They argued that altricial development was a way of avoiding the high thermoregulatory costs of offspring and that intense parental care was necessary in order to meet the high energy requirements of rapidly growing, endothermic young. This paper proposes the completely reverse scenario, in which the selection for intensified parental care started a self-reinforcing chain of behavioural and morphophysiological adaptations leading to endothermy. No single stage of the scenario of the evolution of parental care presented above requires endothermy as a pre-adaptation. If the scenario proposed here is true, the juveniles of early mammals and birds (and their ancestors) were not endothermic, unlike the assumption of Hopson (1973). The thermoregulatory capability of young precocial birds and mammals would be a result of the later evolution of that developmental strategy, which happened independently in several lineages of both birds and mammals.

More recently, Farmer (1998, 2000) proposed that the evolution of endothermy was driven by the development of active incubation, which would lead to the evolution of an increased metabolic heat production (thermogenesis) and control of an elevated body temperature. The immediate advantages were an increased growth rate of the offspring and improved developmental stability. The increased heat production necessary for thermoregulation was achieved by an increased leakiness of plasma

membranes, particularly in the visceral organs (see also Else & Hulbert 1987). Thus, according to Farmer's (2000) model, the high leakiness of membranes and high BMR were 'adaptive' from the very beginning of the evolution of endotherms, whereas a high total DEE was (partly) a consequence of the selection for a high BMR. Such a scenario is, in a sense, the opposite of the one proposed in this study. According to the model in this paper, the high total energy demand associated with feeding offspring required a high metabolic performance from the visceral organs. The increased membrane leakiness was a side-effect of the ability to achieve a high metabolic rate at the cellular level (perhaps associated with the capacity for cross-membrane transport of molecules) (Clausen *et al.* 1991; Ruben 1995). Thus, in this model, the energy loss due to an increased BMR was originally a waste. However, the waste could be used for thermoregulation and incubation, giving all the advantages proposed in Farmer's (2000) model.

Although the two models differ with respect to the suggested proximate mechanisms, they agree on the most important point: the evolution of endothermy (or any other complex adaptation) cannot be understood and explained without looking at the whole life history of organisms. To quote Farmer (1998), the hypotheses are 'distinct from previous theories in proposing that endothermy is primarily beneficial to offspring rather than to the individual organism and is but one character in a mosaic that are all related to parental care'.

4. TESTING THE MODEL

Bennett (1991) alleged that it may be foolhardy to attempt to determine the types of selection that have acted on unknown, extinct organisms in poorly understood environments when we are hardly able to understand the selection forces in populations of extant species. At best, we can attempt to reject some of the hypothetical scenarios of evolution. However, specifying clear falsification criteria is difficult, as discussed by Hayes & Garland (1995) in the context of the aerobic capacity model.

The core of the model proposed here can be expressed as two statements: (i) the evolution of endothermy was triggered by a selection for increased parental effort, in particular feeding offspring, and (ii) the increased total energy expenditure by parents required an increased performance from the visceral organs, which resulted in an increased RMR.

Although the survival of offspring depends on the amount of parental care the offspring receive (Clutton-Brock 1991), it does not imply that an additional effort will always result in increased Darwinian fitness of the parent. An answer to the question about the optimum resource allocation into current and future reproduction requires not only a knowledge of physiology, but also detailed, quantitative knowledge of population parameters, e.g. the density and age dependence of mortality and the state of population dynamics (e.g. Kozłowski 1992). We will never assess those parameters for extinct populations of the hypothetical ancestors of endotherms. Thus, even if we dared to specify the exact conditions under which a correlated evolution of parental care and endothermy should happen, such a hypothesis would not

be falsifiable. However, we can attempt at least one general prediction.

In agreement with fossil data, the model proposed here allows one to predict that the correlated evolution of parental care and endothermy should have happened in widely foraging carnivores rather than in herbivores. First, in herbivorous species, which rely on food which is easy to obtain, the young would not greatly benefit from having the food brought to the nest. Second, low-quality food is difficult to carry and is usually consumed on-site; thus, at the initial stage of the proposed scenario an abrupt change in behaviour would be necessary in a herbivore. Finally and most importantly, the model requires that the costs of locomotor-related activities comprise a large part of the total energy expenditure (otherwise even a large increase in locomotor activity would not result in substantially increased total energy expenditures). This is likely to happen in widely foraging predators (e.g. Secor & Nagy 1994; Gorman *et al.* 1998; see also electronic Appendix A on The Royal Society Web site) but not in herbivores (Garland 1983). Thus, the model would have been falsified if the ancestors of a lineage of endotherms were herbivorous. Neither of the previously proposed hypotheses (Hayes & Garland 1995) allowed one to predict whether the evolution of endothermy should begin in herbivores or carnivores.

Other palaeontological data can contribute to the discussion, but clear falsification criteria are difficult to define. An indication of the nesting behaviour or close association of adults and juveniles in early endotherms and their immediate ancestors would be consistent with the hypothesis. Indeed, some fossil data suggest a possibility of social organization in cynodonts, where adults and juveniles lived together (Blob 1998). However, an absence of nests in the fossil record cannot be treated as a falsification of the model (e.g. a fossil record would hardly remain from the lion's den). Moreover, the evidence of parental care is also compatible with the model proposed by Farmer (2000) and it is not incompatible with the aerobic capacity model.

Where direct tests based on palaeontological data are scarcely available, we are left with indirect inferences based on the behaviour, physiology, morphology and genetic architecture of the extant species. The tests of the aerobic capacity model focused on examining the correlation between the basal and maximum metabolic rates (Hayes & Garland 1995). In the model proposed here an equivalent assumption is that the BMR should be correlated with a maximum rate of energy processing which can be sustained over a long time-scale (SusMR (sustained metabolic rate) *sensu* Hammond & Diamond 1997). In addition, both the BMR and SusMR should be correlated with the capacity of the visceral organs.

A close correlation between the capacity of the visceral organs and maximum rate of energy assimilation or maximum SusMR has been observed at the levels of (i) within-individual phenotypic flexibility, (ii) variation among individuals, and (iii) variation among species. However, the association between the size of the visceral organs and the BMR, and between total energy expenditures and the BMR, is not so clear (see the reviews by Koteja (1991), Weiner (1992), Ricklefs *et al.* (1996), Hammond & Diamond (1997) and Piersma & Lindström

(1997)) (more detailed information is presented in electronic Appendix A).

Thus, similar to the case of the aerobic capacity model, analysis of the phenotypic correlations between the morphophysiological traits in extant species provided only mixed corroboration for the model proposed here. However, as has been pointed out by Hayes & Garland (1995), even if clear correlations were detected, the results would not provide sufficient support for the model. Moreover, the lack of expected correlations would not be enough to falsify the model either. This is because neither of the three sources of observation used in the studies cited above provide information about the additive genetic correlation between the hypothetical trait which is selected (parental effort measured as DEE) and the trait affected indirectly (BMR) in the hypothetical populations which founded the lineages of endotherms (cf. Hayes & Garland 1995).

Although there is no way of assessing the information on genetic correlations in extinct populations, the tests of the evolutionary hypotheses can and should include studies on genetic correlations in extant populations (Garland & Carter 1994; Hayes & Garland 1995). One way of obtaining the information is to study inbred strains. For example, Konarzewski & Diamond (1995) found that variations in intestine and heart mass contributed to variation in the BMR among six inbred strains of laboratory mice, whereas a correlation between the BMR and the mass of the liver or kidney also appeared significant in comparisons of individual mice within the same strain.

A promising tool for testing evolutionary hypotheses is artificial selection (Garland & Carter 1994). Consistent with the model proposed here, laboratory mice selected for a high food intake rate (Bünger *et al.* 1998) and rats selected for increased locomotor activity (Randquist & Bellis 1933) evolved a higher BMR. Recently, Garland and colleagues (Swallow *et al.* 1998*a,b*; Koteja *et al.* 1999*a,b*) selected for increased voluntary wheel running, measured as the number of total daily wheel revolutions. Over the first ten generations, the increase in the distance run (70%) was achieved principally by an increased running speed (46%), rather than time spent in the activity (16%). As expected, an increased aerobic capacity was observed as a correlated response (Swallow *et al.* 1998*b*), but only a small increase in daily food consumption was seen (Koteja *et al.* 1999*b*). In such a situation, an increase in the BMR is expected according to the aerobic capacity model, but not if the assimilation capacity model is correct (obviously, a necessary condition for any change in the BMR is the presence of additive genetic variance for that trait). A clearer distinction between the models would be possible in an experiment with a few replicate lines selected for a high level of maximum sustained running speed and a few other lines selected for increased total time spent in locomotor activity. An evolution towards a higher BMR should occur in the first group according to the aerobic capacity model, but in the second group according to the model in this paper.

Obviously, artificial selection experiments (and other methods of studying genetic correlations) are not a panacea and their results should be interpreted with great caution. Any evolutionary inferences rely on the assumption that the genetic architecture in the experimental population is similar to that in the hypothetical ancestral population and that the environmental conditions of the experiment are relevant in the context of the hypothesis tested. Ignoring the latter may lead to confusion. For example, selection for a high growth rate in domestic fowl chicks did not result in an increased BMR (Visser (1991), after Konarzewski (1995)). At first glance it seems that this result contradicts both the model presented here and the model proposed by Farmer (2000), because both models assumed that an increased growth rate was the major advantage which allowed the evolution of a high BMR. Note, however, that the models assumed a correlation between the growth rate of the offspring and metabolic rate of their parents, who had to work hard to supply enough food (my model) or generate heat for thermoregulation (Farmer's (2000) model). I believe an analogue of increased parental metabolic rate must have occurred during the experiment with the chicks: an increased cost per day of maintaining the experimental colony.

To conclude, studies on genetic correlations will not reveal whether the evolution of endothermy did happen according to a particular model. However, the experiments can provide strong evidence that selection for one of the traits (e.g. parental effort) will result in a change in another trait or traits (e.g. the BMR) in extant populations. Thus, the experiments can show which evolutionary paths are possible.

Since a seminal article by Drent & Daan (1980), the problems of the limits to the long-term, sustainable energy budgets of animals and of the relation between energy budgets and the BMR have increasingly become the focus of research (see electronic Appendix A). I believe the model proposed here will add a wider evolutionary perspective to that framework, similar to the way in which the aerobic capacity model has boosted research on the evolutionary physiology of locomotion, exercise and the limits to aerobic metabolism (Garland & Carter 1994; Hayes & Garland 1995).

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