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Importance of prenatal temperature experience on development of the thermoregulatory control system in birds☆

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Abstract

The goal of this paper is to describe the prenatal developmental processes of the thermoregulatory system occurring during the last third of embryogenesis in precocial embryos and its influence on the postnatal efficiency of thermoregulatory control elements. For this, in embryos of the domestic chicken (*Gallus gallus*) and the Muscovy duck (*Cairina moschata*) the internal core temperature, the heat production and oxygen consumption, respiration rate after internal pipping, the peripheral blood flow in the chorioallantoic membrane were measured and the Q_{10} of heat production was calculated. The experiments show that (1) thermoregulatory behaviour is developed after internal pipping in avian embryos, (2) avian embryos show endothermic reactions, (3) hyperthermia causes a down-regulation of heat production in precocial avian embryos, (4) in contrast to heat production, the efficiency of heat loss is high in precocial embryos, (5) the development of physiological control systems starts with non-coordinated and proximate (immediate) non-adaptive reactions.

It is concluded, that strategies of avian embryos in relation to temperature regulation are developed optimally. Endothermic reactions occur very early during the embryonic development but their efficiency is limited. Due to the van't Hoff rule, low temperatures decrease the net heat production but the trajectories of endothermy are stimulated and related epigenetic adaptation mechanisms are activated. Using behavioural mechanisms, the embryo is protected against super-cooling during the natural incubation process. The heat loss mechanisms are most efficient against heat stress, which occurs only for a very short time during incubation and protect the embryo against disturbances caused by hyperthermia.
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1. Introduction

Following the glossary of terms of thermal physiology [1], endothermy is the pattern of thermoregulation in which the body temperature depends on a high (tachybolic) and controlled rate of heat production (HP). That means that a decrease of ambient temperature (T_a) results in an increase of HP.

The measured HP of endothermic animals at temperatures below the thermoneutral temperature is the result of two dif-ferent processes: the thermoregulatory HP and the energy metabolism following the van't Hoff rule [2]. In avian embryos a drop of colonic temperature (T_c) or temperature of the allantoic fluid (T_{af}) due to low T_a causes mostly a decrease of net HP but the decrease is more moderate as to be assumed by the van't Hoff rule [3] (Fig. 1).

Some results in the scientific literature support the assumption, that in embryos of precocial birds endothermy does not exists: Romijn and Lockhorst [4] could not find any signs of metabolic compensation for cooling in fowl eggs, even in 20-day-old embryos. In the embryonic Willow ptarmigan (*Lagopus lagopus*), no endothermic reactions occur [5] but the magnitude of the decrease in HP during cooling was consistent with some thermoregulatory capacity, that is, that the response was not entirely that of a poikilothermic. Wedge-tailed Shearwater (*Puffinus pacificus*), a semi-precocial bird
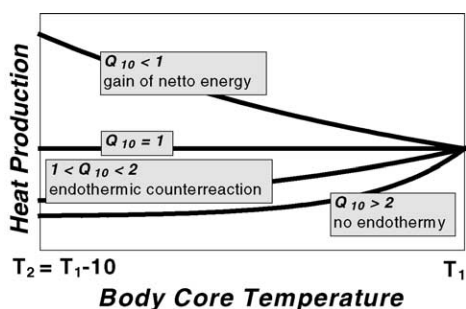

Fig. 1. Schematic relationships between body core temperature and heat production at different Q_{10} [15].

with a long (52 day) incubation period appears unable to initiate and sustain any effective cold-induced thermogenesis before hatching, even though access to oxygen appears to improve substantially during pipping.

In ontogeny, the body temperature will be regulated by different control elements like thermoregulatory behaviour, HP as well as heat loss mechanisms. The importance is different in different phases of development [6]. The aim of this paper is to describe the prenatal developmental processes of the thermoregulatory system occurring during the last third of embryogenesis in precocial embryos and is influence on the postnatal efficiency of thermoregulatory control elements. Some results of the experiments where described elsewhere [2,3,7,9,15,21,22,38].

2. Material and methods

A useful methodology for estimating the function of thermoregulatory control elements in the prenatal period using the example of Muscovy ducks and domestic fowl was developed and described elsewhere [7,8].

Shortly, eggs of the Muscovy duck (*Cairina moschata*) and domestic fowl (*Gallus gallus*) were incubated at 37.5 °C and a relative air humidity of 70% and turned automatically until the start of the experiment. During the experiments internal egg temperature measured as the temperature of the allantoic fluid (T_{af}) was determined using miniature thermistor probes or thermocouples consisted of two glass-fibre insulated thermal wires (NiCr–Ni, with an accuracy of 0.1 °C between 20 and 40 °C). The colonic temperature (T_c) of the embryos was measurable after internal pipping (days 20 or 21 in fowl embryos and days 33–35 in Muscovy ducks embryos). This method was unsuitable earlier in incubation, because of the risk of haemorrhages [9]. After washing the eggshell with alcohol (70%), nearly 1 cm^2 of the eggshell and the underlying egg membranes in the area of the sharp egg pole were removed. The tail feathers of the embryo were identified by their length and their linear form. After locating the tail feathers, the cloaca was easily identified and the thermoelements were inserted through the vent to a depth of 1–2 cm. Finally, the hole in the eggshell was sealed with dental wax.

Oxygen consumption was measured in single embryos using an oxygen-analyser based on the paramagnetic principle. It was connected to metabolic chambers (cylindrical form, volume roughly 290 cm^3) consisting of transparent acrylic.

During the measurements the chamber was supplied with room air by membrane pumps. Magnetic valves were used to switch in succession the single streams of gas from the different chambers to the oxygen analyser. The unanalysed streams of gas were emitted into the room. A separate pump was used to bring room air to the analyser for the measurement of the difference in oxygen concentration after changes caused by embryo. Additionally gas from the chambers passed through a membrane filter and a highly sensitive flow meter. During the experiments, the chambers were placed in a thermostat controlled water bath to obtain precise temperatures.

Respiratory movements before internal pipping were measured after removing the egg shell and the outer shell membrane from above the air cell and replacing it by a special glass vessel. Changes in the vessel pressure fluctuations gave information about the respiratory rate. Respiratory movements after internal pipping were registered by measuring of the pressure changes occurring in the air cell. Besides the respiratory rate, the relative tidal volume and the relative respiratory minute volume could be estimated.

Peripheral blood flow was measured in the chorioallantoic membrane by the instrument MBF3 (Moor Instrument Company, Ltd., Devon, EX13 5DT, England), which uses the laser Doppler principle.

Jacobus Hendrik van't Hoff ideas concerning the relationships between ambient temperature and the velocity of chemical reactions were summarised by the reaction–velocity–temperature (RVT) rule (van't Hoff rule) and described the relationships between temperature and reaction velocity in a chemical solution. Based on the van't Hoff rule, a temperature increase by 10 °C increases the reaction velocity by a factor of 2.0–4.0 [11].

Later, the Q_{10} idea was applied to biological systems. In this case, k_1 is the performance of the examined biological system at one temperature (T_1) and k_2 at another (T_2). T_1 is always the lower than T_2. Biological systems described by Q_{10} may include oxygen consumption or HP [7,8] and the firing rate of neurones [10].

From the practical point of view in biological systems the Q_{10} may be calculated using the equation:

$$Q = \frac{k(T + n)}{kT}$$

if the temperature difference (n) is equal to or near 10. When the temperature differences (n) are much smaller, the formula:

$$\log Q = \frac{10}{T_2 - T_1} \times \log\left(\frac{k_2}{k_1}\right)$$

should be used. Other notations [11] are $Q_{10} = (k_2/k_1)10/(T_2 - T_1)$ or $\log Q_{10} = 10 \times [(\log k_2 - \log k_1)/(T_2 - T_1)]$ The logarithmic notation is necessary because the theoretical ba-

Table 1
Threshold temperature (T_{af} °C) of $Q_{10} = 2.0$ (heat production) in fowl and Muscovy duck embryos

Fowl embryo					Duck embryo				
31.5			34.5 °C		31.5 °C			34.5 °C	
DI	n	T_{af}	n	T_{af}	DI	n	T_{af}	n	T_{af}
12	4	34.02 ± 0.36	6	36.27 ± 0.35	20	6	35.08 ± 0.50	5	36.46 ± 0.42
13	6	34.98 ± 0.25	4	36.82 ± 0.57	21	6	35.60 ± 0.17	4	36.97 ± 0.73
14	5	35.58 ± 0.28	6	36.43 ± 0.89	22	6	35.33 ± 0.37	5	36.46 ± 0.45
15	6	35.45 ± 0.48	6	37.27 ± 0.39	23	6	35.83 ± 0.40	5	36.62 ± 0.39
16	6	34.93 ± 0.67	6	36.83 ± 0.24	24	6	35.20 ± 0.27	4	36.35 ± 0.19
17	6	35.03 ± 0.65	6	37.20 ± 0.79	25	6	35.03 ± 0.69	3	36.37 ± 0.32
18	6	34.95 ± 0.54	1	36.70	26	6	34.90 ± 0.29	4	36.35 ± 0.26
19	6	35.48 ± 0.44	3	37.40 ± 0.26	27	6	35.07 ± 0.34	3	36.27 ± 0.32
20	6	34.87 ± 0.59	0		28	6	35.67 ± 0.32	2	36.10 ± 0.42
21	6	34.43 ± 0.48	2	37.15 ± 0.49	29	6	34.92 ± 0.44	3	36.83 ± 0.11
					30	5	34.56 ± 0.76	5	36.66 ± 0.30
					31	6	34.32 ± 0.68	3	36.43 ± 0.40
					32	5	34.24 ± 0.61	1	36.40
					33	5	34.84 ± 0.65	2	36.60 ± 0.28
					34	5	35.40 ± 0.28	4	37.70 ± 0.48

DI: day of incubation [20].

sis of Q_{10}, the Arrhenius equation, is an exponential function [1].

Whittow and Tazawa [12] showed that, in fowl embryos at a very early stage of development (aged about 12 days) in which no endothermic reaction occurs, Q_{10} of HP is 2.0–2.4. Hence, a Q_{10} of more than 2.0 demonstrates the absence of endothermy. A Q_{10} lower than 2.0 indicates that an endothermic reaction occurs. When the Q_{10} is lower than 1.0 the increase in HP due to the thermoregulatory mechanisms is greater than the decrease in HP due to the van't Hoff rule and a net increase in HP occurs with decreasing core temperature.

Using this method, we estimated the Q_{10} of HP at various T_a and search for the point of T_a were the Q_{10} was lower than 2.0. At this temperature only exothermic reactions in avian embryos occurred (Table 1).

3. Results and discussion

The results of the experiments can be summarised in the following five topics:

3.1. Thermoregulatory behaviour in avian embryos is developed after internal pipping

In first series the influence of low ambient temperatures on call producing activity in duck embryos were investigated. The eggs were dipped for 2–8 s in a water bath controlled at 20–22 °C. Immediately after this, the call frequency of the embryos was recorded continuously and the call rate was calculated every minute.

After internal pipping, i.e. 3–4 days before hatching, acoustic communication occurs between the embryos of the same clutch and between embryos and the incubating mother [13]. Three types of calls are most important in embryos of

Cairina moschata, the distress call, the trill call and the double call. Whereas trill and double calls are be used for communication between the embryos, distress calls produced by the embryo in uncomfortable situations seem to give a signal for the incubating mother to help.

Immediately after immersing the egg in cold water, the distress call rate of the embryo increases because of the cold stimulus (Fig. 2). After rewarming, this rate decreases again. Thus, there are close relationships between cooling and calling rate. These observations are in agreement with results of experiments carried out by Evans et al. [14], in Ringbilled Gulls *(Larus delawarensis)*. Embryos of this species vocalised strongly when body temperature dropped below 36 °C. When cold-induced calls triggered a 4-min period of rewarming by an artificial heater, embryonic temperature may be stabilised. Cold induced vocalisations are signals of the offsprings need for warmth. If vocal thermoregulation by pipping embryos is a potentially adaptive mechanism, in embryos the chain thermoreceptors—afferent transmission of information—activation of muscles integrated in call production must be developed.

3.2. Avian embryos develop endothermic reations

The measured HP of endothermic animals at temperatures below the thermoneutral temperature is the result of two different processes: the thermoregulatory HP and the energy metabolism following the van't Hoff rule. In contrast to older birds, a decrease in body temperature of avian embryos, due to low incubation temperature usually causes a decrease in net HP but the decrease is more moderate than would be assumed from the van't Hoff rule.

Before we started with any experiments [3,7,15], we assumed that a moderate decrease of T_a results in a small decrease of core temperature and a following activation of deep
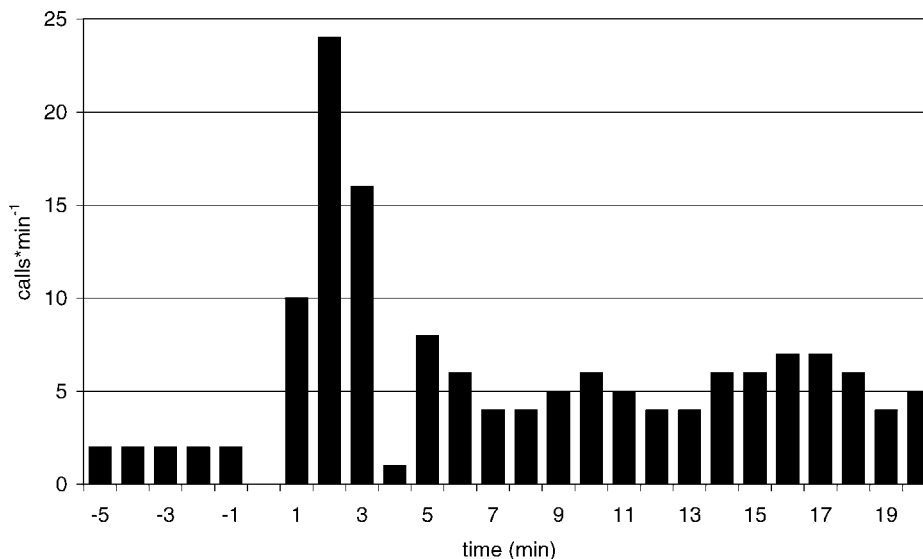
Fig. 2. Call rate of Muscovy duck (*Cairina moschata*) embryos before and after inserting the eggs in a water bath controlled at 20°–22° [49]. The cold stimulus was given between −1 and 1 on the time scale. After this the egg was brought in a room tempered at 37.5 °C. Shown are results of one embryo.

cold receptors which should increase the net heat production. Further, with decreasing core temperature a threshold temperature should be reached, where thermoregulatory drive no more exists and thermoregulatory HP ceases. The results do not support this hypothesis.

Using the results published by Nichelmann et al. [3] and illustrated in Fig. 3, the time course of Q_{10} in 34-day-old Muscovy duck embryos was calculated using 0.1 °C steps (Fig. 4). Some times, between 39.0 and 37.5 °C T_{af} the Muscovy duck embryo showed a net increase in HP during the cooling procedure, it is also endothermic between 38.0 and 36.4 °C T_{af} but showed a net decrease in HP; endothermy disappeared at T_{af} lower than 36.4 °C (Table 1).

In domestic fowl, younger embryos from days 14–17 crossed the Q_{10}-threshold of 2.0 at T_{af} below 36.6 °C.

However, from day 18 onwards, values were below 2.0 at all T_{af} temperatures between 35.8 and 39.1 °C. When T_{a} was lowered to 31.5 °C, even a fowl embryo on day 21 reached Q_{10} values above 2.0 only at the end of a 3 h test (T_{af} = 32.0 °C; HP = 5.29 J g^{-1} h^{-1}; Q_{10} = 2.1). Following the theoretical considerations, given by Nichelmann et al. [3,15] it can be postulated, that embryos of these ages show endothermic reactions. These disappear at core temperatures lower than 34.0, perhaps because the activity of thermo-sensitive neurones ceases at these temperatures (Table 1).

Tzschentke and Basta [16,17] showed that Muscovy duck embryos aged 33 and 28 days have cold-, warm- and thermo-insensitive neurones activated in a similar fashion as in 1–5 day-old ducklings.
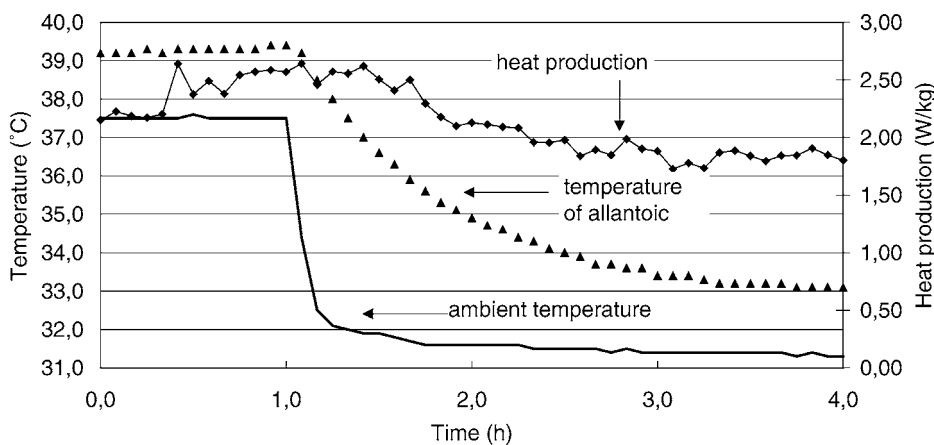

Fig. 3. Time course of ambient temperature, temperature of the allantoic fluid, and heat production of a single 34-day-old Muscovy duck embryo, incubated at 37.5 °C [7]. The scale of heat production is given at the right site, the scale of temperature of the allantoic fluid as an index of body core temperature and the scale of ambient temperature is given the left site.
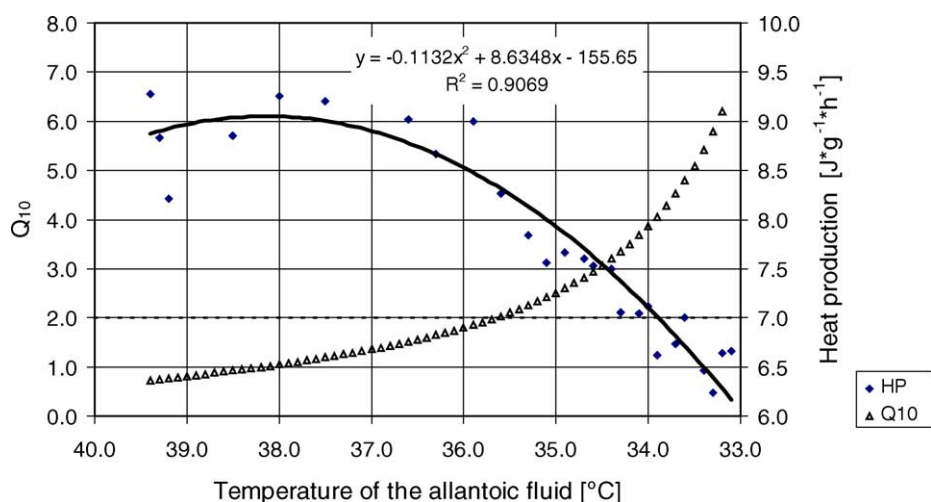
Fig. 4. Influence of the temperature of the allantoic fluid (T_{af}) on heat production (HP) and Q_{10} in the same Muscovy duck embryo as shown in Fig. 3. For details of calculation see [3].

The results presented show that fowl embryos between days 14–21 of development have a $Q_{10} < 2.0$ at body temperatures between 34 and 39 °C. It is postulated that embryos at these ages realise endothermic reactions.

The threshold temperature (T_{af}) of $Q_{10} = 2.0$ showing the transition to endothermic reactions in all investigated Muscovy duck and fowl embryos at all age groups is given in the Table 1. At transient temperature changes between 37.5 and 31.5 °C it was situated between 34.02 ± 0.36 and 35.03 ± 0.65 °C for the fowl embryos and between 34.24 ± 0.61 and 35.83 ± 0.40 °C for Muscovy duck embryos. Whereas at transient temperature changes between 37.5 and 34.5 °C in fowl embryos the values were 36.27 ± 0.35 and 37.40 ± 0.26 °C and were 36.10 ± 0.42 and 37.70 ± 0.48 °C in Muscovy duck embryos (Table 1).

In the 34.5 °C group not all embryos demonstrated thresholds, but endothermic reactions were found mainly in the older embryos during the whole experiment [17,18].

At least, from the theoretical point of view there are two alternative explanations for the increasing Q_{10} at low temperatures.

Firstly, in the experiments presented here, we have measured the oxygen consumption of the avian embryos and subsequently calculated the HP. The HP values are exclusively aerobic measurements and do not include anaerobic metabolic rate. Obviously, it cannot be excluded that anaerobic processes may occur during the influence of low ambient temperatures in avian embryos but they are not able to influence the Q_{10}.

Secondly, according to Whittow and Tazawa [12] the transition from poikilothermy to homeothermy in precocial birds is seen to take place in four stages. Altricial birds seem to be subject to the Arrhenius limitation until after they hatch [12].

Nichelmann et al. [3,8] showed that, in embryos of domestic fowl and Muscovy duck, a Q_{10} lower than 2.0 may occur before the plateau phase, demonstrating that a rela-

tive or absolute oxygen deficiency may not be the cause of the measured low Q_{10}. This assumption is supported by observations of Lange et al. [18] showing that the incubation temperature has an influence on the duration of the plateau phase but not on the level of HP and oxygen consumption during this period. Hence, it is unlikely that incubation temperature can change the oxygen conductivity of the eggshell in an acute experiment.

In earlier experiments, Nichelmann et al. [19] found that the HP of Muscovy duck embryos reached a maximum at 37.5 °C but then decreased with increasing at T_a to 40.5 or 39.5 °C. The relationship between HP and T_a could be described as a parabolic function with the maximum (y_{max}) at 37.5 °C. From day 26 of incubation, HP increased at Ta above 39.0 °C (for instance from 1.189 ± 0.080 to 1.375 ± 0.056 W kg^{-1} at day 28 and from 1.403 ± 0.241 to 1.642 ± 0.201 W kg^{-1} at day 32). These results demonstrate that embryos of Muscovy ducks have a thermoneutral temperature (temperature of a minimal HP) of 40.5 °C up to the 25th day of incubation, when it decreases to 39.0 °C. The maximum values of HP (summit metabolism) were measured at 37.5 °C (normal incubation temperature).

The results of experiments, published by Nichelmann et al. [20] show that the velocity of body temperature changes in Muscovy duck and fowl embryos have an influence on the threshold temperature of endothermy, and support the assumption that the dynamic component of central or peripheral thermosensors may be developed very early. The faster the core temperature changed the lower is the threshold temperature of endothermic reactions (Table 1).

3.3. In precocial avian embryos hyperthermia causes a down-regulation of heat production

In Muscovy duck embryos Q_{10} values were between 0.8 and 1.2, beginning on day 20 at T_a at the start of the heating

period (T_{an}). At ambient temperatures at the end of the heating period (T_{ah}) they were also below 2 on day 21; and on days 22, 25, 29–32 of incubation they were below 1 with a minimum of 0.54 on day 30. In fowl at T_{an}, there was an extremely high Q_{10} of 3.42 on day 12, in combination with unexpectedly low Q_{10} values at T_{ah} on days 12 and 13. From day 16, Q_{10} values were between 1.5 and 2, at day 20 only 0.78. There was a local maximum of Q_{10} at normal and high T_a on the last day of incubation. In contrast to the younger embryos, the older embryos had a tendency to reduce their HP at higher body temperature [21]. Usually, Q_{10} was highest at the initiation of the heat load and decreased during the imposition of the heat load in all age groups, with the exception of the younger Muscovy duck embryos.

The data presented here show that a 3 h influence of 39.0 °C results in an increase in the body core temperature of about 1.5 °C. Despite the hyperthermia which was occurring, the HP of Muscovy duck embryos in the experiments of Nichelmann et al. [19] decreased and the oxygen consumption of Muscovy ducks and fowl embryos in the experiments of Janke et al. [21] were diminished. Marder et al. [23] demonstrated that heat-acclimated pigeons (*Columba livia*) have a lower oxygen consumption at extremely high T_a (0.93 ml O_2 h^{-1} at 50 °C; 0.84 ml O_2 h^{-1} at 60 °C) in comparison to moderate temperature (1.13 ml O_2 h^{-1} at 20–25 °C). The actual reduction of HP in moderate hyperthermia has also been found in the postnatal period in other birds and mammals, too. Gelineo [24] showed a secondary decrease of heat production in cold- and warm-adapted pigeons at T_a higher than the thermoneutral temperature. The threshold ambient temperature of this decrease was much the same in both groups (about 36 °C) but the intensity of the HP decrease was greater in the cold-adapted (25.6%) than in the warm-adapted (12%) group. In man, Thauer, and Wezler [26] observed a 5% decrease in HP during hyperthermia. Gelineo [24], Thauer [25], and Thauer and Wezler [26] designated the phenomenon of

HP dropping at high ambient temperature as "second chemical thermoregulation".

Shibata [27], Shibata et al. [28], Hashimoto et al. [29] as well as Uno and Shibata [30] have shown that there is a centre in the mid-brain reticular formation of rats which tonically inhibits metabolic HP. It can be not be excluded that this centre may inhibit HP during slight hyperthermia in man, mammals, and birds and may also be implicated in metabolic depression observed in avian embryos.

3.4. In contrast to heat production the efficiency of heat loss is high in precocial avian embryos

In contrast to the low efficiency of endothermic reactions during embryonic development, the prenatal efficiency of embryonic heat loss mechanisms seems to be higher than that of the heat production mechanisms. First and very slowly respiration movements occur before internal pipping [31–34].

Panting reactions were found in Muscovy duck embryos between internal and external pipping [35,36] at the same time there are changes in blood flow in the chorio-allantoic membrane at different T_a [9]. After T_a was increased to 40.5 °C, T_{af} increased soon and parallel to T_a and was after some minutes higher than T_a and T_c (Fig. 5). T_c however, was kept constant for more than 40 min after the initial T_a increase and was higher than T_{af}.

Only before heating and after T_a had reached a new stable level at the 150th minute of the experiment.

Elsewhere, [37,38] we have postulated a general rule: the activity of organ functions occurs during embryonic development before this function is ultimately necessary to ensure the survival of the embryo. It can be postulated that endothermic reactions during the prenatal period have an ultimate but not a proximate (immediate) influence on the efficiency of thermoregulation. They have a training effect on the control systems and support adaptivity to expected environmental
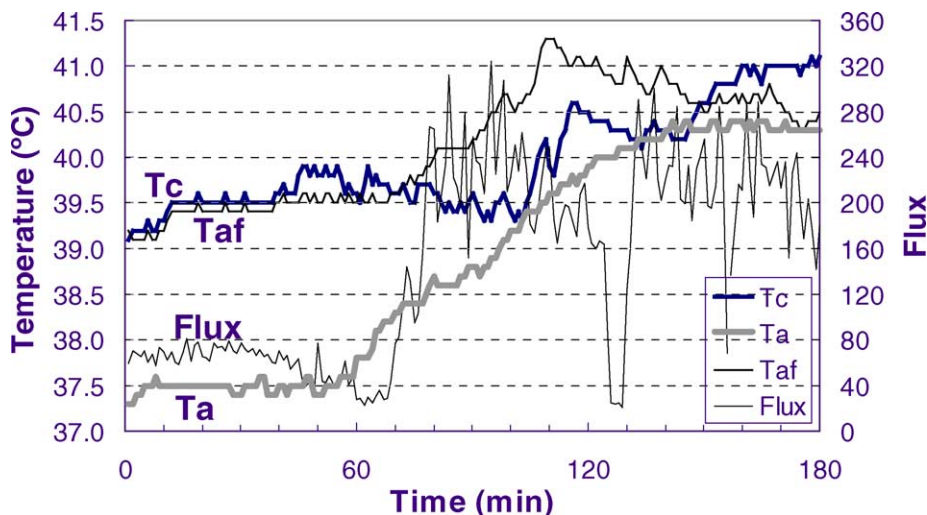

Fig. 5. Time course of ambient temperature (T_a), temperature of the allantoic fluid (T_{af}), colonic temperature (T_c), and blood flow in the chorio-allantoic membrane (flux) during a typical experiment in a fowl embryo after internal pipping [9].

conditions. It may be that they have an influence on epigenetic adaptation mechanisms. Related to epigenetic adaptation process, environmental influences during gestation of mammals or incubation of birds have an influence on gene expression in embryos. The influence of altered environmental conditions during the prenatal period on the later development of physiological control systems in birds and mammals has been described, e.g. for reproductive system and glucose metabolism [39], growth processes [40], thyroid hormones and metabolism [41,42], and the arginine-vasotocin-system.

Tzschentke et al. [43] and Tzschentke and Basta [44] give more general aspects of epigenetic adaptation including epigenetic temperature adaptation. They have shown that in birds incubation at a lower temperature than usual induces postnatal cold adaptation and incubation to a higher temperature warm adaptation.

Their conclusions were supported by some experiments of Modrey [45], carried out in turkeys incubated at the normal temperature of 37.5 °C and at a lower temperature of 34.5 °C. At T_a between 5 and 40 °C, the birds incubated at the lower T_a have had a higher HP than the normally incubated controls in the first 10 days after hatching (Fig. 6) but remarkable and important is that turkeys but not chicken incubated at

high temperatures show the same reaction. The difference between fowl and turkey chickens is not to explain in this time.

3.5. Development of physiological control systems starts with non-coordinated and proximate (immediate) non-adaptive reactions

As has been shown [37,38] training effects occur during the development of body functions and control systems. These are necessary for the complete development of body functions. Another point of view is that the development of physiological control systems starts with non-coordinated and non-specific reactions, which have no proximate (immediate) adaptive effects but are necessary for the ultimate adaptation.

In older birds and mammals the control elements of the thermoregulatory system will be activated in a typical order [46]: (1) with increasing ambient temperature the evaporative heat loss will be activated (2) after this the threshold temperature for the conductance occurs (3) at higher temperatures the biological optimum temperatures is reached and finally (4) the thermoneutral temperature, the threshold temperature for
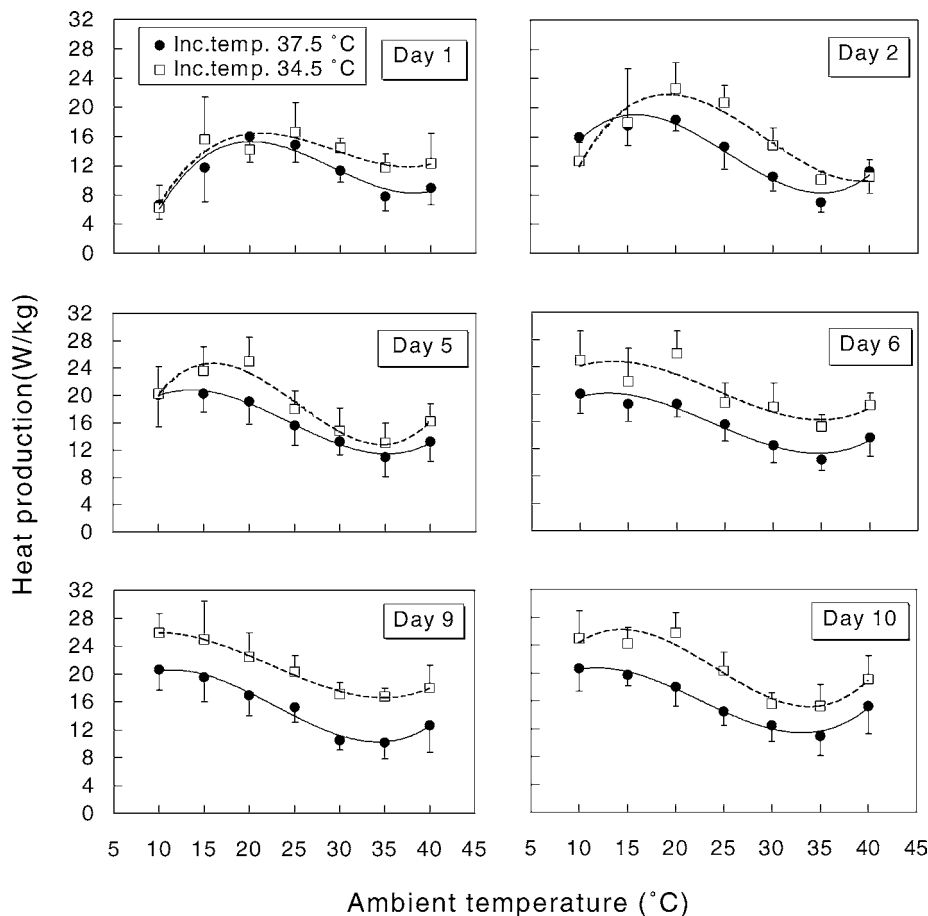

Fig. 6. Relationships between ambient temperature and heat production in 1- to 10-day-old turkey hatchlings incubated at 37.5 °C (control group) or 34.5 °C (cold group) during the last 19 days of incubation [45].

HP [46–49] occurs. In piglets during the first days after birth the control elements will be activated in a non-coordinated fashion, but firstly at the 9th day of life does normal activation modus occurs. These results led to the hypothesis that it is not the direction of change that seems to be most important for the organism but only the fact that a change occurs.

4. Conclusions

The strategies of avian embryos in relation to temperature regulation are optimally developed. Endothermic reactions occur very early during the embryonic development but their efficiency is limited. Due to the van't Hoff rule, low temperatures decrease the net heat production but the trajectories of endothermy may be stimulated and related epigenetic adaptation mechanisms are activated. Using behavioural mechanisms, the embryo is protected against super-cooling during the natural incubation process. The heat loss mechanisms are most efficient against heat stress, which occurs only for a very short time during incubation and protect the embryo against disturbances caused by hyperthermia.

Acknowledgements

References

[1] Glossary of terms for thermal physiology, Jap. J. Physiol. 51 (2001) 245–280.
[2] M. Nichelmann, B. Tzschentke, Avian Poult. Biol. Rev. 14 (2003) 1–19.
[3] M. Nichelmann, A. Burmeister, O. Janke, J. Höchel, B. Tzschentke, J. Therm. Biol. 23 (1998) 369–376.
[4] C. Romijn, W. Lockhorst, Poultr. Sci. 34 (1955) 649–654.
[5] A. Aulie, P. Moen, Comp. Biochem. Physiol. 51A (1975) 605–609.
[6] M. Nichelmann, B. Tzschentke, Comp. Biochem. Physiol. 131A (2002) 751–764.
[7] M. Nichelmann, B. Tzschentke, Orn. Fenn. 76 (1999) 1177–1187.
[8] M. Nichelmann, B. Tzschentke, D. Basta, A. Burmeister, O. Janke, Q_{10} in perinatal thermoregulation. in: H. Tönhardt, R. Lewin (Eds.), III. International Workshop: Investigations of Perinatal Development in Birds, Freie Universität Berlin, 1997, pp. 211–233.
[9] S. Holland, J. Höchel, A. Burmeister, O. Janke, M. Nichelmann, J. Therm. Biol. 23 (1998) 123–128.
[10] E. Simon, H.T. Hammel, A. Oksche, J. Neurobiol. 8 (1977) 523–535.
[11] H. Precht, J. Christopherson, H. Hensel, W. Larcher, Temperature and Life, Springer, Berlin, Heidelberg, New York, 1973, p17ff.
[12] G.C. Whittow, H. Tazawa, Physiol. Zool. 64 (1991) 1371–1390.
[13] M. Rumpf, M. Nichelmann, Zool. Jb. Physiol. 96 (1992) 379–394.
[14] R.-M. Evans, A. Whitaker, M.O. Wiebe, Auk 111 (1994) 596–604.
[15] M. Nichelmann, A. Burmeister, S. Holland, J. Höchel, O. Janke, B. Tzschentke, Development of endothermy in birds: influence of low and high temperatures on heat production and heat loss mehanisms in avian embryos, in: B. Tzschentke (Ed.), 4th Workshop Perinatal Adaptation, Humboldt University of Berlin, 1998, pp. 57–75.
[16] B. Tzschentke, D. Basta, J. Therm. Biol. 25 (2000) 119–123.
[17] B. Tzschentke, D. Basta, Comp. Biochem. Physiol. 131A (2002) 825–832.
[18] B. Lange, M. Nichelmann, A. Paulick, Untersuchungen zum Einfluß der Umgebungstemperatur auf den Sauerstoffverbrauch von Embryonen der Moschusente (Cairina moschata) in: M. Nichelmann, B. Tzschentke, R. Pirow, 1. Workshop Perinatale Anpassungsprozesse (Eds.), Humboldt-Universität zu Berlin, 1993. 71–81.
[19] M. Nichelmann, B. Lange, R. Pirow, J. Langbein, S. Herrmann, Avian thermoregulation during the prenatal period, in: E. Zeisberger, E. Schönbaum, P. Lomax (Eds.), Thermal Balance in Health and Disease. Recent Research and Clinical Progress, P. Birkhäuser Verlag, Basel, 1994, pp. 167–173.
[20] M. Nichelmann, O. Janke, B. Tzschentke, J. Therm. Biol. 26 (2001) 273–280.
[21] O. Janke, B. Tzschentke, J. Höchel, M. Nichelmann, Comp. Biochem. Physiol. 131A (2002) 741–750.
[22] O. Janke, B. Tzschentke, M. Nichelmann, News Biomed. Sci. 2 (2003) 10–12.
[23] J. Marder, Y. Ariele, J. Ben-Asher, A. Israel, J. Zool. 34 (1989) 61–75.
[24] S. Gelineo, C. R. Soc. Biol., Paris 122 (1936) 337–343.
[25] R. Thauer, Erg. Physiol. 41 (1939) 666–805.
[26] R. Thauer, K. Wezler, Zschr. Exper. Med. 12 (1943) 95–128.
[27] M. Shibata, Ann. N. Y. Acad. Sci. 813 (1997) 127–131.
[28] M. Shibata, T. Uno, M. Hashimoto, J. Therm. Biol. 24 (1999) 365–368.
[29] M. Hashimoto, A. Kuroshima, J. Arita, M. Shibata, J. Therm. Biol. 24 (1999) 347–359.
[30] T. Uno, M. Shibata, J. Therm. Biol. 26 (2001) 485–489.
[31] M.A. Vince, B.E. Tolhurst, Comp. Biochem. Physiol. 52A (1975) 334–337.
[32] T.N. Pettit, G.C. Whittow, Resp. Physiol. 48 (1982) 199–208.
[33] H. Tazawa, Embryonic respiration, in: T.J. Seller (Ed.), Bird Respiration, CRC Press, 1897, pp. 3–42.
[34] P. Murzenok, S. Holland, M. Nichelmann, Studies on development of respiration in fowl embryos during internal pipping, in: H. Tönhardt, R. Lewin (Eds.), III. International Workshop: Investigations of Perinatal Development on Birds, Freie Universität, Berlin, 1997, pp. 167–172.
[35] M. Nichelmann, P. Murzenok, S. Holland, Development of heat loss mechanisms in avian embryos. in: V.N. Gourine, M. Nichelmann, V.A. Kulchitzky, Y.F. Pastukhov (Eds.), Temperature Control in Health and Disease, Minsk, 1997, pp. 57–69.
[36] M. Nichelmann, B. Tzschentke, A. Burmeister, S. Holland, O. Janke, Embryonic temperature regulation in the waterfowl, in: R. Rouvier (Ed.), Proceedings 11th European Symposium in Waterfowl, Nantes, Association Groupe Francais de la WPSA, 1997, pp. 206–215.
[37] M. Nichelmann, O. Janke, J. Höchel, B. Tzschentke, News Biomed. Sci. 1 (2001) 15–25.
[38] M. Nichelmann, O. Janke, J. Höchel, B. Tzschentke, Regularities in prenatal development of organ functions and control systems in poultry, in: Proceedings XII International Ongres of the World Veterinary Poultry Association, Cairo–Egypt, 17–21 September, 2001, pp. 116–127.
[39] G. Dörner, Wiss. Zschr. HU 36 (1987) 586–595.
[40] E.M. Widdowson, Definition of growth, in: T.I.J. Lawrence (Ed.), Growth in Animals, Butterworth, London, Boston, 1980, pp. 1–20.
[41] E. Decuypere, Arch. Exper. Vet. Med. 38 (1984) 439–449.

[42] B. Minne, E. Decuypere, Arch. Exper. Vet. Med. 38 (1984) 374–383.

[43] B. Tzschentke, D. Basta, M. Nichelmann, News Biomed. Sci. 1 (2001) 26–31.

[44] B. Tzschentke, D. Basta, Comp. Biochem. Physiol. 131A (2002) 825–832.

[45] P. Modrey, Die postnatele Entwicklung der Temperaturregulation und des Stoffwechsels von Putenküken (Meleagris gallopavo) unter dem Einfluß der Bruttemperatur. Shaker Verlag, Aachen, 1995.

[46] M. Nichelmann, B. Tzschentke, Thermoneutrality: Traditions, Problems, Alternatives. In: T. Nagasaka, A.S. Milton (Eds.), Body Temperature and Metabolism, IPEC, Tokyo, pp. 77–82.

[47] M. Nichelmann, L. Lyhs, Mh. Vet.-Med. 40 (1976) 385–389.

[48] M. Nichelmann, J. Therm. Biol. 8 (1983) 69–71.

[49] M. Nichelmann, B. Tzschentke, Ann. N. Y. Acad. Sci. 813 (1997) 78–86.