Ornis Fennica 76:177–187. 1999

Thermoregulation in precocial avian embryos

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Received 14 August 1998, accepted 1 July 1999

Oxygen consumption was measured and heat production (HP) calculated in Muscovy Duck (*Cairina moschata*) and Domestic Fowl (*Gallus gallus f. domestica*) embryos at different ambient temperatures (Ta) using a closed (Scholander-method) or a half-open system connected to a paramagnetic oxygen analyzer (Magnos, Hartmann and Braun, Germany). After internal pipping, respiratory rate, respiratory tidal volume and minute volume as well as blood flow in the chorioallantoic membrane were estimated in a number of embryos at 40°C. Simultaneously, the temperature of the allantoic fluid (Taf) and colonic temperature (Tc) were measured. In other experiments, Muscovy Duck embryos were incubated at Ta of 34.5°C and HP was compared at different Ta with that of birds incubated at 37.5°C. Generally, a decrease in Ta led to a decrease in Tc, Taf and HP. The estimated HP is the result of the depressing influence of the Q_{10}-effect and the positive influence of CNS-controlled thermoregulatory HP. The older the embryo, the lower the minimal Q_{10} obtained, the lower the threshold Taf for a Q_{10} of 2.0 and the higher the Taf at the minimal Q_{10}. The results suggest that endothermic reactions in precocial birds occur very early during embryonic development. Prenatal temperature experiences seem to stimulate thermoregulatory HP of embryos. During the period between internal and external pipping, panting occurred with increasing body temperature and, in Muscovy Duck embryos, the respiratory rate increased in the Tc-zone between 38.5 and 40.5°C. It seems to be that many organ functions occur during embryonic development, before these functions are ultimately necessary to ensure the survival of the embryo. Prenatal activation of functional systems may have a training effect on the postnatal efficiency of the related adaptive mechanisms.

1. Introduction

Following the *Glossary of Terms of Thermal Physiology* (1987), endothermy is the pattern of thermoregulation in which the body temperature depends on a high (tachybolic) and controlled rate of heat production (HP).

It is generally accepted that newly-hatched precocial birds are able to increase thermoregulatory HP at ambient temperatures (Ta) lower than the thermoneutral temperature [(TNT); (Whittow & Tazawa 1991)]. In our own experiments (Modrey & Nichelmann 1992) it was shown that in 1- to 10-d-old turkeys the relationships between Ta and HP may be described by parabola-like functions. The summit metabolism increased between the first day (15.53 $W*kg^{-1}$) and the fourth day (21.14 $W*kg^{-1}$) and changed little in the following days. At the same time the TNT decreased from 37.7°C at day 1 to 35.4°C at day 4 and to 33.4°C at day 10; HP at TNT increased from 7.96, to 10.2 and to 10.83 $W*kg^{-1}$ at day 1, 4 and 10, respectively. Obviously, the efficiency of thermoregulation is high enough after the 5th day of life to ensure a wide zone of homeothermy. In other poultry species, such as geese, Pekin Ducks (*Anas platyrrhynchos*), Muscovy Ducks (*Cairina moschata*, Koch & Michler 1978) and Domestic Fowls (*Gallus gallus*, Tzschentke 1986) thermoregulatory ability develops in a similar way.

Information on HP during the embryonic development in birds is extremely contradictory (Whittow and Tazawa 1991). Freeman (1964) found a transient metabolic response to cooling in chicken embryos. Internal pipping resulted in further development of the thermogenic response to cooling. In contrast to Freeman's positive finding in Domestic Fowl embryos, Romijn and Lockhorst (1955) could not see any signs of metabolic compensation for cooling in fowl eggs, even in 20-d-old embryos. On the other hand, by measuring the respiratory movements of the hatching Japanese quail (*Coturnix coturnix japonica*) during cooling and warming, Nair and Dawes (1980) suggested that the relatively rapid recovery in frequency during rewarming is partly a reflex effect due to the stimulation of peripheral thermoreceptors. In the embryonic Willow Ptarmigan (*Lagopus lagopus*), no endothermic reactions occur (Aulie & Moen 1975) but the magnitude of the decrease in HP during cooling was consistent with some thermoregulatory capacity, that is, the response was not entirely that of a poikilotherm. Similarly, in the South Polar Skua (*Catharacta maccormicki*), oxygen uptake declined with prenatal cooling, but the Q_{10} of metabolism was only 1.3 between temperatures between 35°C and 30°C, less than the expected value of 2.0 if the oxygen consumption had been related only to temperature (Williams & Ricklefs 1984). Wedge-tailed Shearwater *(Puffinus pacificus)*, an altricial bird with a long (52d) 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 (Mathiu et al. 1992).

The different and partly opposite results given in the literature may be caused by various factors described hereafter.

Species. Generally, altricial birds have no endothermic reactions during the prenatal period (Whittow & Tazawa 1991). The degree of precociality varies in a continuum in non-altricial species. It can be assumed that, because of this, the degree of endothermy may also be different.

The reaction of the same species but of different ages may be different, because enzyme activity, oxygen uptake, the development of the cardiovascular system, the function of the central nervous system and some other processes may be differ with age.

Ambient temperature. An endothermic reaction may only occurs when the perception of the cold stimulus is possible. The activity of internal thermosensors decreases with decreasing local temperature, and at a threshold temperature reception ceases. Below this body temperature endothermic animals show an ectothermic reaction. Experiments of Basta and Tzschentke (1998) have demonstrated that in 28-d- and 33-d-old Muscovy Duck embryos the hypothalamic thermosensors have similar reactions as the sensors in newly hatched ducklings. When, during the cooling process, the internal body temperature falls below the previously mentioned threshold temperature endothermic reactions are impossible.

Duration of cooling. The relationships between the duration of cooling and the measured deep body temperature may be described by an exponential function. Shortly after starting the cooling process the body temperature and, because of this the temperature at the thermosensitive elements in the body core, is higher than at the end of experiment. The thermoregulatory reactions immediately after starting the experiment must be different from those than at the end of experiment.

Because of these difficulties, standardised experiments in two avian species, one with a short incubation period (Domestic Fowl, 21 days) and another with a long incubation period (Muscovy Duck, 35 days) were carried out to find out evidences of endothermic reactions in embryos of precocial birds and to clear some of the questions stated above.

2. Material and Methods

2.1. Incubation

Experiments were carried out in Muscovy Duck (D18 – D35) and Domestic Fowl embryos (D14 – D21). Eggs were obtained from Grimeaud and Brinkmann, 58802 Balve-Beckum, Germany (Ducks) and Lohmann Tierzucht, GmbH, 27454 Cuxhaven, Germany (chicken). They were incubated at 37.5°C and at a relative air humidity of 70% and turned automatically until the start of the experiments.

2.2. Methods

The experiments were carried out in three series.

2.2.1. Series 1

In series 1 as well as in series 2, 5 to 6 eggs were investigated at each Ta. Starting at D18 of incubation and finishing at D34 the oxygen consumption of Muscovy Duck embryos were measured at temperatures of 34.0, 35.5, 37.5, 39.0 and 40.5°C after 100 minutes of temperature exposure, using a Scholander respirometer (Lange et al. 1994, Nichelmann et al. 1994).

2.2.2. Series 2

In the second series, the Muscovy Duck eggs were incubated to the 24th day at 37.5°C. After this, half of the eggs were incubated at the same temperature to hatching, the other half at 34.5°C. Beginning at D24 the oxygen consumption in both groups was measured, using the method described in the first series at Ta of 34.5, 36.0, 37.5, 39.0 and 40.5°C (n = 10 embryos in each group an each actual temperature). Again, the duration of temperature exposure was about 100 minutes.

2.2.3. Series 3

The influence of low Ta (31.5°C and 34.5°C) on different body temperatures (colonic temperature Tc; temperature of allantoic fluid Taf) and oxygen consumption were measured between D20 and D34 of incubation in Muscovy Duck and between D12 and D21 in chicken embryos. In Muscovy Duck embryos, after internal pipping respiratory rate and the blood flow in the chorioallantoic membrane were estimated also at a Ta of 40°C. Because the methods used have been described extensively elsewhere (Nichelmann et al. 1998, Holland et al. 1998) only a brief account is given here.

Equipment. For the measurement of body temperatures (Taf and Tc) and oxygen consumption, single eggs were placed in a watertight metabolic chamber (volume about 290 ml). For respiratory measurements a special incubator was used, equipped with a copper cover to give the effect of a Faraday cage.

Oxygen consumption. The oxygen consumption of each embryo was determined by using an oxygen analyzer (Magnos 4, Hartmann & Braun AG, Berlin). On the basis of these data HP was calculated using a respiratory quotient (RQ) of 0.72 (Decuypere 1984).

Body temperatures. The egg shell was removed at the sharp pole in a diameter of about 1cm . After the shell membrane and the chorioallantoic membrane had been penetrated without injuring major blood vessels, the embryo's tail and cloaca could be exposed. The thermistor probe was inserted 1 to 2 cm into the colon and fixed to the tail feathers with adhesive tape.

The thermistor probe for the measurement of Taf was inserted through the hole at the sharp pole and directed about 2.5 cm towards the blunt pole. The thermocouple could be placed very close to embryos.

Respiratory activity. Around the time of internal pipping breathing activity occurs (Murzenok et al. 1996) and results in measurable pressure fluctuations in the air cell. By installing a tube into the air cell the periodic pressure fluctuations were measured using a Statham element (Hugo Sachs Elektronik KG, 79232 March, Germany) in combination with a Gould recorder (Gould Inc., Test & Measurement Group, Valley View, Ohio 44125, USA).

The recorded pressure fluctuations give information about the respiratory rate, the relative tidal volume and the relative respiratory minute vol-

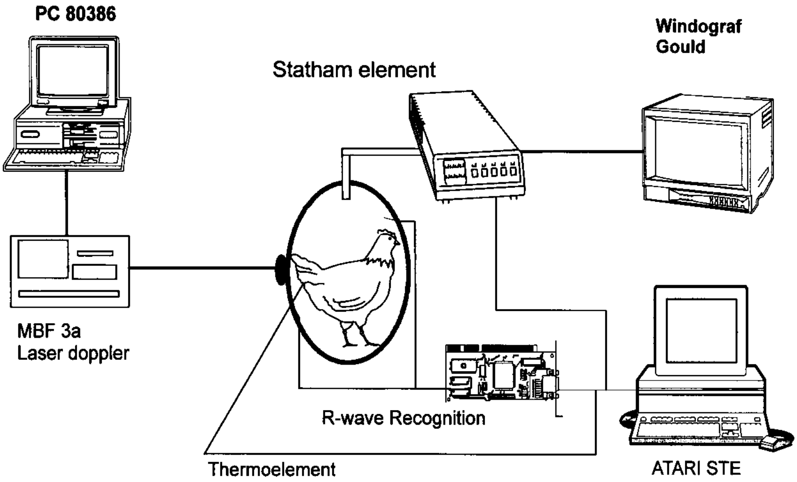

Fig. 1. Connections of the instruments to register the body and ambient temperatures, the respiratory activity and the chorioallantoic blood flow simultaneously. The data were recorded on-line by a computer ATARI STE in ASCII format and could be analysed with common statistical software.

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Chorioallantoic bloodflow. To record peripheral blood flow in the chorioallantoic membrane, the laser Doppler principle was used. When light pulses reflected from a moving object their frequency is shifted. The amount of shift is dependent on the speed of the moving object. In these experiments the instrument MBF3 (Moor Instrument Limited Company, Devon, EX13 5DT, UK) was used. For this, a 5 × 5 mm piece of the egg shell was removed without damaging the shell membranes. The laser Doppler probe was fixed directly on the egg membrane and the mean red cell flux, the red blood cell concentration and the mean red blood cell speed were recorded.

The connections of the instruments to register the temperatures (Taf, Tc and Ta), the respiratory activity and the chorioallantoic blood flow are given schematically in Fig. 1.

3. Results

3.1. Series 1

In the 100-min exposure experiments of the first series, either an increase or a decrease in Ta resulted in decreased HP in 19- to 25-day-old embryos. For instance, on D21 HP was 0.526 ± 0.104; 0.818 ± 0.098; 0.940 ± 0.102; 0.579 ± 0.049 and 0.478 ± 0.097 $W{*}kg^{-1}$ at 34.0; 35.5; 37.5; 39.0 and 40.5°C, respectively. The relationship between HP and Ta could be described as a parabolic function with the extreme value y_{max} at 37.5°C Ta (Fig. 2). From the 26th day of incubation HP increased at Ta above 39.0°C (for instance from 1.189 ± to 0.080 $W{*}kg^{-1}$ to 1.375 ± 0.056 $W{*}kg^{-1}$ at D28 and from 1.403 ± 0.241$W{*}kg^{-1}$ to 1.642 ± 0.201 $W{*}kg^{-1}$ at D32).

3.2. Series 2

The experiments of series 2 show that Muscovy Duck embryos incubated at low temperatures (34.5°C) had at D27 and on the following days at all investigated actual Ta a higher HP than embryos incubated permanently at 37.5°C (variance analysis, $p < 0.05$). The difference was highest at 36.0°C and 40.5°C Ta (Fig. 3).

3.3. Series 3

3.3.1. Heat production

Generally, in the experiments of the third series, a decrease in Ta usually resulted in a decrease of Taf, Tc and HP in Muscovy Duck embryos as well as in chicken embryos. One example related to Muscovy Duck embryos is given in Fig. 4. In some embryos at the last day of incubation, shortly before hatching, a small increase in HP was obtained after starting the cooling procedure. At normal incubation temperatures (37.5°C) the HP of avian embryos rises after the plateau phase, which oc-

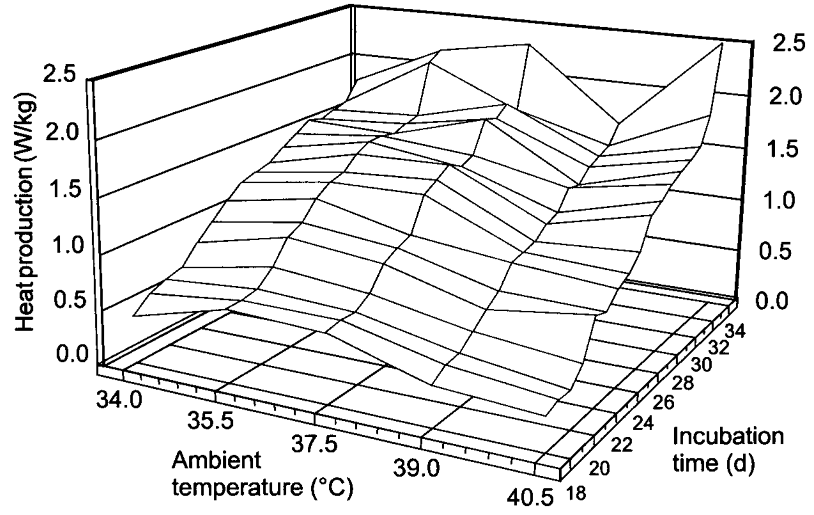

Fig. 2. Influence of incubation temperature (ambient temperature) on heat production in Muscovy Duck embryos aged between 18 and 34 days.

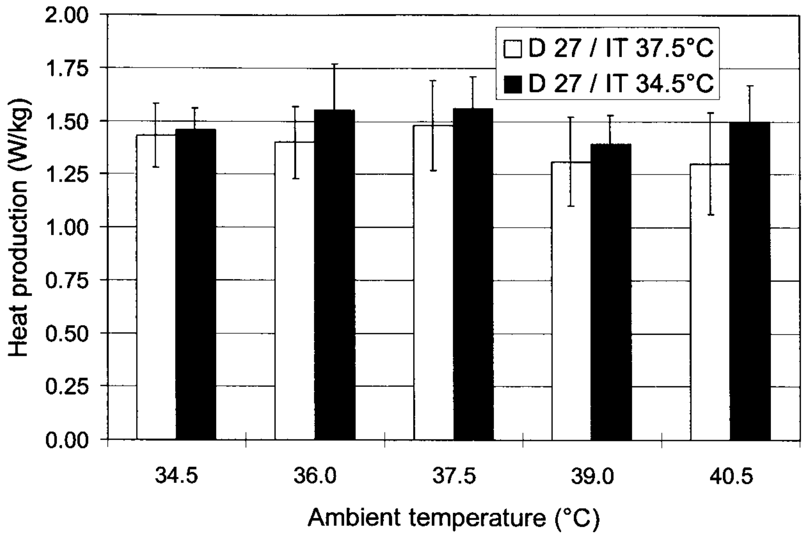

Fig. 3. Heat production of 27-d-old Muscovy Duck at different actual ambient temperatures. The eggs were incubated between D0 and D24 at 37.5°C. In the following days half of them were incubated at 34.5°C, the other at 37.5°C. At D 27 the oxygen uptake of both groups were tested at different temperatures between 34.5 and 40.5°C.

curs in Muscovy Ducks between D25 and D31 and in Domestic Fowl between D17 and D19.

Using the results shown in Fig. 4, the time course of Q_{10} in 34-day-old Duck embryos was calculated using 0.1°C steps (Fig. 5). Details of calculation are given by Nichelmann et al (1998).

Generally, between 39.0°C and 37.5°C Taf this Muscovy Duck embryo showed a net increase in HP during the cooling procedure, it was also endothermic between 37.5 and 34.1°C Taf; however it showed a net decrease in HP and the disappearance of endothermy at Taf lower than 34.1°C. The threshold temperature (Taf) of $Q_{10} = 2.0$ for all investigated Muscovy Duck and chicken embryos is given in Table 1.

Generally, the older the embryo, the lower the minimal Q_{10} obtained , the lower the threshold temperature for a Q_{10} of 2.0 and the higher the Taf at the minimal Q_{10}.

In Domestic Fowl, younger embryos from D14 to 17 crossed the Q_{10}-threshold of 2.0 at Taf below 36.6°C; however, from D18 on, values were below 2.0 at all temperatures between 35.8 and 39.1°C Taf. When Ta was reduced to 31.5°C, even a chicken embryo on D21 reached Q_{10}-values above 2.0 only at the end of a 3-h test (Taf 32.0°C, HP 5.29 $J*g^{-1}*h^{-1}$; Q_{10} 2.1).

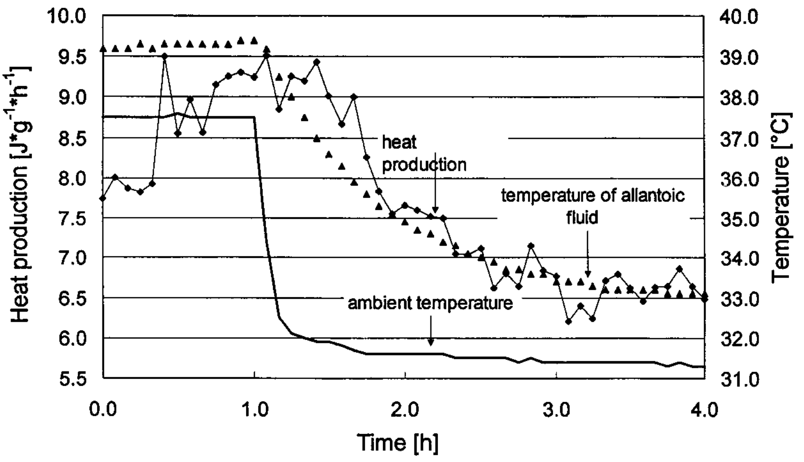

Fig. 4. Time course of ambient temperature, temperature of the allantoic fluid and heat production of a single 34-d-old Muscovy Duck embryo, incubated at 37.5°C.

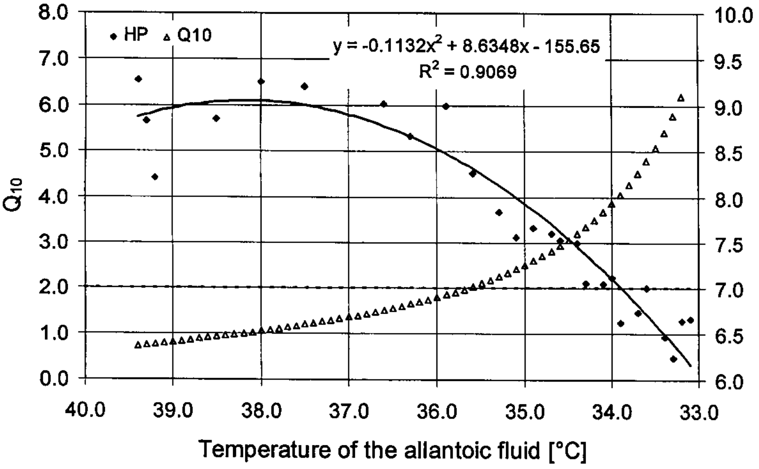

Fig. 5. Influence of the temperature of the allantoic fluid on heat production and Q_{10} in the same Muscovy Duck embryo as shown in Fig. 4. For details of calculation see Nichelmann et al. (1998).

3.3.2. Influence of ambient temperature on respiratory activity

During the period between *internal* and *external pipping*, panting occurred in avian embryo with increasing Tc (Fig. 6).

During panting in Muscovy Duck embryo, the respiratory rate increased in the Tc zone between 38.5 and 40.5°C. At temperatures higher than 40.5°C, a secondary decrease occurred, although the tidal volume increased at this Tc. There was a strong positive correlation between respiratory rate and respiratory minute volume; the higher the respiratory rate the lower the tidal volume.

3.3.3. Chorioallantoic blood flow

When Ta increased to 40.5°C, Taf in chicken embryos increased shortly after and parallel to Ta (Fig. 7).

Tc, however, remained constant for more than 40 minutes after the beginning of the increase in Ta. Over this period, the blood flow in the chorioallantoic membrane increased with increasing Taf. It is assumed that heat produced in the body core may be transported by the blood stream to the chorioallantoic membrane. This heat transfer mechanism clearly bypasses the extra-embryonic fluids. The increasing Taf increases the temperature difference between egg shell and environment and intensifies the heat flux from the egg to the environment. In chicken embryos, cooling the eggs results in a decrease in colonic temperature and a decrease in chorioallantoic blood flow if the blood flow is relatively low at normal incubating temperature. Obviously, at blood flows initially lower than 30 arbitrary units, a further decrease during the cooling process is impossible.

In some cases (Fig. 7) the difference between Tc and Taf will be increased when panting occurs, because heat from the body core is transported via the respiratory system directly to the environment, bypassing the allantoic fluid.

4. Discussion

Generally, the increased measured HP in endothermic animals at temperatures below the thermoneutral temperature is the result of two different processes: the thermoregulatory HP controlled by the thermoregulatory neural network and the energy metabolism following the van't Hoff rule (Nichelmann et al. 1998). In contrast to older birds and mammals, a decrease of body temperature in avian embryos, due to low incubation temperature usually causes a decrease in net HP but the decrease is less than would be predicted by the van't Hoff rule.

Whittow and Tazawa (1991) have shown that in chicken embryos at a very early stage of development, in which no endothermic reactions occur, Q_{10} is 2.0 to 2.4. In the altricial Wedge-tailed Shearwater (*Puffinus pacificus*), the Q_{10} throughout the incubation period was about 2.0 and, also, the temperature-related course of body temperature did not show any signs of endothermic reactions: this bird seems to be ectothermic during embryonic development (Mathiu et al. 1992). In contrast to this, the precocial embryos of Muscovy Duck and Domestic Fowl have a $Q_{10} < 2.0$ at moderately decreased body temperatures (Taf 33.9 to 35.5°C in Domestic Fowl and 34.0 to 35.7°C in Muscovy Ducks; Table 1). A Q_{10} of more than 2.0 demonstrates the absence of endothermy. A Q_{10} lower than 2.0 shows that an endothermic reaction is occurring. When Q_{10} is lower than 1.0 the increase in HP due to thermoregulatory mechanisms is greater than the decrease in HP due to the van't Hoff rule and a net increase of HP occurs with decreasing core temperature (Nichel-

Table 1. Threshold temperature (Taf;°C) of $Q_{10} = 2.0$ (heat production) in chicken and Muscovy Duck embryos. DI = day of incubation.

Chicken embryos			Duck embryos		
DI	n	Taf	DI	n	Taf
12	3	33.95 ± 0.35	20	6	35.00 ± 0.47
13	6	34.95 ± 0.31	21	6	35.35 ± 0.10
14	5	35.40 ± 0.19	22	6	35.25 ± 0.27
15	6	35.32 ± 0.66	23	6	35.92 ± 0.46
16	6	34.83 ± 0.60	24	6	35.18 ± 0.29
17	6	35.03 ± 0.61	25	6	34.98 ± 0.66
18	6	34.92 ± 0.47	26	6	34.85 ± 0.26
19	6	35.48 ± 0.25	27	6	35.07 ± 0.29
20	6	34.85 ± 0.56	28	6	35.67 ± 0.32
21	6	34.47 ± 0.45	29	6	34.85 ± 0.48
			30	5	34.56 ± 0.78
			31	5	34.18 ± 0.79
			32	6	34.02 ± 0.77
			33	5	34.92 ± 0.61
			34	5	35.36 ± 0.34

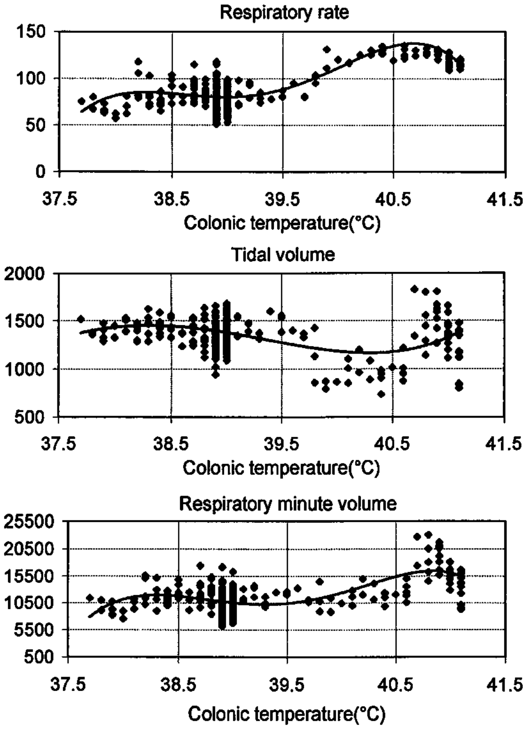

Fig. 6. Influence of colonic temperature on respiratory rate, tidal volume and relatively respiratory minute volume of one Muscovy Duck embryo after internal pipping at D34 of incubation. The respiratory rate is given in n*min^{-1}, the tidal volume and the relatively respiratory volume in arbitrary units.

mann et al. 1998). The results suggest that embryos of Muscovy Ducks and Domestic Fowls show endothermic reactions some days before the plateau phase occurs and continue these reactions to hatching.

As shown in Fig. 4, some embryos are able to increase their HP slightly and decrease the Q_{10} to values below 1.0 immediately before or after external pipping while Ta decreases (Fig.5). At normal incubation temperatures, the HP of avian embryos increases following the plateau phase. The observed increase in HP during the cooling procedure may be due to the post-plateau-phase increase, but may also be due to an increase in thermoregulatory HP (Nichelmann et al. 1998). It is most probable that both factors have an influence on the observed HP but further experiments are necessary to quantify their relative importance.

This results are only partially in agreement with the assumption of Whittow and Tazawa (1991) that in precocial birds there are four perinatal stages in the development of endothermy: (a) an Arrhenius-limited stage in which the embryo's metabolic rate is directly related to its temperature, with a Q_{10} value of about 2.0 caused by a deficit of corresponding enzyme activity and/or by a lack of central nervous influence on HP; (b) an oxygen-conductance-limited stage in which the oxygen uptake of the embryo is limited by the rate of diffusion of oxygen through the egg shell and the chorioallantoic membrane, in relation to oxygen demand by the embryo; (c) a power-limited stage in which the embryo has a limited capacity to produce heat in response to cooling; (d) full-blown homeothermy.

Tazawa et al. (1987) have postulated that the oxygen-conductance-limited stage occurs mainly in the plateau phase of oxygen consumption between internal and external pipping. At this stage, the embryo's thermoregulatory control and effector mechanisms are sufficiently developed to be operative, but are repressed by the low conductance of the eggshell to O_2 diffusion. The embryo's resting metabolism is still less than the eggshell's conductance limit; a slight increase in O_2 consumption might occur when the egg is cooled, but it will not exceed the O_2 conductance limit. This explanation may be true but will not give a full explanation of the early endothermic reactions occurring in experiments presented in this and other (Nichelmann et al. 1998) papers of our group.

It was shown in earlier experiments (Nichelmann et al. 1994, Nichelmann & Tzschentke 1997, Tzschentke & Nichelmann, 1994, 1997, 1999) that avian prenatal cold experiences led to a downward shift of the thermoregulatory set point and to an marked increase of HP during a postnatal cold load in Muscovy ducklings.

The cold experiences led to an increase in the efficiency of HP. In the experiments of series 2 we have shown (Fig. 3) that prenatal cold experiences are able to increase the thermoregulatory HP of Muscovy Duck embryos aged between D27 and D34 at actual Ta between 34.5 to 40.5°C. This increase is significant (variance analysis, $p < 0.05$) and can not be explained by the assumption that the metabolic rate during the plateau phase is ex-

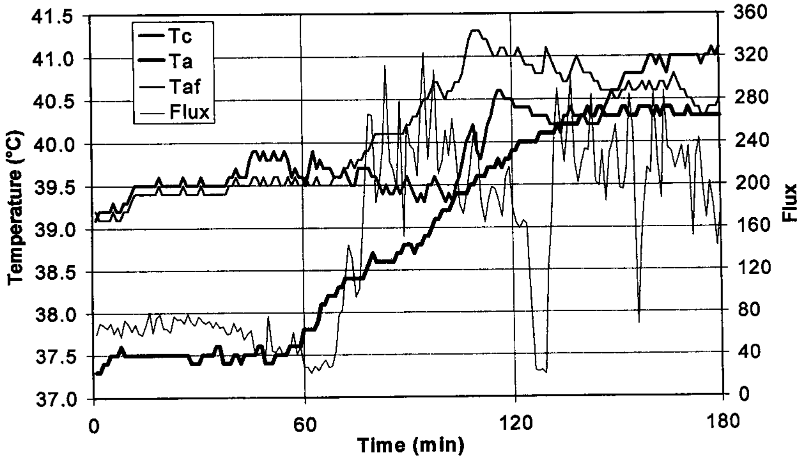

Fig. 7. Time course of ambient temperature (Ta) temperature of the allantoic fluid (Taf), colonic temperature (Tc) and blood flow in the chorioallantoic membrane (flux) during a typical experiment in a chicken embryo after internal pipping.

clusively limited by the oxygen diffusion through the egg shell. We can postulate that in this phase of development, also, a power limitation of HP may exist which is partly abolished by prenatal cold experiences.

Besides the endothermic reactions in the final days of incubation, embryos of precocial birds activate other thermoregulatory effector systems. Respiration movements occur before internal pipping (Murzenok et al. 1996), panting reactions were found in Muscovy Duck embryos between internal and external pipping and, at the same time, changes occur in blood flow in the chorioallantoic membrane.

Obviously, the efficiency of these thermoregulatory effector systems is not high: the existing thermoregulatory HP has only a very small influence on embryonic body temperature. It can not prevent a decrease in body temperature at low Ta but can only delay the fall in Tc. The panting during hyperthermia after internal pipping is characterized by high humidity of the inspired air at high Ta and because of this the evaporative heat loss is limited: the difference in temperature and water vapour pressure between inspired and expired air are small. The changes of blood flow in the chorioallantoic membrane may be more effective for heat loss. It is assumed that heat produced in the body core will be transported by the blood stream to the chorioallantoic membrane. This heat transfer mechanism clearly bypasses the extra-embryonic fluid. During the first 60 to 75 minutes of heating the egg (Fig. 7) Taf increases above Ta and Tc.

Because of the low efficiency of thermoregulatory effector systems in avian embryos it could be argued that thermoregulatory mechanisms are unnecessary in avian embryos, given that (1) the embryos are kept warm by the incubating parent in most birds for the most of time and (2) the thermal tolerance of the embryos protects them to some extent from overheating and cooling (Whittow & Tazawa 1991). But it seems to be a general rule in the development of body functions in avian embryos, that the functional development of organ functions starts very early, before hatching. For example, contractions of heart muscle cells occur in chicken embryos at D2, before morphological differentiation into atrium and ventricle exist and before blood transport is possible (Seidl et al. 1981). Sympathetic innervation of the heart is fully developed before D24 in ducklings (Höchel 1998) and at D16 in chicken embryos (Höchel et al. 1999).

The activity of organ functions occurs firstly during embryonic development, before this function is ultimately necessary to ensure the survival of the embryo.

Acknowledgements: The English of the text was improved before publication by Dr. Murdo MacLeod, Roslin Institute (Edinburgh), Roslin, Scotland, UK. The research was supported by a grant of Deutsche Forschungsgemeinschaft (Ni 336/3-1). Parts of the experiments were carried out by Dr. Astrid Burmeister, Dr. Barbara Lange, Dr. Sven Holland, Tanja Thiele, Oliver Janke and Anke Paulick.

Selostus: **Pesäjättöisten linnunpoikasten lämmöntuoton kehitys**

Myskisorsan (Cairina moschata) ja kanan (Gallus domesticus) lämmöntuoton kehitystä alkionkehityksen aikana mitattiin hapenkulutuksen avulla (ns. epäsuora kalorimetria). Lämmöntuottomittausten lisäksi mitattiin internal pipping -vaiheessa (jolloin linnut puhkaisevat sikiökalvonsa, mutta eivät vielä munan kuorta) hengityksen tiheys, vaihtoilma ja minuuttitilavuus sekä verenvirtaus sikiökalvoissa (chorioallantois). Samalla mitattiin rakkokalvon ja viemärisuolen lämpötila. Nämä mittaukset tehtiin 40°C:ssa. Toisessa koesarjassa verrattiin 34.5°C:ssa ja 37.5°C:ssa haudottujen myskisorsien lämmöntuottoa.

Ympäristön lämpötilan lasku aiheutti yleensä rakkokalvon ja viemärisuolen lämpötilojen sekä lämmöntuoton alenemisen. Lämmöntuottoa alentaa lämpötilasta sinänsä johtuva Q_{10}-vaikutus, mutta samalla keskushermoston ohjaama lämmönsäätelyjärjestelmä, mikäli se on kehittynyt, pyrkii nostamaan sitä. Mitä vanhempi alkio oli kyseessä, sitä pienempi oli laskennallisesti arvioitu Q_{10}-vaikutus, sitä alempana oli lämpötila, jossa Q_{10}:n kriittinen arvo 2.0 saavutettiin ja sitä korkeampi oli lämpötila, jossa Q_{10} oli pienimmillään. Tämä osoittaa, että jo hyvin nuoret alkiot kykenevät keskushermoston ohjaamaan lämmöntuottoon, vaikkakin sen jäähtymistä estävä vaikutus on aluksi varsin pieni.

Haudontalämpötila näyttää vaikuttavan lämmönsäätelyjärjestelmän myöhempään toimintaan: eri lämpötiloissa haudottujen poikasten lämmöntuotto oli erilainen vakiolämpötiloissa mitattuna.

Myös kuumuudelta suojautumisen mekanismit näyttävät kehittyvän hyvin varhaisessa vaiheessa. Internal pipping -vaiheen jälkeen kananpojat kykenivät läähätyksen avulla tapahtuvaan lämmönpoistoon ja myskisorsillakin hengitystiheys nousi, kun rakkokalvon lämpötila kohosi lähelle 40°C.

Alkionkehityksen aikana tapahtuva lämmönsäätelymekanismien aktivaatio, vaikkakaan se ei riitä varsinaiseen toimivaan lämmönsäätelyyn, näyttää olevan olennaista näiden järjestelmien kehitykselle ja myöhemmälle toiminnalle.

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