Development of avian thermoregulatory system during the early postnatal period: development of the thermoregulatory set-point

Barbara Tzschentke & Martin Nichelmann

Tzschentke, B. & Nichelmann, M., Institut für Biologie, Humboldt-Universität zu Berlin, Abt. Sinnesbiologie, AG Perinatale Anpassung, Invalidenstr. 43, D-10115 Berlin, Germany. E-mail: barbara.tzschentke@rz.hu-berlin.de

The development of colonic temperature and of heat production in 1- to 10-d-old chicken, turkeys and Muscovy ducklings was investigated after short-term (1h) exposure in climatic chambers to ambient temperatures between 10 and 40°C. In additional experiments the development of colonic temperature and preferred ambient temperature was studied in a temperature gradient tunnel (ambient temperature range 10–45°C). The decrease in biological optimum temperature (identical with the ambient temperature at which the organism is exposed to minimal thermal load) and in the preferred ambient temperature with increasing age indicated that the lower colonic temperature during the first days after hatching is caused by changes of the thermoregulatory set-point. Compared with normally incubated ducklings, an incubation temperature (34.5°C) lower than the usual 37.5°C during the last week of embryonic development may induce a lower thermoregulatory set-point. These birds have a higher postnatal cold tolerance, they prefer lower ambient temperatures and have a higher heat production at low ambient temperatures at the first day post-hatching.

1. Introduction

Many studies in precocial birds have shown that the deep body temperature in hatchlings is lower than in adult birds (Spiers et al. 1974, Myhre et al. 1975, Myhre 1978, Hissa et al. 1983, Burmeister et al. 1988, Jurkschat et al. 1988, Modrey & Nichelmann 1992). For instance, the colonic temperature of chicks of Willow Grouse (*Lagopus lagopus*) increased from 39.4 ± 0.5°C on the 1st day to 40.3 ± 0.5°C on the 12th day post-hatching (Myhre et al. 1975). Generally, the lower deep body temperature in juvenile birds seems to be the result of a lower thermoregulatory set-point and does not indicate a failure of thermoregula-

tion. The lower thermoregulatory set-point of hatchlings may be an energy saving mechanism by reducing the thermal gradient between the animal and its surroundings (Hissa et al. 1983).

There are some problems in testing the hypothesis that the lower deep body temperature of hatchlings is really caused by a lower thermoregulatory set-point.

Firstly, "... the physiological correlate of the set-point of temperature regulation has remained hypothetical" (Glossary of terms for thermal physiology 1987). In the eighties the set-point concept changed from the classical hypothalamic set-point hypothesis (Hammel 1965, 1968) to the hypothesis of an integrative or additive body tempera-
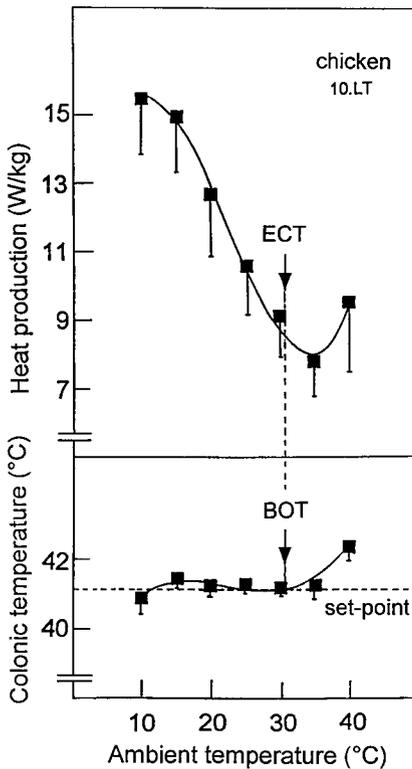
Fig 1. The biological optimum temperature (BOT) was calculated from relationships between ambient temperature and colonic temperature (lower part) and relationships between ambient temperature and heat production (upper part, BOT is identical with the effective critical temperature (ECT)) in 10-d-old chickens. The broken line indicates the colonic temperature at BOT, which can be used for determination of changes in the thermoregulatory set-point.

ture, for instance weighted mean body temperature, resulting from the interaction of different temperature sensor populations (Simon 1986, 1987, Boulant 1991, Lovegrove et al. 1991).

Secondly, "... in temperature regulation the set-point may change temporarily beyond its normal set-range, due to interference with the regulations of nonthermal variables..., or due to pathological, nonthermal influences... It is assumed that the processes of acclimat(izat)ion and adaptation may change the set-point (or set-range) in temperature regulation..." (Glossary of terms for thermal physiology 1987).

Thirdly, how is it possible to determine changes of the thermoregulatory set-point caused by dif-

ferent exogenous and endogenous influences (e.g. age, acclimat(izat)ion)?

The concept of the biological optimum temperature (BOT, Nichelmann 1983) gives one possibility for determination of changes of the thermoregulatory set-point. BOT is defined as the ambient temperature (Ta) at which the thermoregulatory system is minimally activated and the homeothermic organism is exposed to minimal thermal load. The BOT may be determined from (1) relationships between Ta and rectal or colonic temperature (Tc) and (2) relationships between Ta and heat production (HP). The relationships between Ta and Tc in different mammalian and bird species can be described by parabolic curves (Nichelmann et al. 1974). Tc increases with decreasing Ta. The BOT is identical with the threshold temperature for increasing cold load (Fig. 1). In young birds and mammals the relationship between Ta and Tc often is not polynomial. With decreasing Ta Tc is also diminished. Under these conditions BOT must to be determined from the relationships between Ta and HP (Fig. 2).

We hypothesize that all changes in Tc measured at BOT are caused by changes in the thermoregulatory set-point.

Fourthly, homeothermic organisms thus have the option of using either behavioural or autonomic effector systems, or both, in attaining effective thermoregulation with minimal disruption of other homeostatic systems (Schmidt 1984). The effective contribution of each effector system to regulation of body temperature might be different under different circumstances, so that for investigations of changes of thermoregulatory set-point results from both effector systems are necessary.

The aim of this study was (1) to test the hypothesis that the lower deep body temperature of hatchlings is caused by a lower thermoregulatory set-point. This was done by measuring the Tc at BOT and under conditions of temperature selection using a temperature gradient. Further, the goal was (2) to investigate if a decrease in incubation temperature (34.5°C instead of the usual 37.5°C) during the last days of incubation influences the postnatal thermoregulatory set-point in birds.

2. Material and Methods

The experiments were carried out in 1-to 10-d-old Muscovy ducklings (*Cairina moschata f. do-*

mestica), chickens (*Gallus gallus f. domestica*) and turkeys (*Meleagris gallopavo f. domestica*) incubated at 37.5°C (first series). A second series was carried out in Muscovy ducklings incubated during the last week before hatching at a lower temperature (34.5°C; n = 156) in comparison to a group incubated at the usual 37.5°C (control, n = 56).

To characterize autonomic thermoregulation, HP and Tc were measured at different Ta's. During the experiments the birds were placed in open-circuit climatic chambers and exposed to 7 different Ta's between 10 and 40°C (at intervals of 5°C) for 1 h. After 1-h exposure to the respective Ta's, HP was determined by measurement of O_2 consumption and CO_2 production. HP (W/kg) was calculated by multiplying O_2 consumption (ml/min) by its caloric equivalent. Before and after the experiments the Tc was measured by using a fever thermometer.

As described in the previous paragraph (Introduction, Figs. 1 and 2) BOT was calculated using the relationships between Ta and HP.

For characterization of the behavioural thermoregulatory mechanisms, the preferred ambient temperature (PT) was determined using a temperature gradient tunnel (Ta range 10–45°C). Groups of 5 birds were kept for 10 days in the temperature gradient immediately after hatching. Food and water were available *ad libitum* in all sections of the tunnel. The birds could move freely in the tunnel. For 9h daily the chosen Ta were observed every 10 minutes. In the first series of experiments Tc was measured every 3 hours.

For statistical evaluation, appropriate methods such as regression and correlation analysis, analysis of variance and t-test were employed.

Fig 2. Relationship between ambient temperature and heat production. The relationship between ambient temperature and heat production can be described by a parabolic curve. With decreasing ambient temperature, heat production at first increases slowly if the ambient temperature drops below the thermoneutral temperature (TNT; at this ambient temperature the heat production calculated from the parabolic curve is minimum) and then increases at a faster rate. The second part of the parabola can also be described by a linear function. The point of intersection of the linear functions which describe the relationships between ambient temperature and heat production below TNT and under thermoneutral conditions (ambient temperatures at which no significant changes in heat production occur) is identical with the effective critical temperature (ECT). The biological optimum temperature (BOT) is near or equal to the ECT (Nichelmann & Tzschentke 1996).

3. Results

3.1. Series 1

3.1.1. Development of heat production and colonic temperature

As examples, Figs. 3, 4 and 5 show the temperature-dependent pattern of HP and Tc in 1-, 5- and 10-d-old chickens, turkeys and Muscovy ducklings. The relationships between Ta and HP as well as Ta and Tc were described by polynomials of the 3rd degree. In comparison to Muscovy duck-

lings the thermoregulatory HP-capacity in 1-d-old chickens and turkeys is so low that Tc decreased with decreasing Ta. In each species investigated no significant differences in HP under thermoneutral conditions between 5- and 10-d-old birds were found (t-test, P < 0.001)

The BOT calculated from the relationships between Ta and HP (BOT_{HP}) and the Tc at BOT using the method described in Figs. 1 and 2 are given in Table 1. With increasing age BOT_{HP} decreased and Tc at BOT increased in all bird species investigated.
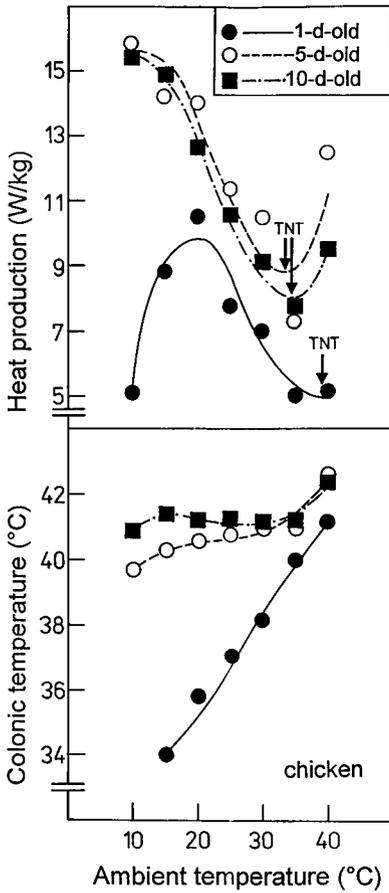
Fig. 3. Relationships between ambient temperature and heat production (upper part) and ambient temperature and colonic temperature (lower part) of 1-, 5- and 10-d-old chickens. The relationships between ambient temperature and heat production can be described by the following polynomials:

$y = 1.4272*10^{-3}x^3 - 0.1236x^2 + 3.1772x - 15.67$ ($r = 0.69$, $n = 38$, 1-d-old chicken),

$y = 1.4182*10^{-3}x^3 - 0.0966x^2 + 1.7070x + 6.69$ ($r = 0.83$, $n = 48$, 5-d-old chicken),

$y = 1.0916*10^{-3}x^3 - 0.0742x^2 + 1.2166x + 9.54$ ($r = 0.88$, $n = 56$, 10-d-old chicken),

(y = heat production in W/kg, x = ambient temperature in°C, n = number of birds investigated).

The relationships between ambient temperature and colonic temperature are described as follows:

$y = -4.1*10^{-4}x^3 + 0.0333x^2 - 0.5795x + 36.77$ ($r = 0.96$, $n = 82$, 1-d-old chicken),

$y = 3.7*10^{-4}x^3 - 0.0255x^2 + 0.5927x + 35.96$ ($r = 0.88$, $n = 112$, 5-d-old chicken),

$y = 3.6*10^{-4}x^3 - 0.0245x^2 + 0.5236x + 37.83$ ($r = 0.81$, $n = 112$, 10-d-old chicken),

(y = colonic temperature in°C, x = ambient temperature in°C, n = number of birds investigated).
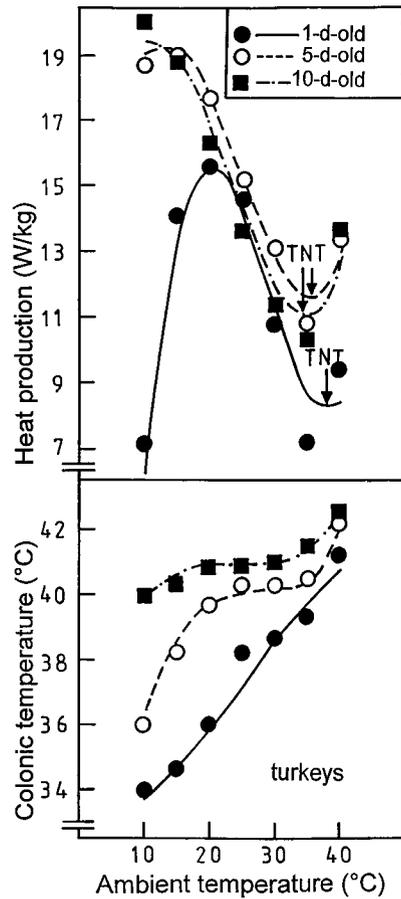
Fig. 4. Relationships between ambient temperature and heat production (upper part) and ambient temperature and colonic temperature (lower part) of 1-, 5- and 10-d-old turkeys. The relationships between ambient temperature and heat production can be described by the following polynomials:

$y = 2.685*10^{-3}x^3 - 0.2311x^2 + 5.994x - 33.38$ ($r = 0.77$, $n = 242$, 1-d-old turkeys),

$y = 1.442*10^{-3}x^3 - 0.1040x^2 + 1.952x + 8.41$ ($r = 0.73$, $n = 245$, 5-d-old turkeys),

$y = 1.694*10^{-3}x^3 - 0.1140x^2 + 1.954x + 9.55$ ($r = 0.76$, $n = 228$, 10-d-old turkeys),

(y = heat production in W/kg, x = ambient temperature in°C, n = number of birds investigated).

The relationships between ambient temperature and colonic temperature are described as follows:

$y = 1.3*10^{-4}x^3 + 0.0103x^2 + 0.0013x + 32.92$ ($r = 0.90$, $n = 167$, 1-d-old turkeys),

$y = 7.3*10^{-4}x^3 - 0.0581x^2 + 1.5584x + 26.03$ ($r = 0.90$, $n = 168$, 5-d-old turkeys),

$y = 4.3*10^{-4}x^3 - 0.0301x^2 + 0.6875x + 35.69$ ($r = 0.82$, $n = 164$, 10-d-old turkeys),

(y = colonic temperature in°C, x = ambient temperature in°C, n = number of birds investigated).

3.1.2. Development of preferred ambient temperature and colonic temperature

Fig. 6 shows the development of Tc and Fig. 7 of PT during the first 10 days post-hatching in chickens, turkeys and Muscovy ducklings. With increasing age PT decreased and Tc measured under preference conditions increased in chickens as well as in turkeys and Muscovy ducklings.

3.2. Series 2

3.2.1. Influence of low incubation temperature on the development of heat production and colonic temperature

HP was higher in cold-incubated ducklings than in normally incubated ones under cold exposure on the first day after hatching (Table 2). Later (days 5 and 10) no differences in HP could be observed between the two groups at Ta of 10°C. In 1-day-old cold-incubated birds, HP at 10°C was 56% higher than in the control.

The Tc in older ducklings incubated at 34.5°C was lower in the Ta-range between 10 and 40°C than in control birds (Fig. 8).

Tc at BOT in 5-d-old cold-incubated ducklings was 40.3°C and in the control 40.6°C, while in 1-d-old ducklings the respective temperatures were 40.0°C (cold-incubated) and 39.6°C (control).

3.2.2. Influence of low incubation temperature on the development of preferred ambient temperature

The PT of ducklings incubated at lower temperature was lower during the first 10 days post-hatching than in birds incubated at the usual incubation temperature (Table 3; analysis of variance P <0.05).

4. Discussion

4.1. Development of thermoregulatory set-point during the early postnatal period in chickens, turkeys and Muscovy ducklings

Both Tc at BOT and Tc under preference conditions increased with increasing age during the first 10 days post-hatching in chickens, turkeys and
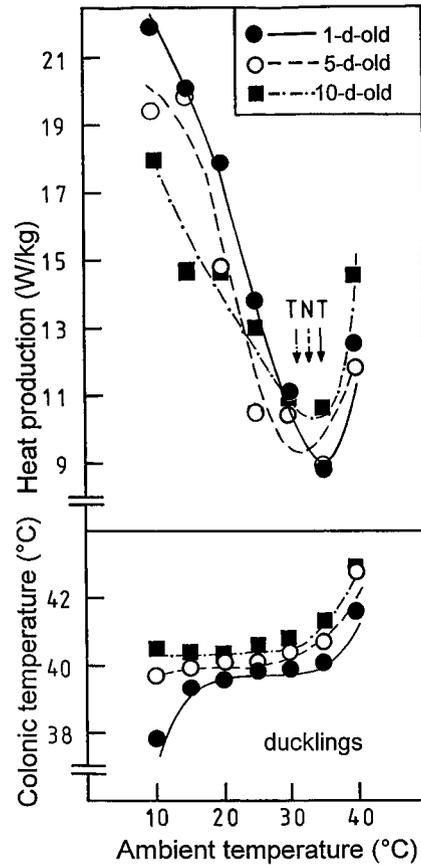
Fig. 5. Relationships between ambient temperature and heat production (upper part) and ambient temperature and colonic temperature (lower part) of 1-, 5- and 10-d-old Muscovy ducklings.

The relationships between ambient temperature and heat production can be described by the following polynomials:

$y = 1.925*10^{-3}x^3 - 0.1361x^2 + 2.4373x + 8.37$ (r = 0.92, n = 84, 1-d-old ducklings),

$y = 1.548*10^{-3}x^3 - 0.0996x^2 + 1.4491x + 14.04$ (r = 0.94, n = 80, 5-d-old ducklings),

$y = 9.610*10^{-3}x^3 - 0.0560x^2 + 0.6646x + 15.76$ (r = 0.82, n = 76, 10-d-old ducklings),

(y = heat production in W/kg, x = ambient temperature in°C, n = number of birds investigated).

The relationships between ambient temperature and colonic temperature are described as follows:

$y = 6.4*10^{-4}x^3 - 0.0503x^2 + 1.2984x + 28.84$ (r = 0.86, n = 56, 1-d-old ducklings),

$y = 4.1*10^{-4}x^3 - 0.0261x^2 + 0.5376x + 36.41$ (r = 0.90, n = 56, 5-d-old ducklings),

$y = 3.2*10^{-4}x^3 - 0.0186x^2 + 0.3476x + 38.29$ (r = 0.94, n = 56, 10-d-old ducklings),

(y = colonic temperature in°C, x = ambient temperature in°C, n = number of birds investigated).
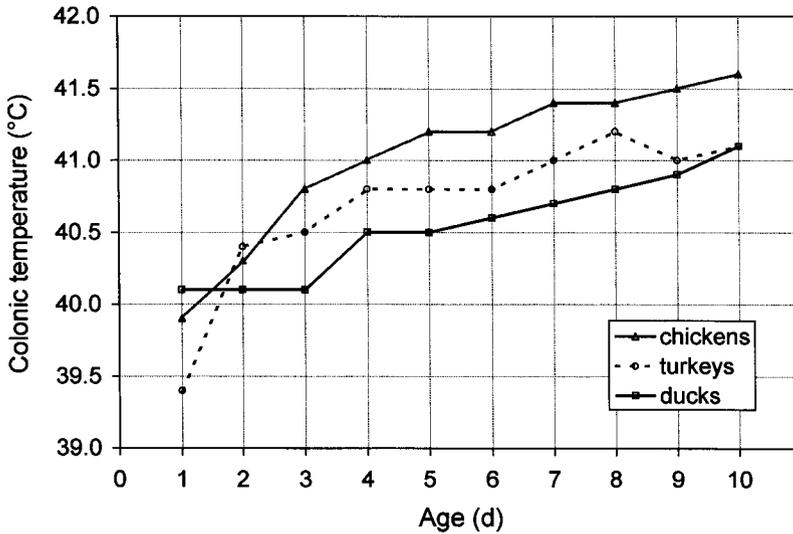
Fig. 6. Age dependent course of colonic temperature during the first 10 days post-hatching. The means were calculated from 10 (chicken), 15 (turkey) and 20 (Muscovy duckling) birds in each age group.

Muscovy ducklings. During the same period the BOT_{HP} and the PT decreased in all bird species investigated (Table 1 and Fig. 6). At BOT the organism is under minimal thermal load (Nichelmann 1983; Nichelmann & Tzschentke 1996). The hypothesis that all changes of Tc measured at BOT are caused by changes in thermoregulatory set-point is supported by the facts that between the 5th and 10th day of life the Tc at BOT increased continuously, while HP under thermoneutral conditions and also at low ambient temperatures remained similar.

The contrasting development of PT (decrease) and Tc under preference conditions (increase)

during the first 10 days post-hatching in all bird species investigated also supports the hypothesis of a lower thermoregulatory set-point after hatching. In a temperature gradient tunnel the birds have the possibility of obtaining warmth from the surroundings to complement their own low HP-capacity. Compared to the autonomic regulation of body temperature, behaviour is a phylogenetically older but very effective means of thermoregulation (Kluger 1979, Satinoff 1980). Already changes in face skin temperature induce behavioural thermoregulatory reactions (Schmidt 1982, 1983). In new-born endothermic organisms thermoregulatory behaviour is essential to maintain a stable

Table 1. Biological optimum temperature calculated from the relationships between ambient temperature and heat production (BOT_{HP}) and colonic temperature at BOT_{HP} (CT_{BOT}) in 1- to 10-d-old chickens, turkeys and Muscovy ducklings.

Age	Chickens		Turkeys		Muscovy ducklings	
(d)	BOT_{HP}	CT_{BOT}	BOT_{HP}	CT_{BOT}	BOT_{HP}	CT_{BOT}
1	36.6	40.0	37.2	40.3	35.6	40.1
2	32.2	40.1	35.0	40.4	34.0	40.4
3	34.1	41.1	32.3	40.0	33.5	40.3
4	32.5	40.9	33.8	40.4	26.2	40.2
5	35.2	41.0	33.8	40.6	32.7	40.5
6	29.7	40.9	33.5	41.0	25.0	40.3
7	33.5	41.2	32.2	40.6	28.5	40.4
8	30.0	41.2	32.2	41.0	26.5	40.3
9	33.4	41.2	31.8	40.9	30.0	40.4
10	30.5	41.2	30.8	41.0	29.7	40.7
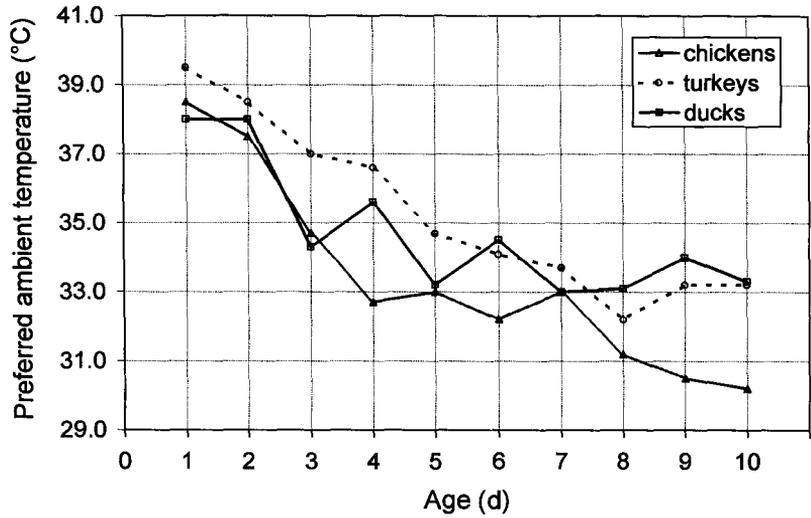
Fig. 7. Age dependent course of preferred ambient temperature during the first 10 days post-hatching. The means were calculated from 10 (chicken), 15 (turkey) and 20 (Muscovy duckling) birds in each age group.
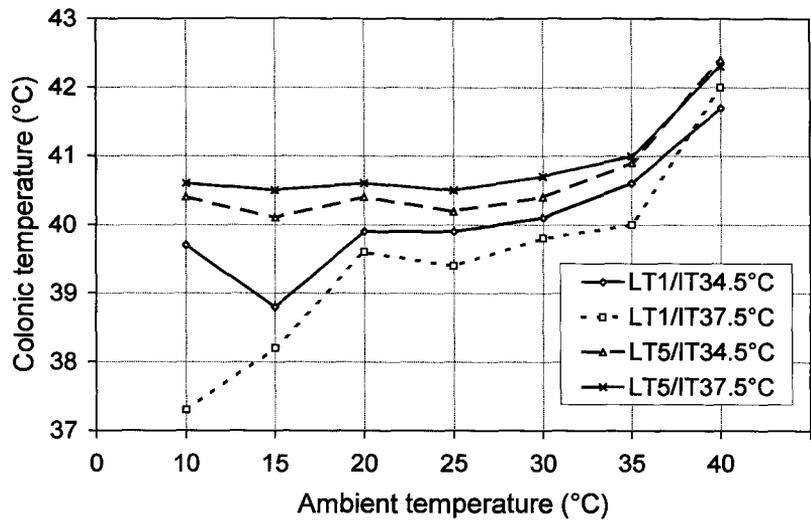
Fig. 8. Colonic temperature of 1- and 5-day-old Muscovy ducklings incubated at 34.5 and 37.5°C.

body temperature, because the autonomic mechanisms are not so much developed. Immediately after hatching chickens are able to select their specific PT range in a temperature gradient (Myhre

Table 2. Influence of incubation temperature on heat production (HP) at an ambient temperature of 10°C in 1-, 5- and 10-d-old Muscovy ducklings (D = day after hatching, n = 15 in each experimental group).

Incubation temperature (°C)	HP (W/kg)		
	D 1	D 5	D 10
34.5	28.2 ± 3.9	20.9 ± 1.2	18.0 ± 1.0
37.5	18.1 ± 2.4	20.2 ± 1.7	17.9 ± 1.1

Table 3. Influence of incubation temperature on preferred ambient temperature (PT) in 1-, 5- and 10-d-old Muscovy ducklings (D = day after hatching, n = 15 in each experimental group)

Incubation temperature (°C)	PT (°C)		
	D 1	D 5	D 10
34.5	38.7 ± 1.4	34.1 ± 3.4	31.6 ± 2.8
37.5	39.1 ± 2.5	36.0 ± 3.4	33.6 ± 3.7

et al. 1975; Tzschentke et al. 1993) with high accuracy. At the first day after birth immature mammals like rats and rabbits are also able to select temperatures (Kleitman & Satinoff 1982, Szelényi et al. 1984, Székely 1986) but often with higher fluctuations (Nichelmann & Barnick 1982).

Similar development of Tc observed under different experimental conditions supports the view that the lower Tc in newly hatched birds is caused by changes of the thermoregulatory set-point.

4.2. Influence of low incubation temperature on development of thermoregulatory set-point in Muscovy ducklings

Prenatal cold load induced an increase in the sensitivity of HP-mechanisms. The higher HP in cold-incubated ducklings (Table 2) explains the higher Tc of the 1-day-old cold-incubated ducklings at Ta's between 10°C and 40°C (Tc of cold-incubated ducklings at a Ta of 10°C: 39.5 ± 1.1, compared with 37.5 ± 2.9 in control birds, Fig. 7) . Because of the higher sensitivity of HP-mechanisms cold-incubated ducklings are able to control their actual deep body temperature at the set-point, unlike birds, incubated at 37.5°C, which have a lower HP.

The Tc in older ducklings incubated at 34.5°C was in the Ta-range between 10 and 40°C lower than in control birds (Fig. 7). However, no differences in HP at low and mild Ta could be observed between the two groups in 5- and 10-d-old ducklings (Herrmann & Nichelmann 1991). At the 5th day post-hatching autonomic thermoregulatory mechanisms are well developed in low as well as in normally incubated (Fig. 5) ducklings. Because of this, we postulate that the thermoregulatory set-point in cold-incubated ducklings is lower than in the controls.

The PT of ducklings incubated at low temperature was during the first 10 days post-hatching significantly lower than in birds incubated at the usual incubation temperature. Because of the fact that new-born animals and birds are able to use temperature selection to regulate their deep body temperature, the lower PT after prenatal cold load supports the hypothesis that avian prenatal cold experience leads to a downward shift of the thermoregulatory set-point. The lower thermoregulatory set-point seems to be a special strategy of epigenetical adaptation to cold conditions in the prenatal period (Tzschentke & Nichelmann 1997).

On the other hand, the PT of 1- to 10-days-old turkeys was higher after a prenatal heat load (38.5°C) than in birds incubated at the usual (37.5°C) temperature (Tzschentke & Nichelmann, 1997). This indicates an elevation in the thermoregulatory set-point after prenatal heat load.

Besides this, prenatal temperature experience to incubation temperatures higher or lower than 37.5°C also induced a clear change in the neuronal hypothalamic thermosensitivity in 10-d-old Muscovy ducklings. Using extracellulare recordings, in warm incubated ducklings the increase in the proportion of cold-sensitive neurons and decline in the number of warm-sensitive neurons in the hypothalamus in relation to all investigated hypothalamic neurons indicates a decrease in the total hypothalamic warm-sensitivity, while the reduction in the number of cold-sensitive neurons in cold-incubated ducks indicates an increase in the total hypothalamic warm-sensitivity (Basta & Tzschentke, 1998).

In conclusion, the presented results - increase of Tc and decrease of BOT and PT between day 1 and 10 post-hatching - support the hypothesis, that in precocial birds after hatching the lower Tc measured under different experimental conditions is caused by a lower thermoregulatory set-point as a special strategy of cold defense.

This development might be influenced by prenatal cold load. In comparison with normally incubated birds prenatal cold load induced besides a higher HP at low Ta at the 1st day post-hatching and a lower PT during the first 10 postnatal days, possibly a further decrease of the thermoregulatory set-point as a sign of increased cold tolerance.

Selostus: **Lintujen lämmönsäätelyjärjestelmän kehitys kuoriutumisen jälkeen: asetusarvon muutokset**

Kuoriutumisenjälkeistä ruumiinlämpötilan ja lämmöntuoton kehitystä seurattiin kanalla, kalkkunalla ja myskisorsalla altistamalla eri ikäisiä poikasia tunniksi 10–40°C ympäristönlämpötiloihin. Toisessa koesarjassa ruumiinlämpötilaa ja poikasten valitsemaa lämpötilaa tutkittiin lämpötilagradientin omaavassa tunnelissa. Kirjoittajat esittelevät ns. biologisen optimilämpötilan (BOT; lämpötila, jossa tarve lämmönpoistoon ja -tuottoon ovat alimmillaan) mittaavan lämmönsäätelyjärjestelmän asetusarvoa paremmin kuin tosiasiallinen ruumiinlämpötila. Sekä BOT että eläinten gradientissa valitsema lämpötila olivat alempia vastakuoriutuneilla poikasilla, mikä osoittaa niiden lämmönsäätelyjärjestelmän asetusarvon olevan alemmalla tasolla kuin vanhemmilla poikasilla. Haudontalämpötilan alentaminen viimeisen haudontaviikon ajaksi 34.5°C:een vaikuttaa lisäksi lämmönsäätelyjärjestelmään siten, että nämä poikaset ovat kylmänkestävämpiä ja ennenkaikkea myös valitsevat alempia lämpötiloja myöhemmän kehityksensä aikana

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