

THERMOREGULATORY HEAT PRODUCTION IN LAYING HYBRID HENS -
SUMMIT METABOLISM

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Thermoregulatory reactions were studied in 96 laying hybrid hens (age 30 to 35 weeks) under moderate (5 to 40 °C ambient temperature, 0.2 m.s⁻¹ air velocity) and extreme environmental conditions (5 to 40 °C ambient temperature, 1.2 m.s⁻¹ air velocity). Effective ambient temperature (EAT) was calculated from the determined heat production, colonic temperature, evaporative heat loss and conductance. The heat production began to decrease in birds exposed to EAT of -50 to -60 °C. At the same time a progressive hypothermia occurred. The summit metabolism was 338% of the heat production under thermally neutral conditions. Total body thermosensitivity oscillated between 3.1 and 3.7 W.kg⁻¹.K⁻¹. The increase in colonic temperature in the range between thermoneutral temperature (TNT) and 5 °C in fully feathered birds is in agreement with this thermosensitivity.

Heat production, feathering, heat loss, effective ambient temperature.

The heat production of homeotherms begins to rise with ambient temperature (T_a) below the thermoneutral temperature (TNT). In fully feathered sexually mature laying hens the heat production does not exceed 50 % at temperatures between thermoneutrality and 5 °C T_a (Nichelmann et al. 1983, 1984).

However, in poorly feathered birds, or in partially or totally defeathered ones substantially higher increase in heat production may be expected at the above-mentioned temperatures. Heat production of partially defeathered "Blue Holland" cocks increased by 140 % between 35 and 5 °C T_a (Romijn 1950). In laying hens (Babcock 390, brown eggshell) with 65 % of body surface defeathered through mechanical effects during cage rearing an increase in heat production by 153 % was observed between 35 and 0 °C (Richards 1977). Light Sussex cocks augmented their

heat production by 167 % at temperatures between 38 and 22 °C (O'Neill et al. 1971). Nichelmann et al. (1978) reported on increasing heat production of a parental flock of laying hybrids between TNT and T_a of 5 °C due to progressive loss of plumage with advancing age. However, no data are available on the maximum possible thermoregulatory heat production increase in the domestic fowl. Owing to good insulation properties of the plumage it may be expected that the summit metabolism occurs only under extreme thermal conditions.

The question of maximum possible heat production increase in laying hybrids is one of not only theoretical but also practical interest. The domestic fowl is genetically acclimated to high T_a so that a special strategy to combat the adverse effects of low T_a can be envisaged (Aulie and Grav 1978). Moreover, in hens kept under intensive husbandry conditions a combination of poor plumage and high air velocity in the immediate surroundings of the birds may dramatically increase their heat loss and activate their thermoregulatory system.

The present paper considers the effects of T_a between 40 °C and 5 °C on heat production of fully feathered laying hybrid hens as compared to thermoregulatory reactions of birds under extreme cold conditions brought about by complete defeathering and air velocity as high as 1.2 m.s⁻¹.

Materials and Methods

Ninety six hybrid laying hens aged 30 to 35 weeks were used. For a period of 4 weeks prior to the experiment, the birds were kept on deep litter at a temperature of 20 ± 1 °C. Commercial food mash and water were available ad libitum. The photoperiod was 16 h light throughout.

Four to six days prior to the experiment, 48 birds were defeathered under a Brevinarcon anaesthesia. The flight feathers of the wings and tail were cut off with scissors. The head feathers were not removed. The birds were kept at a temperature of 26 to 28 °C individually or in pairs until the beginning of the experiment. They were not fasted prior to the procedure.

The hens were individually placed in metabolism chambers adjustable to temperatures between 5 °C and 40 °C (+ 0.7 K). Relative humidity in the chambers was 60 to 75% at temperatures between 15 and 40 °C; at lower T_a it increased to 85%, and the air velocity was 1.2 m.s⁻¹.

The experimental conditions for fully feathered hens were as follows: T_a in metabolism chambers was 5 to 40 °C, relative humidity 60 to 75% at T_a of 15 to 40 °C, 85% at lower T_a ; air velocity 0.2 m.s⁻¹.

Each hen was exposed to the experimental conditions only once for 1 hour. At each T_a six birds each of the feathered and defeathered group were investigated.

Immediately prior to the measurements, the body mass and colonic temperature of the birds were determined. After 1 h exposure to the respective temperatures, the O₂ consumption and CO₂ production of the birds were measured using a Spirolyt II apparatus (VEB Junkalor, Dessau, GDR); the evaporative heat loss was calculated from the water vapour content of the air entering and

leaving the chambers using psychrometers, and the colonic temperature of the birds was again measured using a fever thermometer. Thermal conductance was calculated from the heat production, evaporative heat loss and colonic temperature. Details concerning the measurements and calculations have been described elsewhere (Nichelmann et al. 1973).

Results

Heat production

In feathered hens, the relationship between the T_a and heat production was expressed in terms of a parabolic function (Fig. 1). The extreme value of the parabola, identical with the thermoneutral temperature, was found at 22.3 °C.

The relationship between T_a and heat production below TNT was described by the function in Fig. 2. This implies that below TNT, the heat production increased by 0.11 W.kg⁻¹ per 1 K decrease in T_a .

In feathered hens the heat production of 3.9 W.kg⁻¹ at 25 °C increased to 6.3 W.kg⁻¹ at 5 °C, rising by 62%.

In defeathered birds the heat production increased with falling T_a at temperatures between 40 and 20 °C with a minimum of 5.4 W.kg⁻¹ at 40 °C and a maximum of 13.2 W.kg⁻¹ at 20 °C. At lower T_a their heat production began to fall again. Thus the maximum thermoregulatory increase in heat production of defeathered birds exceeded that of the feathered ones in TNT by 238%.

The relationship between T_a and heat production in defeathered birds was expressed in terms of the function given in Fig. 1. The extreme value of the parabola was found at 17.0 °C.

The relationship between T_a and heat production of these birds at temperatures between 40 and 20 °C was expressed in terms a linear function ($y = -0.3220x + 19.260$). The increase of the curve was with -0.322 W.kg⁻¹ three times steeper than the increase of the function found in fully feathered hens in the temperature range of 5 and 25 °C (Fig. 2).

Colonic temperature

The relationship between T_a and colonic temperature in fully feathered hens was expressed in terms of a polynomial function ($y = 0.0068x^2 - 0.2471x + 43.181$; $r = 0.84$, $n = 48$, $p < 0.01$) given in Fig. 8. The extreme value of this function, 18.8 °C, was identical with the biologically optimal temperature (BOT). Tangents applied to both parts of the parabola intersected at 24 °C (Fig. 3). The intersection lay above the extreme value of the parabolic function, being in good agreement with the graphically estimated BOT (23 °C).

In defeathered hens the colonic temperature decreased continually with lower T_a between 40 and 20 °C (0.11 K per 1 °C T_a change). This decrease became 7.5 times steeper (0.76 K per 1 °C T_a change) as soon as T_a was below 20 °C (Fig. 9). The equations describing the relationship between T_a and colonic temperature of the birds are in Fig. 4.

Table 1
Effect of feathering and T_a on heat production of laying hybrid hens

Ambient temperature (°C)	Heat production		W. kg ⁻¹ defeathered birds
	W. kg ⁻¹ feathered birds	W. kg ⁻¹	
5	6.5±0.5	7.7±0.5	9.9±1.3
10	6.1±0.3	6.8±0.4	12.2±1.2
15	5.1±0.3	5.7±0.3	9.7±1.6
20	5.9±0.7	6.7±0.9	13.3±1.1
25	3.2±0.3	3.6±0.3	8.2±0.8
30	4.5±0.2	5.1±0.2	11.4±1.0
35	4.4±0.4	5.0±0.5	7.8±0.2
40	7.8±0.8	8.8±0.9	5.5±0.5

Values are means ± S.E.M.

Table 2
Effect of feathering and T_a on colonic temperature of laying hybrid hens

Ambient temperature (°C)	Colonic temperature		defeathered birds °C
	feathered birds °C	°C	
5	41.7±0.1		31.7±2.8
10	41.4±0.1		32.8±1.0
15	41.4±0.2		33.9±1.9
25	41.2±0.2		39.7±0.4
30	41.7±0.1		40.1±0.2
35	42.3±0.2		40.6±0.2
40	44.1±0.4		41.5±0.2

Values are means ± S.E.M.

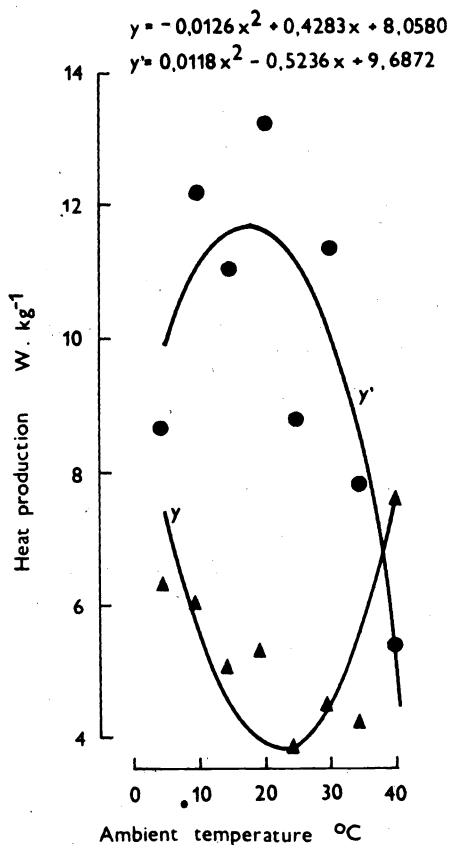


Fig. 1. Relationship between T_a and heat production in fully feathered (▲) and totally defeathered (●) laying hens

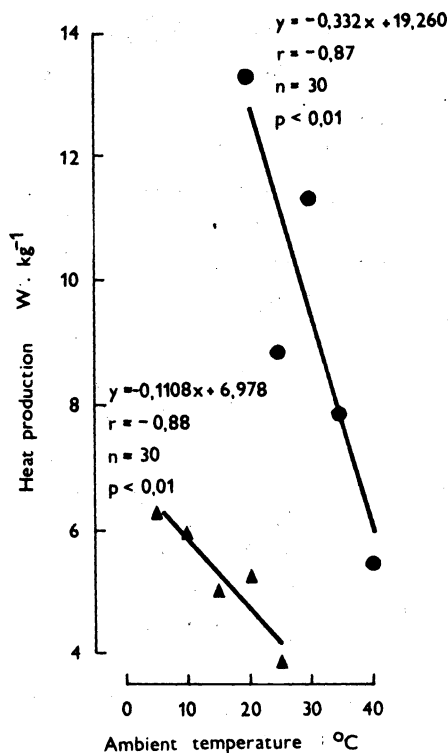


Fig. 2. Relationship between T_a and heat production in fully feathered (▲) and in defeathered hens (●) between 20 and 40 °C

The relationship between the colonic temperature and heat production

The increase in the colonic temperature in the T_a range between TNT and 5 °C is explained by the operation mode of the temperature regulating system. Each decline of T_a results in an elevation of the thermoregulatory set point (Hammel 1972). Provided the functioning of the thermoregulatory system is perfect, the increase in colonic temperature below TNT may be used as a measure of the thermoregulatory set point adjustment. The relationship between the colonic temperature and heat production at these temperatures was defined in terms of the function in Fig. 5. Elevation of the curve with 3.3 W.kg⁻¹ indicates that

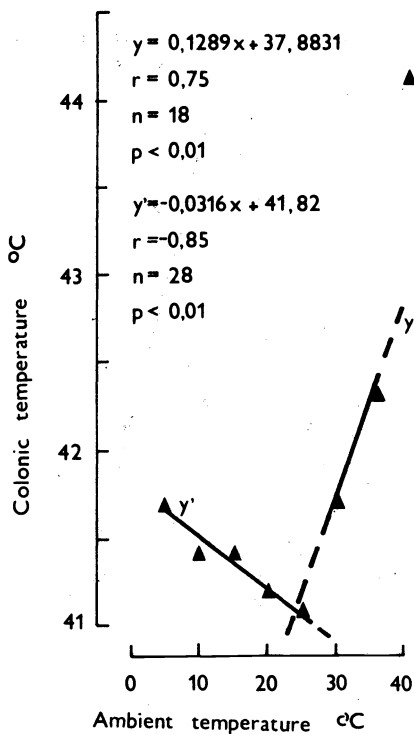


Fig. 3. Linear relationship between T_a and colonic temperature above and below the biologically optimal temperature in fully feathered hens

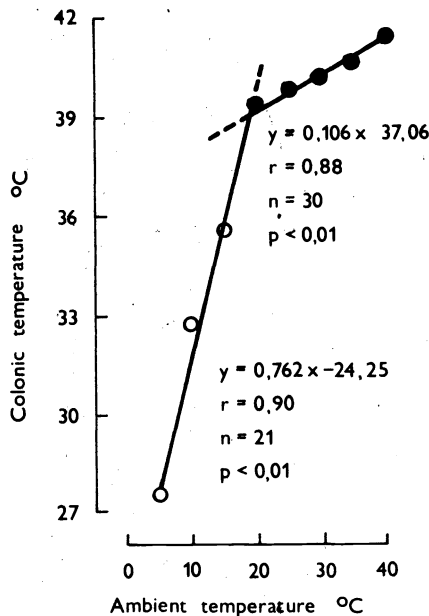


Fig. 4. Relationship between T_a and colonic temperature in at T_a between 5 and 20 °C and between T_a 20 and 40 °C in defeathered hens

the adjustment of the thermoregulatory set point by 1 K results in an augmentation of heat production by 3.3 W . kg⁻¹ (Fig. 5).

For an increase of 1 W.kg⁻¹ in heat production a set point elevation of 0.30 K was necessary. This was achieved through a decrease in T_a by 9.5 K in fully feathered hens. In defeathered birds, the slight decrease in colonic temperature in T_a range between 40 and 20 °C was accompanied by a considerable rise in heat production (Fig. 6). This increase amounted to -3.1 W.kg⁻¹.K⁻¹ and increased further to 3.7 W.kg⁻¹.K⁻¹ provided the data obtained at 25 °C were not included in calculation.

The sharp decline in colonic temperature observed at T_a below 20 °C led to a remarkable fall in heat production. The respective equation is given in Fig. 7.

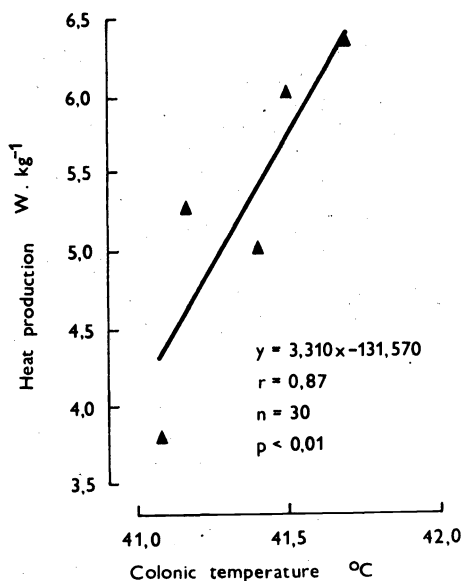


Fig. 5. Relationship between colonic temperature and heat production in defeathered hens at T_a below the summit metabolism temperature

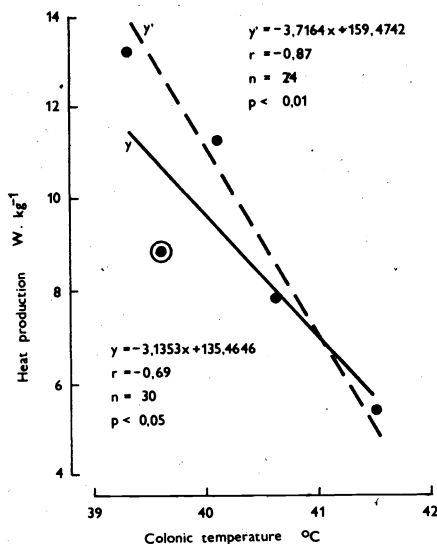


Fig. 6. Relationship between colonic temperature and heat production in defeathered hens at T_a between 20 and 40 °C (the a curve y does not cover the values obtained at 25 °C)

Evaporative heat loss

In feathered hens, the evaporative heat loss was expressed in terms of an exponential function. The evaporative heat loss began to rise continually above a T_a of 15 °C and at 40 °C it amounted to 0.8 W.kg⁻¹. The threshold temperature for rising evaporative heat loss was 11.3 °C (Fig. 8) as indicated by the course of the straight line expressing the relationship between the T_a and evaporative heat loss above and below the threshold temperatures.

In defeathered birds, the evaporative heat loss also increased above a T_a of 15 °C. The calculated temperature threshold for these birds was 8.9 °C (Fig. 9). Analysis of variance revealed no differences in evaporative heat loss between the two groups of hens.

Thermal conductance

In feathered birds, the thermal conductance was between 2.1 and 3.2 W.m⁻².K⁻¹ in the temperature range between 5 and 25 °C. It increased with each T_a rise by 0.0448 W.m⁻².K⁻¹. Above 27.6 °C this rise was augmented to 0.2418 W.m⁻².K⁻¹. The respective course of the curve is shown in Fig. 8.

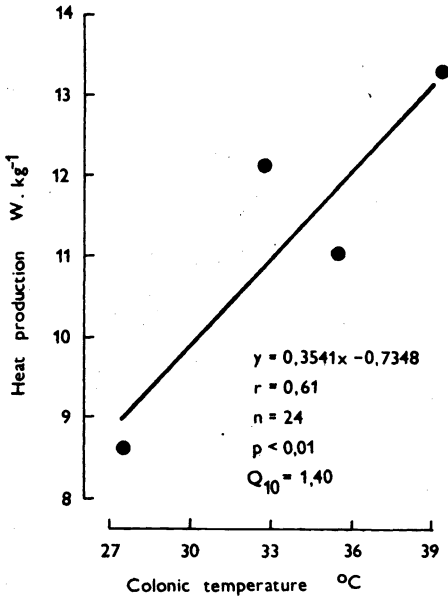


Fig. 7. Relationship between colonic temperature and heat production in defeathered hens at T_a between 5 and 20 °C

In contrast, thermal conductance in defeathered birds fell by $0.362 \text{ W.m}^{-2}.\text{K}^{-1}$ at temperatures between 5 and 25 °C and rose by $0.470 \text{ W.m}^{-2}.\text{K}^{-1}$ at temperatures between 25 and 40 °C (Fig. 9). Thermal conductance of defeathered hens surpassed considerably that of the feathered birds at each temperature studied.

Discussion

The relationship between the T_a and heat production throughout a wide range of T_a may be expressed in terms of a polynomial function of a higher order (Hensel et al. 1973; Bligh 1972) in agreement with generally accepted models based on Giaja's (1938) work. The heat production rises with falling T_a to a maximum - the summit metabolism - at an extremely low T_a . Below this temperature it begins to decline. The increase of the function changes only slightly within the temperature range between just below the TNI and above that of summit metabolism so that this fraction of the polynomial function may be expressed with high significance in terms of a linear function. Indeed, numerous published data indicate such a course of the curve (Scholander et al. 1950; Versteegen et al. 1978; Mount 1979).

The actual heat production of a homeotherm is influenced not only by the T_a but also by a variety of thermal and other climatic factors. Particularly important are air humidity, air velocity and thermal radiation as well as factors capable to change the insulation of the animal body. They change the heat output of the animals, and with potent stimulation, also that of internal thermoreceptors. The thus elicited thermoregulatory reaction

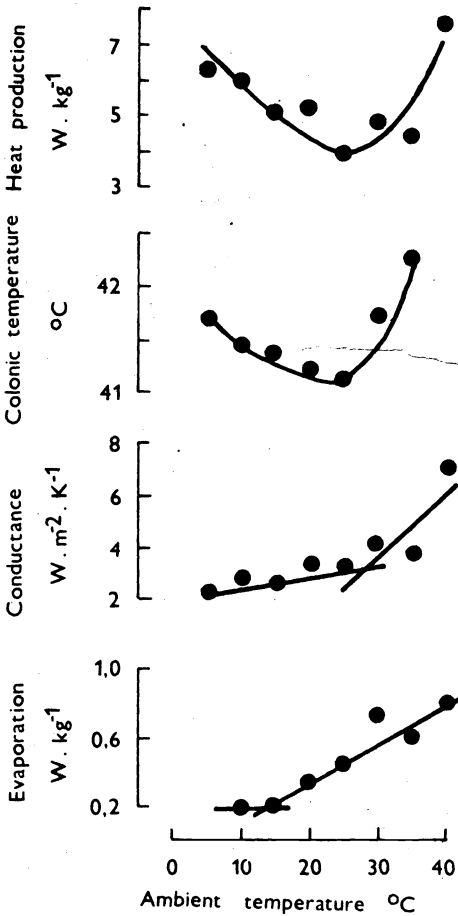


Fig. 8. Relationship between T_a and evaporative heat loss, thermal conductance, colonic temperature and heat production in fully feathered hens

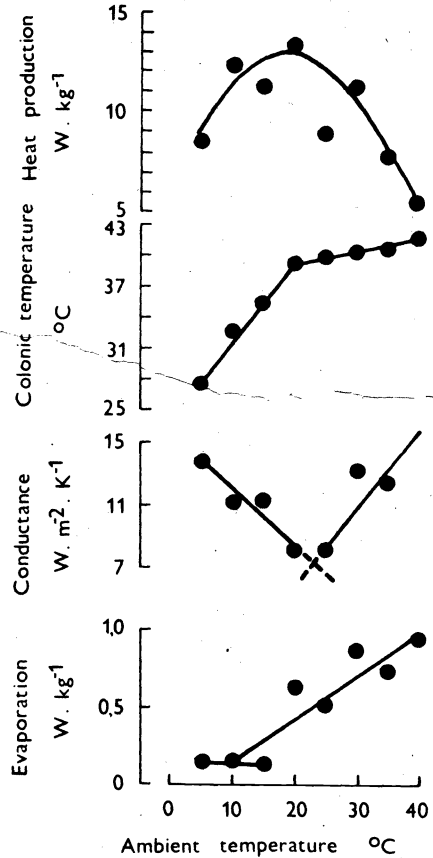


Fig. 9. Relationship between T_a and evaporative heat loss, thermal conductance, colonic temperature and heat production in defeathered hens

is a function of thermoregulatory inflow from the population of thermoreceptors in hypothalamic thermoregulatory centre. The route of receptor activation (i. e. changes in T_a or other above-mentioned factors) is here of no importance.

Environmental factors relevant to thermoregulation have been characterized by the term of effective ambient temperature (EAT) (Blight and Johnson 1973). According to these authors, all actual environmental situations that result in the same thermal sensations in an individual have the same T_a . As a measure of the EAT in homeothermic animals the thermoregulatory effects of heat production may be employed. This implies - first as a working

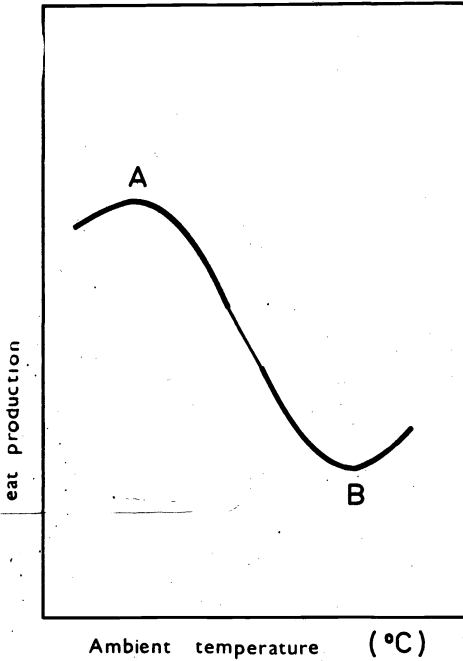


Fig. 10. A schematic presentation of the relationships between T_a and heat production over a broad temperature range

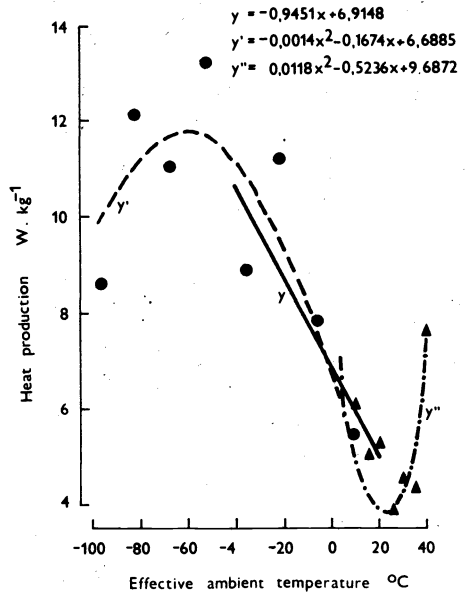


Fig. 11. Relationship between EAT and heat production. The temperature range between -96 and 9 °C is expressed in terms of the function y' , the temperature range between -36 and 20 °C in terms of the function y , and the temperature range between 5 and 40 °C in terms of the function y'' .

hypothesis - that all environmental factors leading to identical heat production have the same T_a . As a reference, a situation should be employed in which the air velocity would not exceed 0.2 m.s^{-1} and the air humidity would oscillate in a medium range (Goll et al. 1986). Using this concept in interpretation of present results, both parabolic functions expressing the relationship between T_a and heat production in both groups of hens can be viewed as portions of one curve. A schematic drawing of the relevant conditions is shown in Fig. 10.

The heat production values obtained at low air velocities and with intact feather coat of the birds are plotted in the right part of the curve (Fig. 10, part A), the same parameters for the defeathered hens are in the left part (Fig. 10, part B). The courses of the straight lines describing the relationship between T_a and heat production below T_{NT} in fully feathered birds ($0.1108 \text{ W.kg}^{-1}.\text{K}^{-1}$) and between 40 °C and T_{SM} in defeathered hens ($-0,332 \text{ W.kg}^{-1}.\text{K}^{-1}$) differ in their slopes (Fig. 2). In other words, in hens with removed feathers and exposed to high

air velocity, one K of T_a change led to such an increase in heat production that would only occur after a 3 K change in T_a for fully feathered birds at an air velocity of $0.2 \text{ m} \cdot \text{s}^{-1}$. Thus 1.0 K temperature change under the conditions of increased air velocity and almost total defeathering is equal to 3.0 K change in the effective ambient temperature. Both functions shown in Fig. 2 indicate that the heat production of defeathered birds at 40°C is equal to that of fully feathered ones at 9°C . This finding along with that of a 1:3 ratio in the effect of temperature change upon the heat production of feathered and defeathered birds provide a basis for calculation of the EAT summarized in Table 3. The course of the curve constructed on the basis of these data and showing the relationship between T_a and heat production, is shown in Fig. 11. The TSM of laying hens lay at an EAT of -50 to -60°C .

In the present experiment, the heat production of hens at TSM attained 338% of its value found at TNT. This thermoregulatory increase in heat production is somewhat lower than the values found by Alexander and Williams (1968) in newborn lambs (i. e. 430%) and in older lambs (540%). In Pekin ducks a five-fold increase in heat production was elicited by whole-body cooling through intrainestinal thermodes (Inomoto and Simon 1981).

Table 3

Actual ambient temperature T_a and effective ambient temperature (EAT) in fully feathered and defeathered laying hybrid hens

Feathered birds Air velocity $0.2 \text{ m} \cdot \text{s}$		Defeathered birds Air velocity $1.2 \text{ m} \cdot \text{s}$	
T_a ($^\circ\text{C}$)	EAT ($^\circ\text{C}$)	T_a ($^\circ\text{C}$)	EAT ($^\circ\text{C}$)
5	5	5	- 96
10	10	10	- 81
15	15	15	- 96
20	20	20	- 51
25	25	25	- 36
30	30	30	- 21
35	35	35	- 6
40	40	40	+ 9

The increase in heat production observed in our study was relatively low compared with that occurring during an intensive muscular activity. Birds with the body size range similar to that of the domestic fowl are capable to augment their heat production 10 times during flight or running on a treadmill. The O_2 consumption of resting domestic fowl (2.48 kg body mass) at TNT amounted

to 9.5 ml.kg⁻¹.min⁻¹, whereas during a run of 9 km.h⁻¹ it increased to 112.5 to 115.0 ml.kg⁻¹.min⁻¹ (Brackenbury and Avery 1980). No explanation for the differences in the maximum possible increase in heat production during a thermoregulatory reaction at low T_a and during a maximum muscular activity (running, flying) can be offered.

In the present study, a continuous fall in colonic temperature was observed in defeathered hens at T_a declining from 40 to 20 °C. This fall was accompanied by a considerable increase in heat production of 3.1 to 3.7 W.kg⁻¹ per K of T_a change. This change in heat production can be employed as a measure of thermosensitivity of the thermoregulatory system assuming that the temperature change is equal in all receptor fields. Whole body thermosensitivity of 5 to 6 W.kg⁻¹ at low and medium T_a was determined in Pekin ducks with core temperature decreased by an intestinal thermode, and body thermosensitivity of 3.2 W.kg⁻¹ at high T_a (Inomoto and Simon 1981).

The relatively low thermosensitivity of our experimental birds as compared to other species may lay in different experimental methods employed as well as in species differences in receptor thermosensitivities.

Our observations on elevated heat production in feathered birds between T_{NT} and 5 °C accompanied by a simultaneous increase in colonic temperature suggest a rather low thermosensitivity of the temperature regulation system in domestic fowl. This phenomenon may be connected with a thermoregulatory set point adjustment at decreasing T_a (Nichelmann and Lyhs 1976; Nichelmann 1983; 1984).^a The function depicted in Fig. 5 shows that a change in thermoregulatory set point by 1 K results in an increase in heat production of 3.3 W.kg⁻¹. This value is in good agreement with the whole body thermosensitivity of 3.1 to 3.7 W.kg⁻¹ determined in our experimental birds.

Below the EAT of -50 to -60 °C the colonic temperature of defeathered hens began to drop sharply. At the same time their heat production decreased, leading in turn to further colonic temperature decline. For the effect of temperature a Q_{10} of 1.4 was calculated (Calder and King 1974). Assuming that in a living organism a Q_{10} of 2.0 expresses the effect of a temperature change on biochemical reaction rates, a Q_{10} value of 1.4 means that in domestic fowl with a colonic temperature lower than 39.5 °C the heat production is indeed decreased through local effect of temperature on metabolically active cells but that efferent effects from the thermoregulatory centre are still in operation to prevent this decrease.

The control elements of the thermoregulatory system activated in a typical sequence in fully feathered hens (Nichelmann and Lyhs 1976; Nichelmann 1983, 1984; Nichelmann et al. 1985) showed a different pattern in defeathered birds (Fig. 9). Of interest is the relationship between the maximum heat productions of fully feathered birds at 20 °C (3.9 W.kg⁻¹) and the defeathered ones at 40 °C (5.4 W.kg⁻¹): both temperatures are thermoneutral for the respective groups of birds. The heat production of defeathered birds was still substantially higher due to their high radiation heat loss.

Both the evaporative heat loss and thermal conductance began to increase at an ambient temperature at which the organism of the bird was exposed to a considerable thermal load. The heat loss was thus enhanced at a temperature at which hypothermia occurs. The reasons for this seemingly paradoxical reaction are not understood and require further study.

Termoregulační produkce tepla u hybridních nosnic

U nosnic hybridů ve věku 35 až 40 týdnů byly sledovány termoregulační reakce při mírné (5 - 40 °C teplota prostředí a 0,2 m.s⁻¹ rychlost proudění vzduchu) a při extrémní (5 - 40 °C teplota prostředí a 1,2 m.s⁻¹ rychlost proudění vzduchu) teplotní zátěži. Z naměřených hodnot energetického metabolismu, teploty v kolonu, evaporačních ztrát tepla byla vypočtena efektivní teplota prostředí. Energetický metabolismus nosnic počal klesat při efektivní teplotě prostředí -50 až -60 °C a zároveň nastoupila progresivní hypotermie. Energetický metabolismus za těchto podmínek převyšoval o 338 % jeho hodnoty naměřené v termoneutralním prostředí. Termosensitivita termoregulačního systému se pohybovala mezi 3,1 a 3,7 k.kg⁻¹.K⁻¹. Tato termosensitivita dostatečně vysvětluje vzestup teploty těla nosnic v rozmezí termoneutralní teploty prostředí a 5 °C.

Termoregulační produkce tepla u hybridních nesušek

У несušек гибридов в возрасте 35 - 40 недель проводили наблюдения за терморегуляторными реакциями при умеренной (5 - 40 °C температура окружающей среды и 0,2 м.ц⁻¹ скорость воздушного течения) и при крайней (5 - 40 °C температура окружающей среды и 1,2 м.ц⁻¹ скорость течения воздуха) температурной нагрузке. На основе полученных величин метаболизма энергии, температуры в ободочной кишке и температурных потерь выпариванием, была вычислена эффективная температура окружающей среды. Метаболизм энергии несušек стал понижаться при эффективной температуре окружающей среды -50 - -60 °C и одновременно проявилась прогрессивная гипотермия. Энергетический метаболизм в данных условиях превышал на 338% величины, полученные в термoneutralной среде. Термочувствительность терморегуляторной системы достигала пределов 3,1 и 3,7 Вт.кг⁻¹.К⁻¹. Приведенная термочувствительность в достаточной степени объясняет увеличение температуры тела несušек в пределах термoneutralных температурных величин окружающей среды и 5 °C.

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