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Development of temperature regulation in the grey partridge *Perdix perdix*

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The development of temperature regulation in grey partridge *Perdix perdix*, *Galliformes* chicks at the age of 0-40 days was studied using three different approaches: 1) heat production was measured by indirect calorimetry of chicks subjected to various ambient temperatures; 2) the ability to resist cooling was studied by subjecting chicks to an ambient temperature of 0°C with either dry or wetted plumage; 3) behavioural responses were studied in a thermal gradient using a video camera and an image processing system. The development of homeothermy was not linear. Absolute metabolic rates increased with age at all temperatures, while the maximal mass-specific heat production ($W \cdot kg^{-0.75}$) doubled between days 1-2 and day 5, but remained unchanged after that. Assuming that the allometric exponent accounts for mass-induced changes in the metabolic rate, this suggests that the increase in maximal heat production before the age of five days can be attributed to both maturation and growth, while the increase after five days can be explained by growth only. At the age of 1-2 days, the chicks' capacity to increase heat production in cold was negligible. In five and 10-11-day-old chicks the capacity was markedly higher, but the maximal heat production occurred already at 25°C. A quantum leap occurred between 10-11 and 15-16 days, when the point of maximal heat production shifted from 25°C to 5°C, which indicates a significant improvement of insulation. Wetted chicks cooled faster than dry chicks until 21 days of age. The relative effect of wetting was maximal at 10-11 days. Behavioural observations suggest a drop in the time spent in the warmest section of the thermal gradient after five days and that the coldest part of the gradient (5°C) was hardly visited before 25 days of age. The sequence for attaining homeothermia in the partridge is thus comprised of an early development of significant thermogenesis from day 5 onwards, followed by a rapid increase in insulation around two weeks of age. Despite this fact, especially wet chicks strongly depend on parental heat in cold spells during the first three weeks of their life. The increase in body mass and the development of a water-impermeable plumage enhance the cold resistance in older chicks.

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The geographic range of the grey partridge *Perdix perdix*, *Phasianidae*, *Galliformes* covers Europe and Asia (Potts 1986). In Finland, partridges extend sparsely from southern Finland to the latitude of 65°N. A rough estimate of the total number of partridges is approximately 3,000 - 5,000 pairs. The population size is strongly dependent on weather conditions. Low temperature and lack of food are the ultimate reasons for the temporarily occurring declines in populations. However, in times of suf-

ficient food partridges can well tolerate even the coldest weather conditions in Finland. In adult partridges, the metabolic rate exceeds the basal metabolic rate only by a factor of three at -30°C (Hohtola et al. 1989).

The ability of partridge chicks to respond to cold and the development of temperature regulation has not been studied. It is well known that newly hatched gallinaceous chicks respond to cold mostly by behavioural means. Autonomic mechanisms like insulation and shivering devel-

op later but are more advanced than in altricial nestlings (Ricklefs 1989, Choi & Bakken 1991). On the other hand, their growth rate is slower than in altricial species.

Typically, the level of body temperature (T_b) of galliform chicks is much lower than in adult birds, as shown e.g. in hatchlings of chicken *Gallus domesticus* (Randall 1943, Myhre 1978), Japanese quail *Coturnix coturnix japonica* (Spiers et al. 1974), capercaillie *Tetrao urogallus* (Hissa et al. 1983), turkey *Meleagris gallopavo* (Modrey & Nichelmann 1992), willow ptarmigan *Lagopus lagopus* (Aulie 1976a, Pedersen & Steen 1979), black grouse *Lyrurus tetrix* (Myhre & Steen 1979), White Beltville turkey *Meleagris gallopavo* (Jurkschat et al. 1989), and ring-necked pheasant *Phasianus colchicus* (Gdowska et al. 1993). This does not necessarily follow from a poorly developed thermoregulatory control. Even at thermoneutrality, the preferred T_b in chicks is typically located at a lower level and/or also covers a wider temperature range than in adult birds.

The development of physiological cold defense in birds has two components: 1) an increase in body mass, which reduces the surface/volume ratio, and an increase in the amount of plumage per unit area of skin surface. Both of these factors contribute to a reduction in mass-specific thermal conductance (Dunn 1975); 2) improved thermogenic capacity, i.e. increases in basal metabolic rate, voluntary muscular activity and shivering. Hatchlings do not have the capacity for mammalian-type non-shivering thermogenesis (NST), apparently because they lack brown adipose tissue (Saarela et al. 1989, 1991, Olson et al. 1988). NST has been suggested to occur, however, in leg muscles of ducklings and king penguin *Aptenodytes patagonicus* chicks (e.g. Barré et al. 1985, Duchamp et al. 1992). In contrast, the behavioural component of cold defense is well developed in all precocial birds soon after hatching.

In this work, we describe the development of endothermy in growing partridge chicks and their ability to resist cooling by subjecting them to experimentally decreased ambient temperatures with dry or wetted plumage. Since behavioural temperature regulation of newly hatched chicks is the primary way to keep body temperature constant, we have also studied their behavioural responses. A preliminary report has been presented elsewhere (Marjoniemi et al. 1994).

Material and methods

The study was carried out in the summer of 1992 on 100 partridge chicks in the Zoological Garden of the Department of Zoology, University of Oulu (65°N, 25°E). Eggs were obtained from captive parents housed in an aviary. They were artificially incubated with an air temperature set at 37.8°C and a relative humidity (RH) of 55-60%.

Two days before the estimated hatching-time RH was raised to 80%. On the post-hatching day (day 1) chicks were transferred to open wooden boxes of 1 m², app. 30 chicks in each. The boxes were equipped with a 250 W infra-red lamp hanging 70 cm above the floor. At the age of 3-4 weeks the chicks were transferred to an outdoor aviary (20 m²) fitted with an extra infra-red lamp.

The chicks were offered a mixture of hard-boiled egg, ant pupae, fresh vegetable matter, pellets (Raisio, Finland), water with vitamin (Monivimin, Agri) and mineral supplement ad libitum. Ascorbic acid (0.25%) was supplied at regular intervals. Hard-boiled egg and ant pupae were removed from the diet after two and three weeks, respectively. The rate of change in body mass was constantly followed by weighing a selected group of chicks.

Heat production

Oxygen consumption was measured in chicks of the following ages: 1-2, 5, 10-11, 15-16, 20-21, 30 and 39-40 days. Each chick was used only once in each experiment. The chicks had free access to food and water until 30-120 minutes before the beginning of an experiment. Before measurements, the chicks were weighed to the nearest 0.1 g and a 32-gauge thermocouple was inserted through the cloaca into the rectum for continuous measurement of body temperature (T_b). Immediately thereafter the chicks were placed in the metabolic chamber with the air temperature maintained at the desired value. After an equilibrium period of 30 minutes, oxygen consumption was recorded for 10 minutes, and the chick was returned to its home cage. The oxygen concentration of outflowing air was measured using an S-3A Oxygen Analyzer (Applied Electrochemistry). Oxygen consumption was calculated using routine steady-state equations for open-flow systems.

Two different sizes of chambers were used depending on the age and size of chicks. Maximally the size was 33×23×20 cm (15.2 litres). The selected ambient temperatures (T_a), measured inside the chamber, were 35°, 30°, 25°, 20°, 15°, 10°, 5°, 0°, -5° and -10°C. The airflow through the darkened chamber was 0.5-2.0 litres/minute depending on the size of chick. The flow into the chamber was measured and regulated with a mass flowmeter/controller (HI-TEC F 201C-FA, Bronkhorst). The metabolic rate (in Watts, W) was computed on the assumption that 1 litre of oxygen consumed per hour is equivalent to 5.579 W (Schmidt-Nielsen 1984).

Minimal thermal conductances were calculated from metabolic measurements using the equation $C = M/(T_b - T_a)$, where C = conductance ($W \times kg^{0.75} \times ^\circ C^{-1}$) and M = metabolic rate expressed in appropriate units.

Datapoints were taken, if possible, from the rising part of the heat production curves, where insulation suppos-

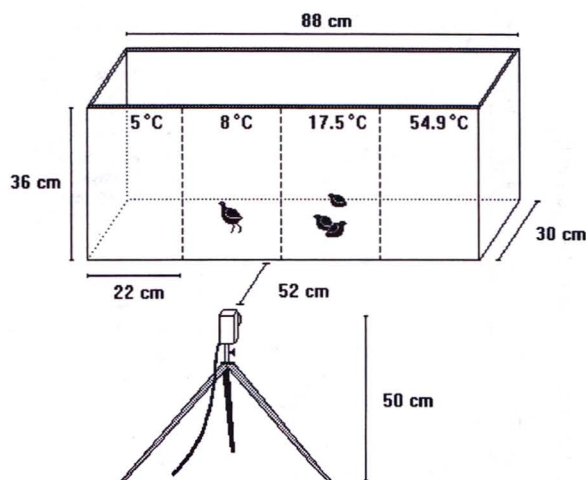


Figure 1. Experimental set up for recording behavioural temperature regulation of partridge chicks in a thermal gradient.

edly is already maximal. The mean change in T_b during the measurements was $0.334 \pm 0.112^\circ\text{C}$ (mean \pm SE). The mean values of T_b for the 10-minute periods were used for calculations.

The ability to resist cooling

The tip of a 32-gauge thermocouple was inserted through the cloaca into the rectum and fixed with adhesive tape. Thereafter chicks were transferred to a chamber with an ambient temperature maintained at 0°C . Body temperature was continuously recorded either for 20 minutes or until it had dropped to 25°C in chicks aged 2, 7 and 11 days or to 30°C in chicks aged 15, 21 and 29 days. After this the birds were allowed to recover for 30 minutes

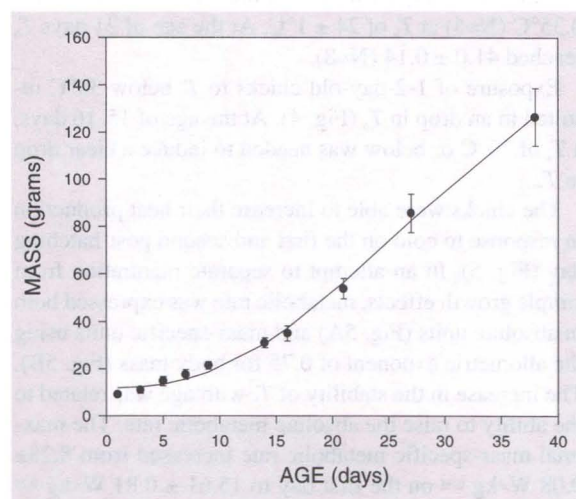


Figure 2. Growth rate of partridge chicks, $N=10$ individuals in each cohort. Vertical bars indicate standard deviation (\pm SD) and the line indicates a logistic equation fitted to the data.

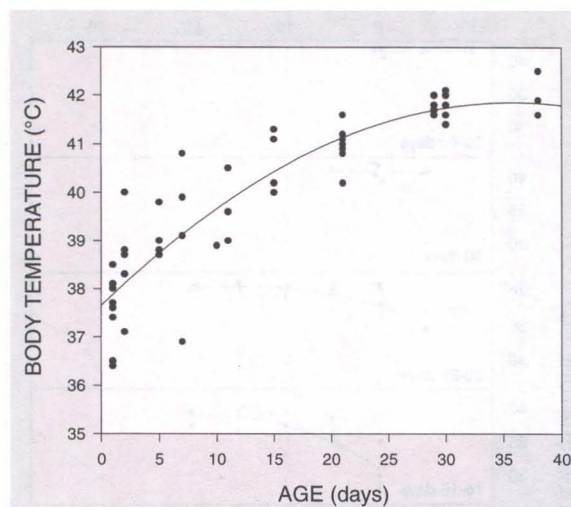


Figure 3. Relationship between body temperature (T_b) and age. The curve is calculated according to the following equation: $T_b = 37.653 + 0.235x - 0.0033x^2$, where x = age in days. Results of the temperature measurements from the metabolic rate experiments and cooling tests were compiled for the graph. Only measurements performed in putatively thermoneutral conditions ($>25^\circ\text{C}$) were included.

under the infra-red lamp. Thereafter they were wetted by spraying the plumage with water until their body mass increased by 5% and the experiment was repeated as above.

Behavioural responses

Fig. 1 describes the experimental procedure for recording behavioural temperature regulation. A box measuring $36 \times 30 \times 88$ cm was divided into 4 sections, each approximately 22 cm wide and the box was set up at 0°C . The temperature gradient was produced by using two infra-red lamps (250 W each). The stabilised temperatures of brown bottles filled with water arranged in each of the four sections were used for recording reference temperatures. The behaviour of the chicks was followed continuously with the help of a video camera (Philips) connected to a computer (386 SX) with an image processing program created by Eero Hatunen and Sami Sallinen (University of Oulu). The activity count in each section was used as an estimate of the presence of the birds in that section. Four chicks at a time were placed in the gradient. The age groups tested were 3, 6, 9, 14, 20 and 25 days old. The chicks did not have access to food or water during the 3-hour test period.

Statistics

Results are expressed as mean \pm SE. The statistical analyses were performed using χ^2 -tests (behavioural data), t -tests and one-way analyses of variance. Regression anal-

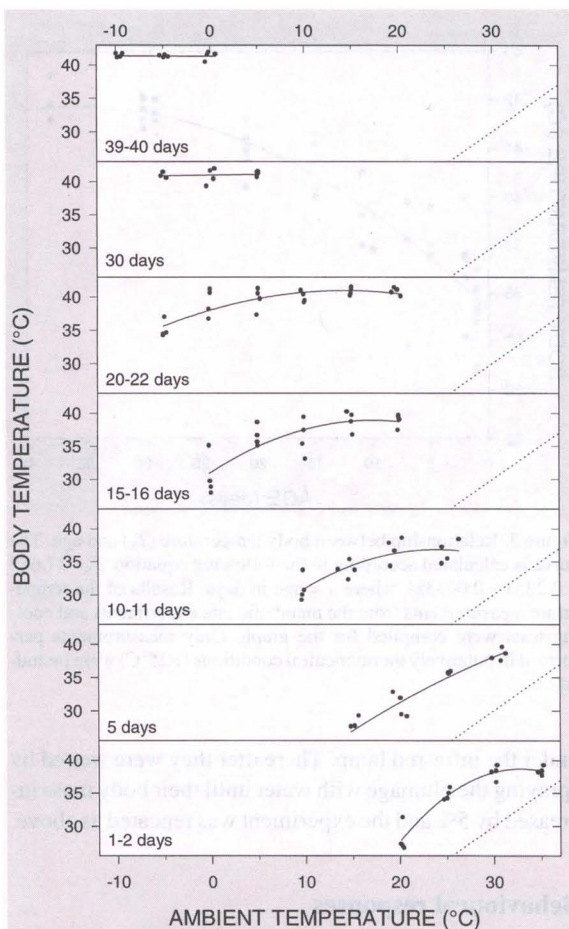


Figure 4. Body temperature of partridge chicks exposed to ambient temperatures of -10° , -5° , 0° , 5° , 10° , 15° , 20° , 25° , 30° and 35°C for 30-minute periods. The results were obtained from the experiments done to measure metabolic rate (see Fig. 5). The dotted, oblique lines indicate the 1:1 relation of body temperature and ambient temperature.

yses were performed using the least squares method. Slopes of regression equations were compared with t -tests. The p -values in the text refer to t -tests unless otherwise mentioned.

Results

Growth rate

The average body mass (BW) in newly hatched chicks was 9.2 ± 0.27 g ($N=10$) and 126.4 ± 3.85 g ($N=10$) at the age of 38 days. BW increased statistically significantly ($P<0.001$) already within the first three days (Fig. 2).

Development of homeothermy

The steady state T_b increased with age (Fig. 3). There was a significant increase in T_b ($P<0.001$) between the ages of

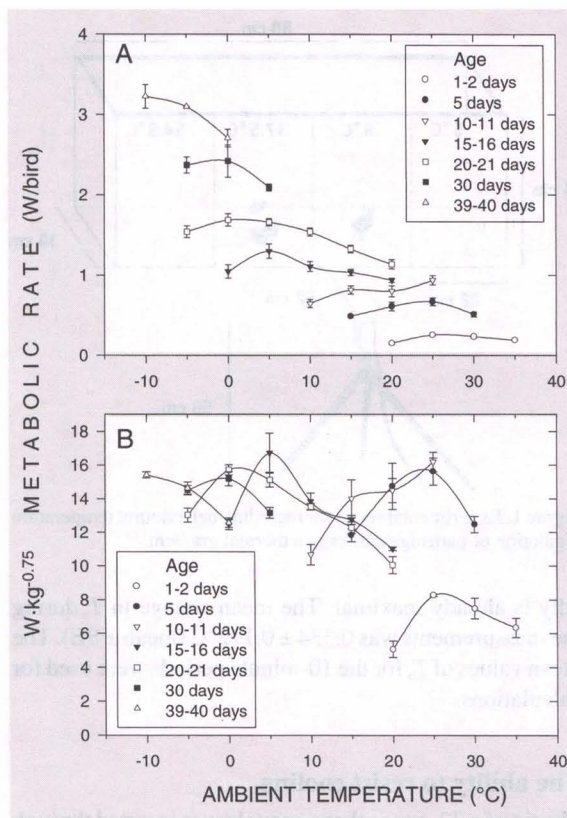


Figure 5. Age dependent changes in the relation of metabolic rate to ambient temperature in partridge chicks. Panel A shows the absolute metabolic rate (in Watts per bird) and panel B the mass-specific metabolic rate (calculated for the allometrically defined metabolic body mass as $\text{W} \times \text{kg}^{-0.75}$). Each point is based on measurements of 4 chicks, but different chicks were used for tests at each temperature. Vertical bars represent SE.

1-2 and 10-11 days from $37.9 \pm 0.24^{\circ}\text{C}$ ($N=15$) to $39.7 \pm 0.35^{\circ}\text{C}$ ($N=5$) at T_a of $24 \pm 1^{\circ}\text{C}$. At the age of 21 days T_b reached 41.0 ± 0.14 ($N=8$).

Exposure of 1-2-day-old chicks to T_a below 30°C resulted in an drop in T_b (Fig. 4). At the age of 15-16 days, a T_a of 10°C or below was needed to induce a clear drop in T_b .

The chicks were able to increase their heat production in response to cold on the first and second post-hatching day (Fig. 5). In an attempt to separate maturation from simple growth effects, metabolic rate was expressed both in absolute units (Fig. 5A) and mass-specific units using the allometric exponent of 0.75 for body mass (Fig. 5B). The increase in the stability of T_b with age was related to the ability to raise the absolute metabolic rate. The maximal mass-specific metabolic rate increased from $8.28 \pm 0.08 \text{ W} \times \text{kg}^{-0.75}$ on the first day to $15.61 \pm 0.81 \text{ W} \times \text{kg}^{-0.75}$ ($P<0.01$) on the 5th day and to $16.19 \pm 0.58 \text{ W} \times \text{kg}^{-0.75}$ ($P<0.01$) on the 10-11th day following hatching. However, the maximal mass-specific metabolic rate ($\text{W} \times \text{kg}^{-0.75}$)

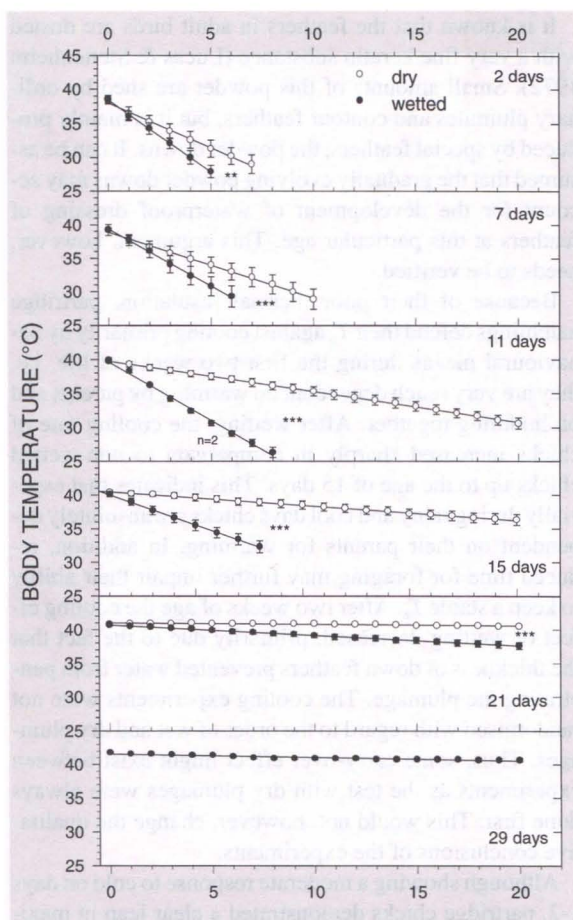


Figure 6. Body temperature of chicks of 2, 7, 11, 15, 21 and 29 days of age during a 20-minute exposure to 0°C with dry or wetted plumage. The asterisks indicate the statistical significances of the differences in slopes of regression lines (*t*-test) between dry and wetted chicks: *** = $p < 0.001$, ** = $p < 0.01$. Each point is based on measurement of four chicks (only two for wetted birds at 11 days). Dry chicks were not tested in the age group of 29-day-old chicks.

did not change significantly after the 5th day (one-way ANOVA, $p > 0.05$).

Subjecting wetted chicks to 0°C produced a significantly faster cooling rate than in dry chicks (Fig. 6). On the second day of life, the slope of regression as a function of T_a in wetted chicks differed significantly from that in dry chicks ($P < 0.01$).

In older chicks the slopes of regression lines of dry and wetted chicks differ highly significantly ($P < 0.001$). The relative effect of wetting was maximal at 10–11 days. In addition, the slopes of cooling rates of 2–7-day-old dry chicks do not differ from each other. After 11 days of age the drop of T_b is significantly slower than in young chicks. Only after 15 days of age did the T_b of wetted birds decrease more slowly than in younger chicks with dry plumage.

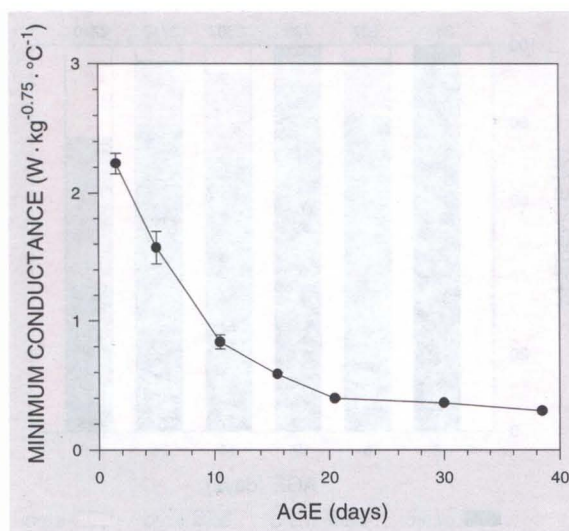


Figure 7. Minimal thermal conductances of partridge chicks as a function of age.

The development of minimum thermal conductance in partridge chicks, calculated in the allometrically defined mass-independent units, showed that the largest decrease occurs between age groups of 5–6 and 10–11-days-old chicks (Fig. 7). The improvement is moderate between days 10 and 20, and after 20 days conductance does not change appreciably.

The time spent in the colder parts of the thermal gradients increased significantly with age ($\chi^2 = 489.69$, $df = 23$, $P < 0.001$, Fig. 8). A marked shift toward cooler areas was seen already in 5-day-old chicks, but the coldest parts were not visited regularly before two weeks of age. The total activity of chicks also increased with age.

Discussion

The onset of homeothermy in *Galliformes* reflects body size; the chicks of larger species demonstrate a greater capacity for cold defence than smaller species immediately after hatching (Matthew 1983). However, the later development of autonomic thermoregulatory effectors is slower in larger species. The pattern of development of temperature regulation in the partridge hatchlings as presented in this work well exemplifies the pattern for smaller *Galliformes*.

As shown in the present work, T_b of partridge chicks is on the average 4–5°C lower after hatching than in adult partridges at thermoneutrality. Both ambient temperature and age had a significant effect on T_b . Chicks aged 1–2 days were not able to keep a stable T_b even at 25°C although they had a moderate capacity to elevate their heat production. Only after the age of 20–21 days were they able to maintain a stable T_b over the range of 10–25°C.

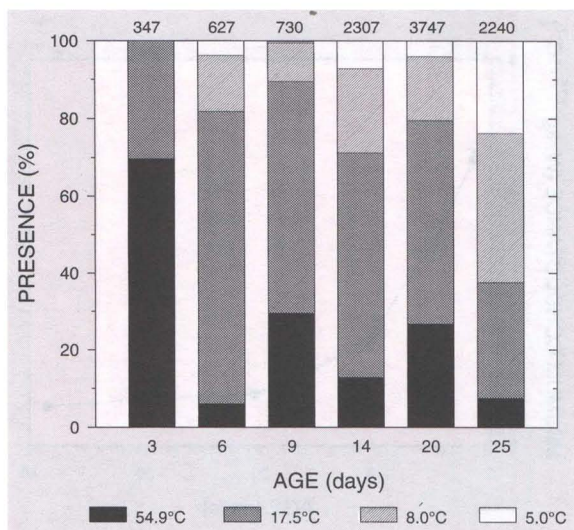


Figure 8. Relative occurrence of movements of partridge chicks in the four different parts of a thermal gradient (compare Fig. 1) given as a function of age in days. The numbers at the top of the graph give total movement activity during the experiments.

Partridge chicks aged 1-2 days showed a significantly lower T_b than 10-11-day-old chicks. On the following days T_b increased, being $41.7 \pm 0.07^\circ\text{C}$ ($N=11$) at the age of 29-30 days, which still differs significantly ($P<0.001$) from the adult temperature ($42.1 \pm 0.07^\circ\text{C}$, Hohtola et al. 1989).

Low T_b has also been measured in hatchlings of other galliform species (see e.g. Randall 1943, Spiers et al. 1974, Aulie 1976b, Myhre et al. 1975, Hissa et al. 1983, Jurkschat et al. 1989, Modrey & Nichelmann 1992, Gdowska et al. 1993). Partridge chicks achieved the adult T_b at the age of 39-40 days. However, their BW (126.4 ± 3.85 g, $N=10$) at this age is about one-third of the adult BW. It takes at least two months to reach the adult BW (ranging from 256 to 368 g, Hohtola et al. 1991). Turkey chicks reach adult T_b at the age of 40 days (Nichelmann et al. 1976, Modrey & Nichelmann 1992).

The difference in the cooling rate between dry and wetted birds was maximal at the age of 10-11 and 15-16 days. This parallels the marked shift that occurs in the temperature that elicited maximal thermogenesis, and indicates that a significant improvement of insulation occurs at this age. Estimations of mass-independent thermal conductance from metabolic and temperature measurements (Fig. 7) confirm that the rate of decrease in thermal conductance is high at this age. The effect of wetting decreases rapidly in older age groups, despite the fact that conductance values show only a very small decrease at this time. This suggests that the plumage reaches its maximum water resistance later than its thermal insulation.

It is known that the feathers in adult birds are dusted with a very fine keratin substance (Lucas & Stettenheim 1972). Small amounts of this powder are shed by ordinary plumules and contour feathers, but it is mainly produced by special feathers, the powder downs. It can be assumed that the gradually evolving powder downs may account for the development of waterproof dressing of feathers at this particular age. This argument, however, needs to be verified.

Because of their poor thermal insulation, partridge hatchlings defend their T_b against cooling primarily by behavioural means during the first two weeks of life, i.e. they are very much dependent on warming by parents and on huddling together. After wetting, the cooling rate of chicks increased sharply in comparison to non-wetted chicks up to the age of 15 days. This indicates that especially during rainy and cool days chicks are absolutely dependent on their parents for warming. In addition, reduced time for foraging may further impair their ability to keep a stable T_b . After two weeks of age the cooling effect of wetting decreased, primarily due to the fact that the thickness of down feathers prevented water from penetrating the plumage. The cooling experiments were not randomised with regard to the order of wet and dry plumages. Thus, some carry-over effect might exist between experiments as the test with dry plumages were always done first. This would not, however, change the qualitative conclusions of the experiments.

Although showing a moderate response to cold on days 1-2, partridge chicks demonstrated a clear leap in maximal mass-specific heat production at the age of five days, a finding which is consistent with the cooling measurements. As shown, the heat generation capacity doubled at this age. In the Japanese quail and bobwhite quail *Colinus virginianus* the elevation of the muscle mass-specific metabolic rate occurred at eight days and 8-15 days, respectively (Choi et al. 1993). Interestingly, maximal metabolic rate, when expressed per unit of standardised body mass using the »allometric« exponent ($\text{kg}^{-0.75}$), did not change after five days. This indicates that the metabolic machinery matures rapidly, and that the subsequent increase in maximal metabolic rate is due to growth only. Of course, this conclusion is strictly dependent on the assumption that expressing metabolic rate in these allometric units accounts for the mass-specific increase of metabolism. Peak metabolic rate does not scale with body mass with the classical 0.75 exponent in precocial chicks (Visser & Ricklefs 1993), which might be argued to invalidate this conclusion. However, the exponent of any interspecific allometric equation for developing birds necessarily has two components: growth and maturation, and would thus not be expected to comply with the normal allometric relation seen in adult birds. We suggest that by accounting for the increase in mass by expressing

the variables in appropriate allometric units, maturation processes can be separated from simple growth.

Interestingly, palpation showed that the hatchlings were able to shiver at the age of five days. This is at variance with earlier studies (Hohtola et al. 1989), which were unable to detect significant electromyographic signs of shivering in the breast or leg muscles of cold-exposed adult partridges. The present results show that neuromuscular pathways for incipient shivering appear early in the partridge. However, electromyographic measurements were not performed in this work and the thermoregulatory importance of shivering in the partridge remains to be studied.

In galliform birds, the development of thermogenesis appears to depend primarily on the heat production of leg muscles, i.e. in concordance with the development of oxidative and glycolytic capacity of muscle fibres over the course of development. Barré et al. (1985) suggested that leg muscles of precocious species might serve as an organ for NST. Leg muscles are the most important tissues in heat generation in avian hatchlings and embryos (e.g. Aulie & Moen 1975, Whittow & Tazawa 1991). They usually comprise a greater proportion of body mass than pectoral muscles in precocial birds at hatching (e.g. Aulie 1976c, Ricklefs 1979). Later, the mass of the pectoral muscles certainly exceeds that of the leg muscles together with their increased capacity for heat production. The pectoral muscles of capercaillie hatchlings accounted for only 2.4% of total body mass but at the age of 80-105 days 21.1% of the total body mass (Saarela et al. 1990). The proportions of leg or pectoral muscles of the partridge were not measured in this work.

Oxidative muscle fibres (SO=slow twitch, oxidative, FOG=fast twitch, oxidative, glycolytic) are primarily responsible for thermoregulatory heat production in muscles of birds (George & Berger 1966, Aulie 1976a, Hohtola & Stevens 1986, Aulie & Tøien 1988), but the proportions of fibre types and their subsequent oxidative development in the partridge hatchlings is not known. Since the capacity for maximal mass-specific heat generation after the age of five days did not increase it is reasonable to assume that the regulatory and biochemical machinery were already well developed at this age. However, as emphasised by Choi et al. (1993) the sudden increase in mass-specific heat generation is not solely determined by the increased oxidative capacity of cells. Maturation of neural control of muscles fibres is also involved.

In conclusion, the sequence by which partridge chicks attain endothermic homeothermy is: 1) an early maturation of mass-specific maximal thermogenesis from day five onwards. At this phase, the chicks are still unable to resist cooling even at moderately cool temperatures; 2) a major increase in insulation on days 5-20 and onwards. At this phase, the chicks can defend their T_b in moderate-

ly cold conditions (10°C or below), but wetted chicks cool rapidly and are dependent on parental warming; 3) development of a water-impermeable plumage, which further increases insulation. These changes together with increased body mass and the concomitant decrease in relative surface area enable adult-like cold resistance at the age of 30 days.

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