Adaptation of homeostatic thermoregulation: comparison of incubating and non-incubating Bantam hens

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Summary. Incubating and non-incubating Bantam hens were exposed to identical thoracic skin cooling to study the difference between their physiological responses with regard to thermoregulatory adaptation to incubation. Under resting conditions thoracic skin temperature (Tths) and metabolic heat production (M) were significantly higher in broody than in non-broody hens, indicating a permanently increased conductance of the brood patch. Thoracic skin cooling from 35 to 25 °C decreased Tths less in broody than in non-broody hens. In broody hens, these coolings induced a large, immediate increase in M, no constriction of brood patch vasculature, and a decrease in colonic temperature (Tc). This decrease in Tc triggered no further increase in M, but induced vasoconstriction in the feet. The coolings induced a smaller increase in M in the non-broody hens, accompanied by pronounced vasoconstriction, and did not affect Tc and foot temperature, Tf. The effects of more severe thoracic skin cooling (between 25 and 15 °C) differed much less between non-broody and broody hens. Vasoconstriction of the brood patch also occurred in the latter. It is concluded that in adaptation to incubation the thoracic skin becomes more sensitive, and its input signal becomes stronger for the control of certain effectors of thermoregulation, allowing a controlled heat transfer to the eggs.

Key words: Incubation - Thermoregulation - Brood patch - Vasoconstriction - Vasodilation

Introduction

Under the control of gonadal and adenohypophyseal hormones (Cheng and Silver 1975; Lea et al. 1981) most incubating birds form brood patches seasonally by losing feathers from species-specific areas of the thorax, abdomen, and thighs. Brood patch skin appears loose and wrinkled, the stratum corneum thickens, and surface blood vessels proliferate. Contact between the egg and the brood patch mediates heat transfer to the embryo, and studies of many different bird species have shown that this heat transfer is controlled to keep egg temperature within rather narrow tolerance limits, usually very close to the optimal development temperature [see review by Haftorn (1988)]. Special circulatory mechanisms for local heat dissipation, and especially for rewarming cold eggs by cold-vasodilation of arterio-venous anastomoses in the brood patch skin, have been suggested (Midtgaard et al. 1985).

The metabolic demands of incubation on the parental bird have long been a controversial topic (e.g., Mertens 1980; Vieck 1981; Walsberg 1983), but several studies have clearly demonstrated the dependency of the incubating bird's metabolic rate on clutch size and egg temperature (Haftorn and Reinertsen 1985; Tøien et al. 1986; Tøien 1989). Several authors even consider the clutch energetically as an extension of the body of the incubating bird (Drent 1975; Haftorn and Reinertsen 1982). However, the exact role of egg temperature in the incubating bird's thermoregulatory system is unclear, especially during cold stress, with its conflicting demands between warming the eggs and stabilizing the deep body temperature.

This study investigates the thermoregulatory adaptation to incubation by thoracic skin cooling in Bantam hens, Gallus domesticus. The differences between the physiological responses of broody and non-broody hens exposed to identical experimental conditions are discussed with regard to their implications for homeostatic regulation in incubating birds.

Materials and methods

Experimental animals. As descendents of tropical birds, Bantam hens are relatively photorefractoric. Thus, at any time of the year their reproductive cycle can be triggered or suppressed by appro-
priorite light regimes. Previous work on metabolic acclimatization in birds shows seasonal adaptation occurring after exposure of the animals to changing light regimes together with changing ambient temperatures (Reinertsen 1984). To compare adaptations to broodiness and non-broodiness 26 Bantam hens were used after careful adaptation and in clearly distinguished states.

Non-broody hens: 13 bantam hens, at least 1 year old (body weight 870 ± 273 g) were acclimatized for at least 2 months in an environmental chamber at 15°C with lights on from 1000 to 1600 hours. The birds had previously incubated successfully, but were studied only after moult and completed refeathering of the thoracic skin.

Broody hens: To induce broodiness, the light phase was increased to 14 h per day (0700-2100 hours) and the room temperature to 20 ± 2°C. Nest boxes were offered. Within 4 weeks, 80% of the hens began to lay and incubate as soon as the clutch was nearly finished (8-16 eggs). The presence of a rooster seemed to be advantageous but not necessary. Incubating hens sat almost continuously on their clutches, leaving the nest only once a day for foraging, drinking, and defecation. Incubation time was artificially prolonged by replacing newly-laid eggs by boiled eggs. Sixteen broody hens (830 ± 179 g), at least 1 year old, were studied after at least 10 days of uninterrupted incubation. Three of these hens were also studied under non-brooding conditions.

Stimulation. For local cold stimulations of the thoracic skin, a flat aluminium box perfused with temperature-controlled water was tied to the hen’s chest. Cristae inside the stimulator rapidly and evenly distributed the 500 ml min⁻¹ perfusion flow. The contact area between the skin of the lateral apterium (defeathered by moult in the broody and shaved in the non-broody hens) and the stimulator was 38 cm². Stimulation temperature changes of 5–25°C were achieved within 15 s.

Measurements and evaluations. Core temperature was measured by small copper-constantan thermocouples (California Fineewire) inserted 5 cm into the colon, and a thermocouple taped to the skin of the back measured Tth. Double-sided adhesive tape (1 cm²) was used to anchor a thermocouple to the thoracic skin to measure Tths in the center of the area in contact with the stimulator. A thermocouple in the waterflow inside the stimulator measured Tstim. In five brooding and in five non-brooding hens, thermocouples were also taped to the skin of the feet between the toes to measure Tf.

Oxygen consumption was continuously measured by an electrochemical oxygen analyzer (Model S-3A, Applied Electrochemistry, Inc., USA) in an open-circuit system. Dry air was drawn through a mask covering the bird’s head and closed by a tightly-fitting rubber septum around the neck. The total volume of mask, connecting tubes, and an interconnected damping chamber was 1200 ml. The flow of about 5 l min⁻¹ guaranteed an oxygen extraction rate of less than 1% and a wash-out time to 99% of steady-state values in less than 1 min (Steffensen 1989). Oxygen consumption was corrected to STPD and converted to M by assuming that 1 ml O₂ g⁻¹ h⁻¹ was equal to 5.548 W kg⁻¹, and assuming Kleiber’s (1961) respiratory exchange ratio of 0.75 for dry seed eaters.

Experimental procedure. All experiments were performed in a climatic chamber at a temperature of 25°C. The birds were fasted overnight with free access to water before experiments. In the morning, after weighing, the hen was placed in a net sling that suspended its trunk but allowed free movement of its wings and feet, which rested on a bar (Fig. 1). After the bird was fitted with thermocouples, stimulator, and oxygen mask, it was allowed to rest for at least half an hour while the stimulator was perfused with water at 40°C to avoid any loss of heat to the aluminium surface, until body temperature and VO₂ stabilized.

Stimulation temperatures of 35, 30, 25, 20, and 15°C were then applied to the thoracic skin in random order. Each stimulation lasted slightly longer than 10 min, and between stimulations Tstim was kept at 40°C until body temperatures and VO₂ had returned to resting levels.

Statistics. Stable prestimulation temperatures and temperature values recorded after 10 min of stimulation were used for the quantitative evaluation plotted in the figures.

Mean values are presented with standard deviations (±SD). The statistical significance (P<0.05) of the differences between the mean values was evaluated by two-tailed t-testing. Linear regressions were fitted by the method of least squares, and the slopes and intercepts were compared by r-testing. Critical points of two-phase regressions were determined by the method of Yeager and Ultsch (1989).

Results

Resting body temperatures and oxygen consumption

Under resting conditions (Tstim = 40°C), Tth, Tf, and Tbs for broody and non-broody hens did not differ (Table 1). However, the temperature of the unstimulated brood patch was significantly higher than that of the shaved thoracic skin of non-broody hens. In broody hens M was about one-third greater than in non-broody hens.

Body temperatures and VO₂ during moderate cold stimulation

Moderate lowering of Tstim (35–25°C) caused a fall of Tbs and an increase of VO₂ in all hens. In broody hens, Tbs decreased less than in non-broody hens (Figs. 3 and 4) and kept a stable level, resulting in a typical “angular” curve (Fig. 2A, left). The increase of VO₂ started with a short overshoot in 32% of all stimulations (n=78) in 11 broody hens, thereafter stabilizing at a plateau within the first minute of stimulation. There was no further significant increase in VO₂ of broody hens during the stimulation period (Table 2). In non-broody hens the first sudden drop of Tbs was followed by a continuous