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Blood flow in the brood patch of Bantam hens: evidence of cold vasodilatation

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Summary. 1. Blood flow was measured in the brood patch of Bantam hens by recording the washout of ^{133}Xe from the tissue in different experimental conditions.

2. In hens incubating 5 eggs at normal temperature, cutaneous and subcutaneous blood flow in the brood patch averaged 0.31 $ml \cdot min^{-1} \cdot g^{-1}$ and 0.15 $ml \cdot min^{-1} \cdot g^{-1}$, respectively.

3. Cooling the brood patch in restrained hens immediately increased cutaneous and subcutaneous blood flow by an average of 83% and 63%, respectively. The increase in blood flow was restricted to the site of cooling, while neighbouring skin areas showed little change in flow. This cold vasodilatation could also be elicited in hens incubating water circulated eggs and was unaffected by local anaesthetics.

4. The observations suggest that the vasodilatation in response to cooling is due to a direct temperature influence on the smooth muscle cells of the brood patch vasculature.

5. It is suggested that the cold vasodilatation may be important for providing increased heat transfer to the eggs at low ambient temperatures or when the parent bird returns to cool eggs after feeding excursions.

Introduction

The proper development of the avian embryo is dependent on a near continuous supply of heat from an external heat source. In the vast majority of birds, the external heat is provided by one of the parent birds which incubate the eggs by sitting on them (Drent 1975). Most birds develop a naked brood patch by shedding the feathers on parts of the breast and belly in the beginning of the breeding season. Along with the defeathering, the size and number of blood vessels in the cutaneous and subcutaneous tissues increase significantly (Lange 1928; Bailey 1952). It is generally believed that these changes, which occur under hormonal control, enhance the transfer of heat from the incubating bird to the eggs (Drent 1975).

Several studies have shown that the incubating bird regulates the temperature of the eggs by adjusting the nest attentiveness and the 'tightness of sit' on the eggs (Irving and Krog 1956; Drent 1970; White and Kinney 1974; Haftorn 1979). In addition to this behavioural regulation, there is also evidence that the incubating birds respond physiologically to egg temperatures that deviate from normal. For example, it has been found that egg cooling increases the breathing rate (Haftorn and Reinertsen 1982), shivering (Tøien et al. 1984), and oxygen consumption (Biebach 1979; Vleck 1981). Furthermore, Gabrielsen and Steen (1979) demonstrated that ptarmigans returning to nests with cold eggs increased their heart rate considerably, and if this response was blocked by administration of propranolol, warming of the eggs took longer time. These studies show that warming of the eggs to normal incubation temperature is facilitated by an increase in heat production, and apparently the heat is distributed to the brood patch by the circulating blood. However, as argued by Tøien (1984), the increase in heart rate during egg cooling may primarily serve to provide more blood for the shivering muscles, and so far there is no direct experimental evidence for changes in blood flow in the brood patch.

In the present study we report on direct measurements of blood flow in the brood patch of Bantam hens and provide evidence that egg cooling results in vasodilatation of the brood patch.

Materials and methods

Animals and incubation conditions

Five Bantam hens and one cock (*Gallus gallus* var. *domesticus*) with body weights of 678±66 g (mean±SD) were obtained from a local poultry breeder and brought into a large aviary in an animal house in late winter. The fowls were given food and water ad libitum and were exposed to natural light conditions and fresh air through a door open to the outside. After egg laying started, nest facilities were offered and four of the hens successively started incubation. Eggs were removed so that each nest contained 5–6 eggs, and before hatching, fresh eggs were returned so that incubation could be prolonged if necessary.

The nests consisted of small plastic buckets sheltered in vertical boxes. The experimental nest was situated outside the aviary and was similar to the others, except that the bowl was reduced in size with cardboard and a scintillation detector was fitted into the side of the box (Fig. 1).

Blood flow measurements

Blood flow in the brood patch was measured by using a modification of the washout technique of Kety (1948). The technique is based on the principle that the washout of a freely diffusible isotope, which is introduced into the tissue, is proportional to the blood flow in that particular tissue. The isotope used in the present study was ^{133}Xe which can be introduced without trauma into cutaneous and subcutaneous tissues by diffusion from the surface of the skin. Since the technique, its theoretical background, and validity have been described thoroughly in previous publications (Sejrsen 1968, 1969, 1971), only a brief outline will be given here.

A small area (ca. 2 cm^2) of the thoracal part of the brood patch was labeled with ^{133}Xe laterally to the midline by exposing the skin to 0.1 ml physiological saline containing 0.1 to 0.5 mCi of the tracer. The depot was applied epicutaneously and covered with a gas tight Mylar membrane. After 2 min exposure, a sufficient amount of ^{133}Xe had diffused into the skin and the surplus was wiped off and recording of the washout started. The recording equipment consistent of a scintillation detector with a sodium iodide crystal (diameter 31 mm, thickness 6 mm) connected to a rate meter which printed the counts at 10 or 20 sec intervals. The washout curves showed a biexponential form, indicating that ^{133}Xe was washed out from two different compartments of the tissue at different rates. It has been shown that the initial fast component of similar curves in humans corresponds to washout of ^{133}Xe from the cutaneous compartment, while the final slower component is washout of the isotope from the subcutaneous tissue (Sejrsen 1969). The difference in the washout rate is essentially due to the high solubility (affinity) of ^{133}Xe in lipid, which is present in high amounts in the subcutaneous tissue (see below). The two components of the washout curve were determined by graphical curve resolution, and subsequently the rate constants (k) were calculated by the method of least squares. Blood flow was then computed according to the equation

$$f = k \cdot \lambda$$

where f is blood flow (ml·min^{-1}·g^{-1}) and λ is the tissue-blood partition coefficient (ml·g^{-1}) for ^{133}Xe. λ is dependent on the amount of water, lipid, and protein in the tissue, and therefore the content of these constituents in the brood patch was determined for one of the hens after the experiments.

The brood patch was separated in its cutaneous and subcutaneous components and the tissues were dried to constant weight at 40 °C in a vacuum oven. Lipid was extracted from the dry residue by a 2:1 mixture of chloroform and methanol. The dry, extracted material was finally combusted at 500 °C to determine the amount of inorganic material. The difference in weight of the dry extracted material and ash was assumed to provide an estimate of the protein content, though the fraction also includes some carbohydrate material. The water, lipid, and protein contents were 70.7%, 1.4%, and 26.3% for the cutaneous tissue, and 61.0%, 24.9%, and 13.2% for the subcutaneous tissue, respectively. Using the solubility coefficients for ^{133}Xe reported by Yeh and Peterson (1963, 1964, 1965) and a hemoglobin content of 9.0 g per 100 ml blood (Sturkie 1976), the tissue-blood partition coefficient was 1.0 ml·g^{-1} for the cutaneous tissue and 4.4 ml·g^{-1} for the subcutaneous tissue.

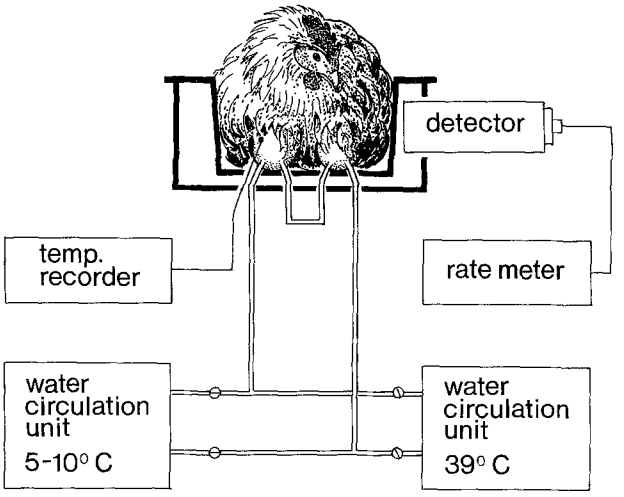

Fig. 1. Experimental set-up for measuring changes in brood patch blood flow during egg cooling in freely incubating hens. In addition to the two water circulated eggs, the nest contains three normal eggs. The brood patch is labeled with ^{133}Xe and the washout rate, which is porportional to blood flow, is recorded by the scintillation detector

Temperature measurements

Colonic temperature, brood patch temperature (measured at the egg-brood patch interface), and the temperature of the artificial eggs were recorded with calibrated copper-constantan thermocouples which were connected either to a spot galvanometer (Radiometer, GVM 22c) through a rotary switch or to a potentiometric recorder (Goertz Electro, RE 501). The reference junctions of the thermocouples were kept in a waterfilled vacuum flask where the temperature was read on a standard mercury thermometer (accuracy±0.05 °C). The accuracy of the temperatures determined with the spot galvanometer was ±0.05 °C while that of the recorder was ±0.5 °C.

Experimental conditions

All experiments were conducted at normal room temperature (20–22 °C). Blood flow was recorded in freely incubating hens and in restrained hens.

1. Freely incubating hens. After labeling of the brood patch with ^{133}Xe, the hen was returned to the experimental nest which contained 5 eggs that were kept warm during the labeling period. Recording of the washout started immediately when the hen had settled on the eggs and continued for about 50 min.

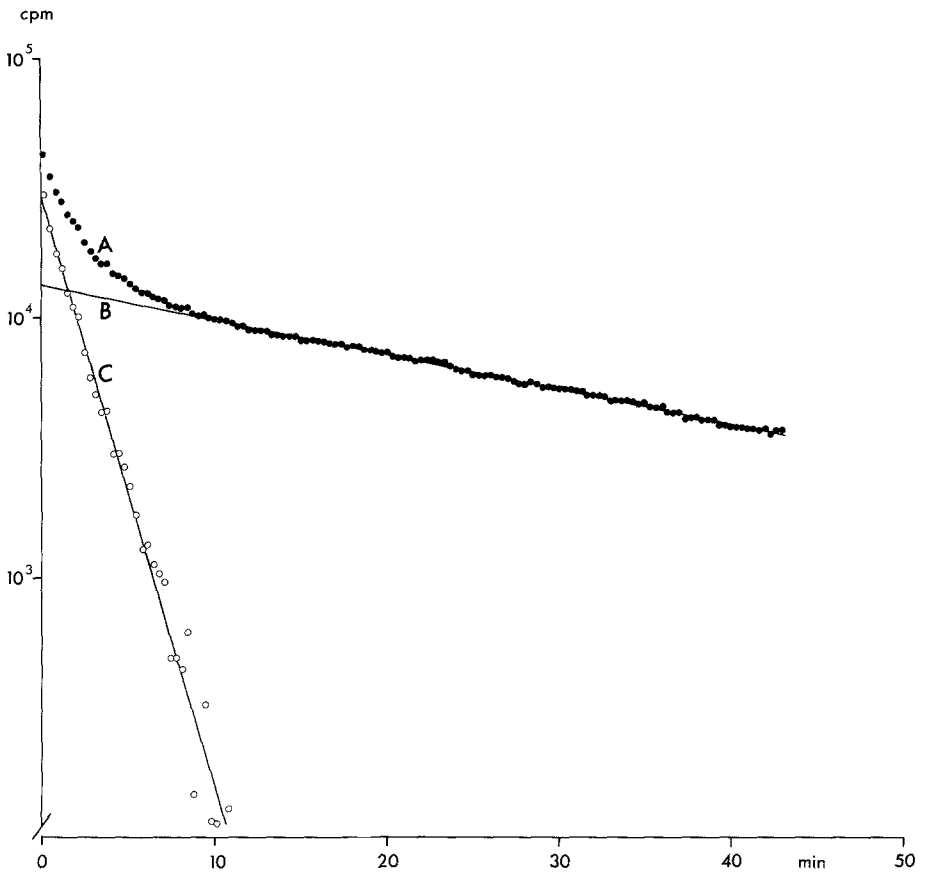

Fig. 2. Washout of ^{133}Xe in the brood patch of a hen incubating 5 eggs with normal temperature. *A* is the recorded washout curve. *B* and *C*, which represent the subcutaneous and cutaneous components, respectively, have been obtained with graphical resolution of the washout curve

In cases where the response to egg cooling was tested, two of the normal eggs were removed and replaced with hollow metallic eggs which were circulated in series with either warm (39 °C) or cold (5–10 °C) water from two thermostatically controlled reservoirs (Heto, Hetofrig) (Fig. 1). Care was taken to place the hen on the nest in a way that was assumed to provide contact between the labeled area of the brood patch and one of the water circulated eggs. After 3–4 min of steady incubation, the artificial eggs were alternately perfused with cold and hot water in 3 min periods. In order to reduce experimental stress to a minimum, thermocouples were not attached to the incubating hen in experiments where blood flow was recorded. The effect of egg cooling on deep body temperature and brood patch surface temperature was recorded in separate experiments.

2. Restrained hens. In this condition, which was applied to obtain information on the response of the brood patch to general or local cooling, the hen was restrained on its back with the head covered with a cloth. A hollow metallic disc (diameter 3 cm) circulated with water from a Hetofrig was used for local cooling while general cooling of the whole patch was accomplished by covering it with a water soaked swab that was ventilated with an air stream. The degree of cooling was monitored by a thermocouple taped to the skin.

Data analysis

Graphical curve resolution and least squares regression analysis were performed with a computer programmed specifically for this purpose. All results are expressed as mean ± standard deviation (SD).

Results

Brood patch blood flow in incubating hens

Although the hens usually resumed incubation immediately when they were returned to the experimental nest, measurements of brood patch blood flow were at times troubled by changes in the recording condition caused by resettling movements of the hens. Figure 2 illustrates the washout of ^{133}Xe from the brood patch in an experiment where the hen incubated quietly during the entire recording period. The biexponential washout curve has been resolved into its initial fast component (C) and slower 'tail' (B) which represent washout of ^{133}Xe from the cutaneous and subcutaneous tissues, respectively. The cutaneous and subcutaneous blood flow calculated from 5 experiments with hens incubating eggs at normal temperature were $0.31 \pm 0.12\ ml \cdot min^{-1} \cdot g^{-1}$ and $0.15 \pm 0.05\ ml \cdot min^{-1} \cdot g^{-1}$, respectively.

Effect of cooling

General cooling of the brood patch in restrained hens immediately increased the washout rate of

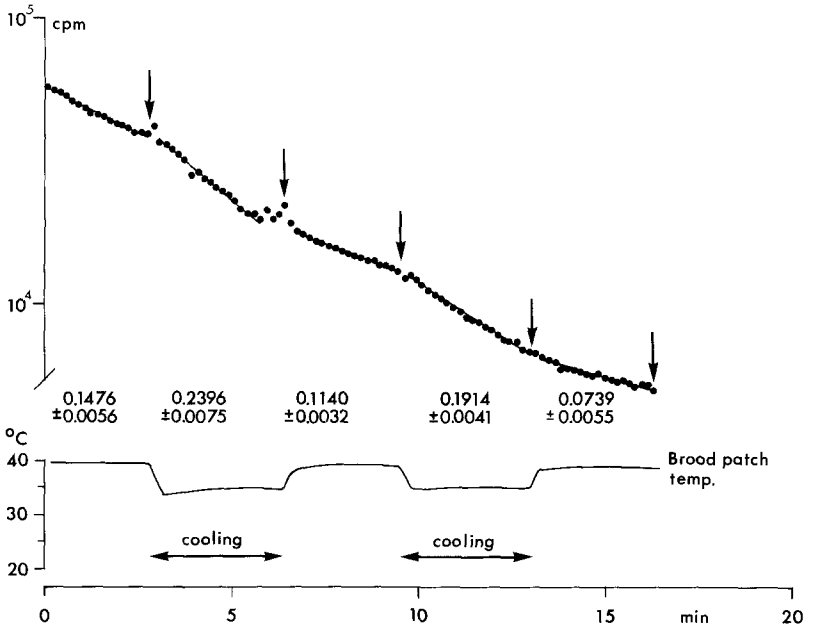

Fig. 3. Effect of cooling on brood patch blood flow in a restrained hen. Spells of cooling increases the washout rate of ^{133}Xe (top curve). The rate constants given below the washout curve show that the blood flow during cooling is increased with a mean value of 94% in comparison to precooling and postcooling levels. This experiment was conducted in the cutaneous phase of the washout curve

^{133}Xe (Fig. 3). The increase in blood flow in response to cooling was $83 \pm 26\%$ ($n=7$) for the cutaneous tissue and $63 \pm 22\%$ ($n=6$) for the subcutaneous tissue. If cooling was restricted to the labeled area, a similar increase in blood flow was observed, while cooling the adjacent skin (2–3 cm from the labeled area) caused a slight decrease (6–8%) in blood flow. The associated decline in skin temperature was about 15 °C immediately below the cold disc and less than 1 °C in the neighbouring skin. These experiments indicate that vasodilatation only occurs in the area where the cold stimulus is applied, while neighbouring areas may respond with vasoconstriction.

The vasodilatory response could also be elicited in freely incubating hens, although the response was more variable. Shifting from hot to cold water in the perfused eggs increased blood flow with an average of 23% in 6 experiments, while in 8 experiments there was no change or a slight decrease in blood flow. In line with the results from local cooling experiments, it is likely that the vasoconstrictor response or lack of response to egg cooling were seen in experiments where the artificial eggs were not in direct contact with the labeled area of the brood patch.

In order to determine whether the observed vasodilatation is a neural mechanism, six experiments were performed with restrained hens in which the brood patches were anaesthetized with lidocaine (ca. 2 ml 0.5%, injected subcutaneously around the nerves that enter the brood patch from its lateral border, or directly in the area which was subsequently labeled with ^{133}Xe). The volume and concentrations used were assumed to provide complete nerve blockade after 30 min, since similar doses in humans effectively block nerve transmission in somatic as well as autonomic fibers (Henriksen 1977). The mean rate constant of the washout curve in precooling periods ($0.1023 \pm 0.0325\ min^{-1}$) was not significantly different ($P > 0.1$, t-test) from that found without local anaesthesia ($0.1410 \pm 0.0416\ min^{-1}$), indicating that nerve blockade did not alter the level of blood flow. The increase in cutaneous blood flow in response to general cooling of the brood patch was $110 \pm 71\%$, which is not significantly different ($P > 0.1$, t-test) from the value obtained without nerve blockade.

Body and brood patch temperatures

Body temperature and the temperature of the brood patch measured during incubation in the four hens averaged 41.7 ± 0.3 °C and 40.8 ± 0.7 °C, respectively. Shifting from hot to cold water in the artificial eggs had a marked influence on body and brood patch temperature. After circulating 6 °C water for a period of 8 min, body temperature and brood patch temperature (contralateral to the artificial eggs) decreased with 1.2 ± 0.7 °C ($n=6$) and 1.1 ± 0.9 °C ($n=6$), respectively.

Discussion

The appearance of the washout curve for ^{133}Xe in the brood patch of the hens (Fig. 2) corresponds

to the biexponential washout curves seen in the human skin (Sejrsen 1971). The absolute blood flow values derived from the washout curves are dependent on the tissue-blood partition coefficient (λ) for ^{133}Xe, which again depends on the composition of the tissue and blood (Yeh and Peterson 1965). In the present study, the value of λ calculated for the cutaneous tissue (1.0 $ml \cdot g^{-1}$) is comparable to the 0.7 $ml \cdot g^{-1}$ used in humans (Sejrsen 1971), the difference being due to the lower hemoglobin content in chicken blood. In contrast, λ for the subcutaneous tissue of the brood patch (4.4 $ml \cdot g^{-1}$) deviate considerably from the 10.0 $ml \cdot g^{-1}$ reported by Larsen et al. (1966) for the rat. This difference is mainly due to the low lipid content in the subcutaneous tissue of the thoracic skin of the fowl.

Being a freely diffusible tracer, ^{133}Xe enters capillaries as well a larger blood vessels such as arteriovenous anastomoses (AVAs). Since AVAs are present in the brood patch of birds (Midtgård 1984) it cannot be excluded that a small part of the blood flow measured in the present study is due to washout of ^{133}Xe through these vascular structures. Wolfenson et al. (1981) have measured capillary blood flow in various tissues of the laying hen by using 15 μm microspheres. They found that blood flow in the breast skin increased from 0.05 $ml \cdot min^{-1} \cdot g^{-1}$ in the normothermic hen to 0.35 $ml \cdot min^{-1} \cdot g^{-1}$ during heat stress. Although the values obtained with the ^{133}Xe washout technique and microspheres are not directly comparable, it appears that the blood flow associated with dissipating heat from the breast skin during hyperthermia is comparable to what is necessary for incubating 5 eggs in a thermoneutral environment. However, it is surprising that breast skin blood flow in incubating hens does not exceed that of the hyperthermic laying hen, especially when considering that the vascularity of the thoracic skin increases greatly during formation of the brood patch (Lange 1928; Bailey 1952). The reason for this may be that the increased vascularity concerns the AVAs rather than the capillaries, and that AVA blood flow is more important in delivering heat to the eggs than capillary blood flow. However, recent experiments with sheep have shown that AVA and capillary blood flow can be equally important in dissipating heat from the skin (Hales 1985).

The major objective in the present study was to determine the response of the brood patch vasculature to cooling. Although the changes that we recorded are small in comparison to the 7-fold increase in breast skin blood flow which Wolfenson et al. (1981) found for the heat stressed hen, our findings are important in that the response is opposite to what would be expected for cutaneous blood vessels. While mild cooling of the skin generally decreases blood flow, the brood patch vasculature responds with a promptly onset increase in blood flow. However, cold vasodilatation is not unique to the brood patch, since this phenomenon, although different in nature, also has been observed in the hands of humans (Lewis 1930; Greenfield et al. 1951; Krog et al. 1960; Folkow et al. 1963) and in the feet of birds (Johansen and Millard 1974; Murrish and Guard 1977). Immersion of the hands in water at temperatures close to zero °C elicits transient vasoconstriction followed by longer lasting vasodilatation. The dilatory response depends on a number of different mechanisms, but apparently vasodilatory nerves are not involved (Greenfield et al. 1951; Folkow et al. 1963). In contrast, the prompt increase in blood flow that occurs when the foot of the Antarctic fulmar (*Macronectes giganteus*) is immersed in icewater is a neural vasodilatory response (Johansen and Millard 1974; Murrish and Guard 1977). Active vasodilatation can also be elicited in the feet of ducks and chickens (McGregor 1979), and it appears that the dilatory nerves are restricted to the AVAs (Hillman et al. 1982). Ultrastructural observations confirm the presence of possible vasodilatory nerve terminals near AVAs in the feet of ducks (Molyneux and Harmon 1982). We have not established the nature of the mechanism that underlies the cold vasodilatation in the brood patch, nor do we know whether AVAs are involved. However, the fact that the dilatory response was purely local and was unaffected by nerve blockade seems to suggest that nerves are not involved. Further experiments, such as perfusion of isolated tissue, are of course needed to confirm this. If nerves are proven not to be involved it is likely that the vasodilatory response is due to a direct temperature influence on the vascular smooth muscle fibers. A vasodilatory mechanism of this kind has been reported for the rabbit facial vein (Winquist and Bevan 1980).

The variable response of the brood patch vasculature to egg cooling in the freely incubating hens is most likely related to differences in the position of the artificial eggs with respect to the skin area in which blood flow was recorded. Being a local response, vasodilatation would only be observed in cases of direct contact between the labeled area and the cold eggs, whereas a decrease in blood flow would be recorded if adjacent areas were cooled. Although temperature is a poor measurement of blood flow, the observation of a de-

crease in brood patch surface temperature on the contralateral side to the cold eggs is also suggestive of vasoconstriction. The vasoconstrictor response in adjacent areas may be a reflex mechanism involving brood patch thermoreceptors or could be elicited centrally due to the pronounced decrease in deep body temperature seen during spells of egg cooling. The decline in colonic temperature occurs immediately upon egg cooling and is believed to be mediated by the circulating blood rather than being a local heat conduction phenomenon.

It is obvious that an increase in brood patch blood flow, together with other physiological changes that occur in response to egg cooling, implies that more heat is transferred to the eggs. This mechanism may be considered advantageous to incubation in several respects: (1) heat transfer to the eggs will be augmented during incubation at low ambient temperature; (2) eggs that have been cooled, for instance if the incubating bird has left the nest to feed, will heat up faster than they would in the absence of the mechanism; and (3) in being a local response, the vasodilatation will serve to distribute heat preferentially to cold eggs in a clutch, which will tend to diminish temperature gradients between the different eggs. While cold vasodilatation in the breast skin obviously is important during the breeding season, it is clear that the same response is disadvantageous to the bird outside this period of the year. It is a question whether the vasodilatory mechanism is universally present in the breast skin or only concerns the new blood vessels that develop in the brood patch. It has been shown that full brood patch vascularization can be elicited by administration of a combination of estrogen and prolactin (Jones 1969), and, until further experiments have been made, it is tempting to speculate that changes in the level of one or both of these hormones during the incubation period could alter the sensitivity of the brood patch vasculature to thermal stimulation.

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