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Heat Stress Effects on Capillary Blood Flow and its Redistribution in the Laying Hen

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Abstract. The effect of heat stress on capillary blood flow (CBF) distribution was examined in laying hens, using 15 micron microspheres, by determining CBF before and after elevating body temperature by 1–2° C. No change was evident in unfeathered metatarsal skin, although its temperature increased by 7° C. Breast skin CBF change was 3.5 times larger than that of back skin. Comb CBF increase was larger than in wattles. CBF in upper respiratory tract increased proportionally to increment in respiratory frequency. Digestive system CBF was reduced by hyperthermia: the effect was pronounced in its upper organs (46% of normal) and decreased along the tract. CBF increased 4-fold in an expiratory abdominal muscle, a smaller rise occurred in a pectoral muscle and no change in a leg muscle. CBF in the tibia fell to 64% of normal. In the reproductive system, CBF fell to 58% of control level in the uterus, to 70–80% in the larger ovarian follicles and infundibulum with no significant changes in magnum and isthmus. Cerebral CBF increased during hyperthermia.

Heat stress significantly reduced CBF to inner body organs, with marked differences between systems as well as within systems. Changes were more pronounced on 2° C hyperthermia than on 1° C hyperthermia.

Key words: Capillary blood flow – Heat stress – Thermoregulation – Microspheres – Laying hen

Introduction

The involvement of cardiovascular function in thermoregulation is only poorly documented in birds relative to mammals. In mild heat stress, during which fowls maintain first phase of panting, i.e. continuous rapid breathing, cardiac output is increased by 20–30% from normal by increased heart rate (+15%) and stroke volume (+10%), while arterial pressure drops by 10% and peripheral resistance by 30% (Frankel et al. 1962; Whittow et al. 1964). These changes are similar to those reported in mammals.

Skin temperature over unfeathered areas changes, as a result of vasomotor function, over a wider range than in the feathered areas of the skin (Richards 1974). The heat loss from the unfeathered limbs may reach up to 50% of total metabolic heat production (Steen and Steen 1965). The thermally induced vasomotor changes in birds were mostly characterized for the legs owing to their obvious importance in heat dissipation in these species (Johansen and Millard 1973; Bernstein 1974; Baudinette et al. 1976). Recently, it was shown that blood flow to the wattles of cocks is increased by release of the alpha-adrenergic tone (Nolan et al. 1978). The forementioned studies are limited in their interpretation, since blood flow was monitored in the main vessel supplying the area and the thermally induced change was attributed to skin blood flow, without it being actually measured. The overall view on the distribution of blood flow in the body was not clarified, as blood flow was not simultaneously measured in other regions. This is, however, feasible if the labelled microspheres technique is used.

A cardiovascular involvement in respiratory water loss seems also required for the maintenance of both the activity of respiratory muscles and the evaporation from the respiratory surfaces. In both the dog and sheep mild hyperthermia was associated with a significant increase of blood flow to the upper respiratory tract and respiratory muscles (Hales 1973b; Hales and Dampney 1975). There is, however, no information on the panting birds.

The alteration of peripheral vascular function is associated with changes in body core blood flow. In mammals a reduction of blood flow to the kidneys and the digestive tract during hyperthermia was found (Hales 1973a; Rowell 1974). Some studies also indicated a reduction in the blood flow to the reproductive system, which was suggested to impair embryonal development (Leduc 1972; Oakes et al. 1976;

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Roman-Ponce et al. 1978). We know of only one short report on regional blood flow in birds, in which a decrease in blood flow to the uterus and the jejunum was stated to occur in heat acclimated hens (van Handel-Hruska et al. 1977). This reports a study on the effect of heat stress on distribution of capillary blood flow in laying hens as measured by radioactive microspheres.

Methods

Animals. The study was carried out on 8–15 month old crossbred White Leghorn × Rhode Island Red hens, mean body weight 1,900 ± 270 (SD) g, mean laying rate 75–80%. The hens were housed between the experiments in an open shed, in individual battery cages, exposed to the natural outdoor air temperatures (8–21°C). They were fed ad libitum a commercial layers food mixture, and were lit about 15 h per day.

Experimental Procedure. The hens were brought to the laboratory, weighed to ± 15 g, and set on their side on a plastic net within a flat wooden frame. They were restrained by stretching thin rubber bands over the body and tying the legs to the wooden frame. This allowed for light movements, but prevented interfering with latter procedures. Blood vessels were cannulated and deep colonic and foot skin temperatures, oxygen consumption, respiratory and heart rates, arterial pressure, arterial blood pH and P_{CO_2} and blood flow distribution were determined as earlier described (Wolfenson et al. 1978). Cannulations were performed under local anaesthesia (Lidocaine, 2%). The labelled microspheres were injected via the brachial artery to the root of the aortic arch above the aortic valve, since it was proven unfeasible to reach the left ventricle by retrograde insertion of the cannula through either the carotid or the brachial arteries. An accurate location of the end of the cannula above the aortic valve was found essential for attaining a proper distribution of the microspheres into the circulation. In preliminary experiments it was found that the mean distance from the insertion point in the brachial artery is 8.0 ± 0.5 cm. The cannula was, therefore, marked at 1 cm intervals to ascertain depth of insertion. Blood pressure in the cannula was monitored on approaching the root of the aorta. As the end of the cannula reached the aortic valve, a change in the pressure record was evident. The cannula was then withdrawn by 1–2 mm and fixed at this depth of insertion. The skin incision on the inner surface of the wing was then sutured to prevent dessication. Since the microspheres were injected to the root of the aorta and not into the left ventricle, their uniform distribution between upper and lower body organs could not be presumed. To account for this we used as reference organs the brachial artery, which served to calculate blood flow to the organs supplied by the brachiocephalic arteries and the sciatic artery, which served as a reference organ for the organs supplied by the descending aorta. Blood was drawn at the rate of 1.3 to 1.7 ml · min^{-1} from these two reference organs into weighed syringes simultaneously with the injection of the microspheres, using a multichannel infusion/withdrawal pump (Harvard Apparatus, Model 907 A). The microspheres, mean diameter 15.0 ± 1.8 (SD) μ, were labelled with ^{51}Cr and ^{141}Ce (3 M-Nuclear Products or New England Nuclear). An initial dose was injected after the animal responses stabilized and served as a control; the next dose was injected after warming the animal to a controlled degree of hyperthermia. This was achieved by blowing hot air over the animal.

Data Analysis. The data on lower body organs blood flow are based on 13 successful experiments. Out of these, in 4 experiments problems in blood withdrawal for the upper reference organ or low activity in this sample prevented calculation of blood flow in upper body organs. This and some counting failures resulted in unequal replicate numbers. Statistical evaluation was carried out by Student's paired "*t*" test.

Results

Validity of the Method. In addition to its earlier assessment (Wolfenson et al. 1978), the validity of the method was also estimated by simultaneously administering differently labelled microspheres. The relationships between such independent measurements indicate the validity of a procedure in which one isotope is used for the control state and the other to assess the effect of a treatment within one animal. The results obtained on injecting in a sequence or simultaneously two differently labelled microspheres in 8 hens were examined by regression analysis. The regressions were separately calculated for the lower and the upper body organs, according to the particular reference organ referred to.

Lower body organs: Isotope A = 0.01 + 1.02 (Isotope B)
$r = 0.96$, $s_b = 0.03$, $n = 78$, $P < 0.001$.

Upper body organs: Isotope A = −0.02 + 1.07 (Isotope B)
$r = 0.95$, $s_b = 0.05$, $n = 56$, $P < 0.001$.

These regression equations are not statistically different from the identity equation. As such they indicate the feasibility of using differently labelled isotopes to assess the distribution of blood flow in one animal at two different states.

The principle underlying the microsphere method is that the microspheres are not recirculated in the vascular system. Microspheres of 15 μ diameter may recirculate if they evade the capillary bed by passing through arteriovenous anastomoses (AVA) larger than 15 μ in diameter, to be later trapped in the capillary bed of the lungs. In birds the bypassing microspheres are also trapped in the venous portal systems of the kidneys and the liver which are interconnected by the coccygeomesenteric vein. Injecting 15 μ diameter microspheres into a peripheral vein of the fowl resulted in their almost 100% trapping in the lungs (Boelkins et al. 1973) and when injected into a vein of the leg they were trapped in the ipsilateral kidney, liver and lungs, with no measurable residual radioactivity in other tissues (Odlind 1978). It may hence be concluded that the results here presented estimate capillary blood flow in the different organs. However, the radioactivity measured in the liver, kidney and lungs following the injection of 15 μ microspheres may also result of microspheres passing through AVA in the lower body organs.

Thermal and Respiratory Responses. Parameters of cardiorespiratory and thermoregulatory functions are

Table 1. Means (± SE) of thermal state and cardiorespiratory functions of 13 laying fowls in either normothermia or hyperthermia. Statistical significance of differences: $*P < 0.05$, $***P < 0.001$

Parameter	Normothermia	Hyperthermia
Air temperature (°C)	21.2 ±0.5	
Body temperature (°C)	41.4 ±0.1	42.9 ± 0.1***
Skin temperature (°C)	29.3 ±1.6	36.5 ± 0.7***
Resp. frequency (breaths · min^{-1})	34 ±2	177 ±17***
Oxygen consumption (ml · min^{-1} · kg^{-1})	13.9 ±0.7	16.2 ± 1.0
Heart rate (beats · min^{-1})	355 ±6	405 ± 7***
Mean arterial pressure (mmHg)	132 ±4	119 ± 3*
Arterial blood pH	7.46±0.01	7.47± 0.01
Arterial blood P_{CO_2} (mmHg)	30.8 ±0.6	22.7 ± 0.9***

Table 2. Organ weights (means ± SE) in 13 laying fowls

Organ	Weight (g)	Organ	Weight (g)
Wattles	1.9 ±0.2	Liver	49.8 ±2.4
Comb	8.5 ±0.9	Kidneys	14.5 ±0.5
Tongue	1.2 ±0.1	Infundibulum	2.2 ±0.1
Larynx	0.90±0.03	Magnum	29.4 ±1.3
Cerebrum	1.7 ±0.1	Isthmus	7.8 ±0.3
Proventriculus	5.7 ±0.3	Uterus	15.4 ±0.7
Gizzard	18.6 ±0.8	Follicle[a] 1	0.49±0.03
Duodenum	5.1 ±0.3	Follicle 2	0.43±0.03
Jejunum	8.0 ±0.4	Follicle 3	0.34±0.02
Ileum	5.0 ±0.4	Follicle 4	0.28±0.03
Pancreas	2.9 ±0.1		

[a] Follicle weights excluding yolk, numbers design descending order of size

presented in Table 1 and weights of various organs in Table 2. These experiments were carried out during the winter, at a room temperature of 21° C. Mean body temperature during the hyperthermal state was 42.9° C, an increment of 1.5° C from the normothermic state ($P < 0.001$). This increment in body temperature was associated with significant increases in foot skin temperature (+7° C, $P < 0.001$) and respiratory rate, while oxygen consumption increase (+16.5%) was statistically non-significant. Heart rate also increased by 14% ($P < 0.001$), while blood pressure was 10% lower ($P < 0.05$). The P_{CO_2} in arterial blood fell to 73% of the control level ($P < 0.001$), which reflects a wash-out of CO_2 as a result of panting, while pH remained at the control level.

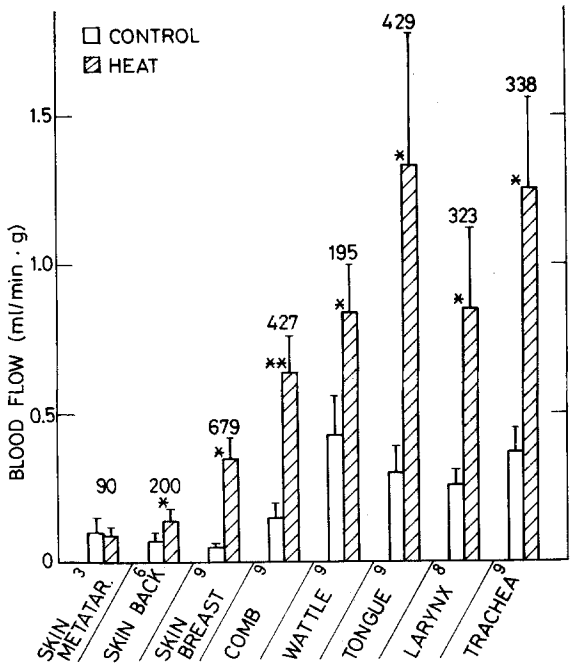

Fig. 1. Capillary blood flow (means ± SE) during normothermia and hyperthermia in organs active in heat dissipation. Numbers above columns denote precentage change from control value. Number of replicates denoted by number at base of column. Statistical significance of differences: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

Blood Flow to Organs Active in Heat Dissipation. These values are presented in Fig. 1. They indicate as a whole an increase in blood flow (BF) during hyperthermia. A notable exception is the unfeathered metatarsal skin, in which no significant change in capillary BF occurred, in spite of the fore-mentioned marked increase in skin temperature. The extent of change varied from organ to organ. In the back skin BF was doubled to 0.14 ml · min^{-1} · g^{-1} while a seven fold increment was evident in the breast skin (to 0.35 ml · min^{-1} · g^{-1}). In the comb, hyperthermia was associated with a 430% increase in the mean BF of the anterior, intermediate and posterior areas of the comb. In the control state, BF was lesser in the posterior area than in other areas of the comb. During heat stress, these relations were modified, as BF increased to 540% in the posterior part, while it increased to only 320% in the anterior part. The vasomotor change was less reflected in capillary BF to the wattles, which only doubled to 0.84 ml · min^{-1} · g^{-1}. Marked increases in BF were observed in the upper parts of the respiratory tract involved in the evaporative water loss during panting: BF increased to 320–430% of the control level, an increment comparable to the rise in respiratory frequency.

Blood Flow to the Digestive Tract, Kidneys and Liver. The results presented in Fig. 2 indicate the changes in

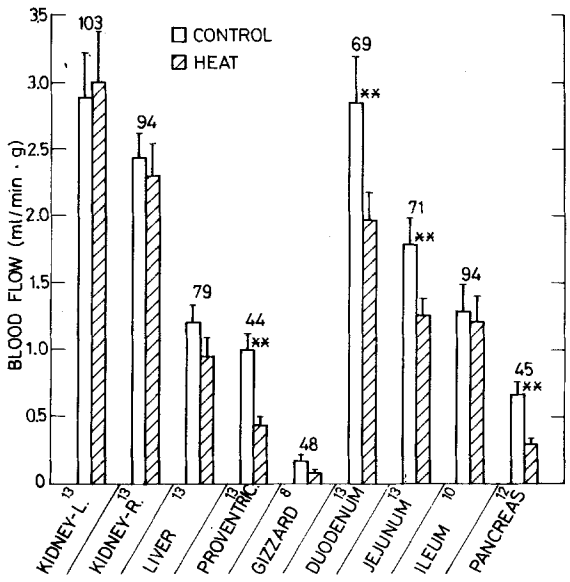

Fig. 2. Capillary blood flow (means ± SE) in inner body organs during normothermia and hyperthermia. Legends as in Fig. 1

BF induced by hyperthermia. The overall trend of a decrease in blood flow in the digestive tract was the opposite of that recorded in the organs active in dissipation of heat. The largest reductions were observed in the specialized parts of the system: the proventriculus, the gizzard and the pancreas, in which BF decreased to 44–48% of control values. In the duodenum and jejunum it decreased to 69–71% of the control levels, while in the ileum the reduction noted was statistically non-significant. The rate of blood flow to the kidneys was not significantly affected by hyperthermia. BF to the right kidney was smaller than that to the left one, in both the control and the hyperthermic states. BF to the liver also was not significantly affected by hyperthermia. These effects of hyperthermia on BF to the kidneys and the liver should however be viewed with caution, considering the forementioned reasons.

Blood Flow to Bone, Muscle, Brain and Endocrine Glands. Among the three muscles documented here (Fig. 3), BF in the control state was the highest in the abdominal muscle (M. external abdominal oblique). This muscle is one of the 10 expiratory muscles in birds. BF in this muscle increased by 400% during hyperthermia, contrasting the smaller 180% ($P < 0.001$) increase in pectoral muscle (M. pectoralis major) BF and the lack of change in the leg muscle. During hyperthermia, BF to the tibial bone was reduced to 64% of control values. BF was not significantly modified in the thyroid and the adrenals, while that in the brain increased to 143% of the control level.

Blood Flow to Reproductive System. The distribution of BF during hyperthermia was examined in 13 hens. The

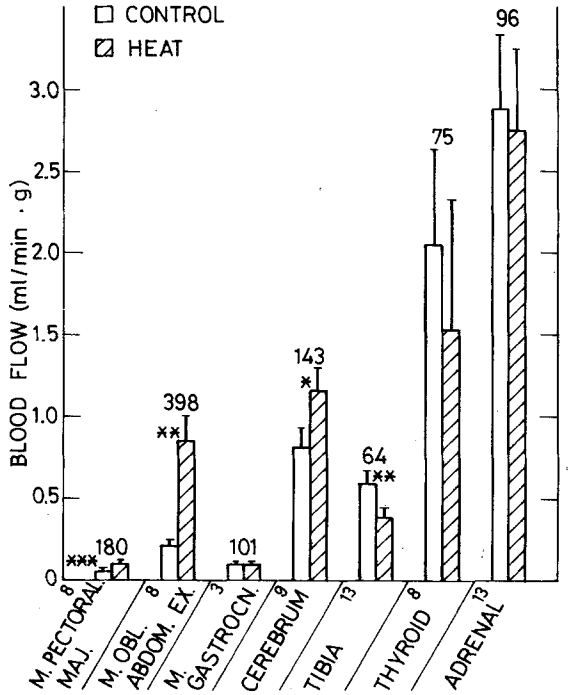

Fig. 3. Capillary blood flow (means ± SE) in inner body organs during normothermia and hyperthermia. Legends as in Fig. 1

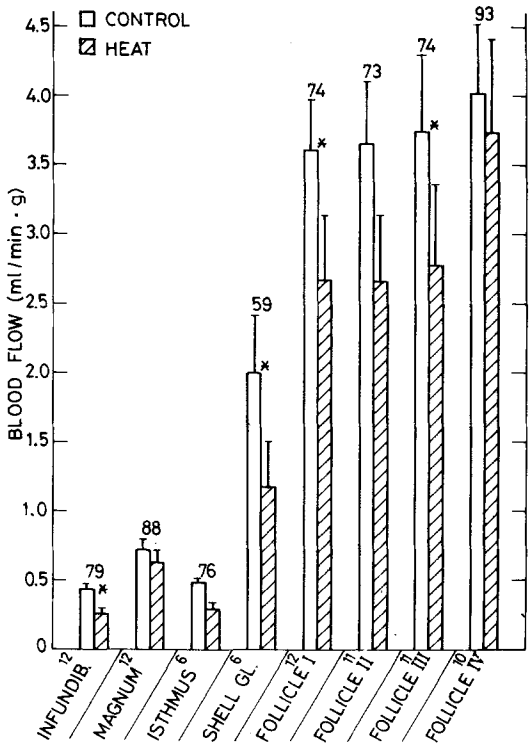

Fig. 4. Capillary blood flow (means ± SE) in reproductive system organs during normothermia and hyperthermia. Legends as in Fig. 1

rates of BF in the uterus and the isthmus was examined in 6 experiments carried out in the evening hours, during which BF to these organs is stable (Moynihan and Edwards 1975). In the earlier hours of the day, BF

Table 3. Means (± SE) of thermal state and cardiorespiratory functions of 6 laying fowls in moderate hyperthermia (+ 1° C) and of 7 laying fowls in severe hyperthermia (+2° C). Statistical significance of differences: $^{**}P < 0.01$, $^{***}P < 0.001$

Parameter	Moderate hyperthermia		Severe hyperthermia	
	Control	Treatment	Control	Treatment
Air temperature (°C)	21.7 ± 0.8		20.7 ±0.4	
Body temperature (°C)	41.5 ± 0.2	42.5 ± 0.1***	41.3 ±0.2	43.3 ± 0.2***
Skin temperature (°C)	31.0 ± 2.5	35.2 ± 0.9	27.8 ±2.2	37.4 ± 0.9**
Resp. frequency (breaths · min^{-1})	34 ± 5	147 ±22***	34 ±2	202 ±22***
Oxygen consumption (ml · min^{-1} · kg^{-1})	13.0 ± 1.0	16.0 ± 1.9	16.6 ±1.0	16.3 ± 1.3
Heart rate (beats · min^{-1})	362 ±10	391 ±13	350 ±8	418 ± 4***
Mean arterial pressure (mmHg)	132 ± 5	117 ± 4	131 ±6	120 ± 6
Arterial blood pH	7.48± 0.01	7.48± 0.02	7.44±0.01	7.46± 0.01
Arterial blood P_{CO_2} (mmHg)	30.5 ± 0.9	23.7 ± 1.3**	31.1 ±0.9	21.9 ± 1.2***

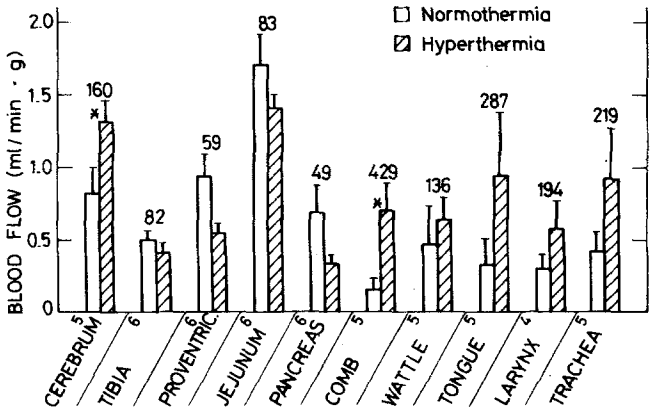

Fig. 5. Effect of 1° C hyperthermia on capillary blood flow in representative organs. Legends as in Fig. 1

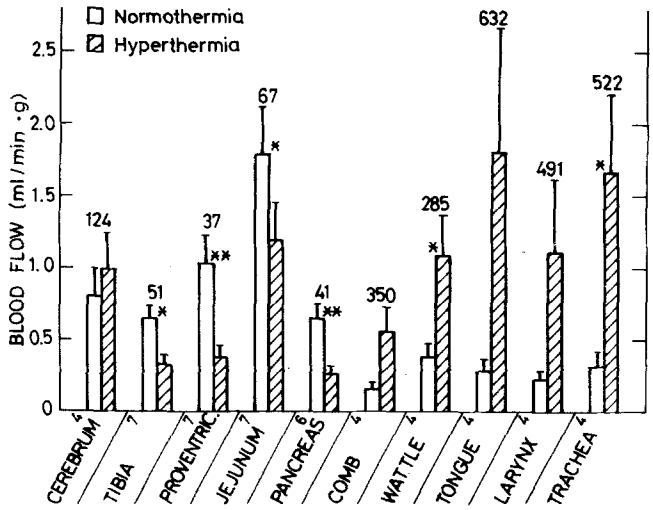

Fig. 6. Effect of 2° C hyperthermia on capillary blood flow in representative organs. Legends as in Fig. 1

levels depend much on the presence of the egg in the segment. It is increased 3- to 4-fold in the isthmus with egg present in it, while in the uterus BF increases from entrance of the egg to reach maximal steady values 4 h later. Among the various parts of the reproductive system, that in the uterus was the most sensitive to hyperthermia (Fig. 4); BF in it was reduced to 58% of the control values (2.0 ml · min^{-1} · g^{-1}). Smaller changes in BF were recorded in the infundibulum, while that in the isthmus and the magnum were not significantly modified. In the three largest ovarian follicles similar reductions, of about 30%, were noted with no change in the fourth follicle.

Relationship of BF to Degree of Hyperthermia. The extent to which the degree of hyperthermia affected the distribution of BF was examined by classifying the animals according to the level of hyperthermia at which they were maintained: 7 fowls in which body temperature was maintained at about 2° C above their control level and 6 fowls in which it was maintained at about 1° C above the control level. The two groups differed significantly in their body temperature, skin temperature, respiratory frequency and heart rate, while oxygen consumption, mean blood pressure and pH were similar in both groups; in the higher body temperature group blood P_{CO_2} was slightly lower, but the difference was not significant (Table 3). The two groups differed in BF values in 10 out of the 34 organs examined (Fig. 5 and 6). In the cerebrum, BF increased to 160% in the 1° C hyperthermia group, while in the 2° C hyperthermia group only a non-significant increase relative to control levels was found. In the tibia the respective reductions at 1° C and 2° C hyperthermia were to 82% (NS) versus 50% ($P < 0.05$) of control values, in the proventriculus 60% (NS) versus 37% ($P < 0.01$), in the jejunum 83% (NS) versus 67% ($P < 0.025$) and in the pancreas 49% versus 41% (both significant at $P < 0.005$). These indicate a trend for an enhanced reduction in BF to inner body organs with increasing degree of hyperthermia with the probable exception of the cerebrum.

The opposite trend was evident in the organs involved in heat dissipation, with the exception of the comb. In the wattles, BF increase relative to the control level was 136% (NS) in the 1° C hyperthermia group

and 285% in the 2° C hyperthermia group ($P < 0.05$). In the respiratory organs, 2–3-fold increases were recorded (NS) in the 1° C hyperthermia group, while in the 2° C hyperthermia group the increases were larger (5–6-fold).

We calculated the relationship between the increment in respiratory frequency (F) and the percentage increase in BF above the control level (Y) in the trachea, tongue and larynx. The regression equations are presented below.

Trachea $Y = -53.7 + 3.34F$, $r = 0.65$, $P < 0.10$.
Tongue $Y = -452 + 6.10F$, $r = 0.78$, $P < 0.025$.
Larynx $Y = -552 + 5.60F$, $r = 0.79$, $P < 0.025$.

These regressions indicate a positive relationship between the increase in respiratory frequency during hyperthermia and the relative increase in BF to the organs active in respiratory water loss.

Discussion

The control levels of cardiorespiratory functions and thermal state were within the range normal for fowls of this sex and age as reported in a number of studies (Whittow et al. 1964; Frankel and Frascella 1968; Kawashiro and Scheid 1975). The pH values found in this study are similar to those reported by Frankel and Frascella (1968) but higher than those reported by Kawashiro and Scheid (1975). In preliminary measurements in nonlaying hens we found higher pH values. It is thus possible that the lower levels in our control measurements are related to the high rate of laying, since metabolic acidosis was shown to develop during the egg shell formation (Simkiss and Taylor 1971). The similarity of the control data to those of other studies indicates that the experimental situation in which BF was measured did not alter the responses of the animals; it also indicates that it is feasible to examine the distribution of BF in unanaesthetized fowls.

Thermoregulatory Responses. In the hyperthermic animals, mean body temperature increase above control level was 1.5° C. In this state, the animals were in first phase of panting characterized by a continuous rapid breathing, as defined by Frankel et al. (1962). The metatarsal skin temperature increased by 8° C, while in the feathered skin an increase in air temperature from 20 to 30° C was shown to induce only a 2° C increment in skin temperature (Richards 1971), demonstrating the role of the unfeathered skin areas in the temperature regulation of the fowl (Steen and Steen 1965; Baudinette et al. 1976).

The 16.5% increment in oxygen consumption which occurred in the hyperthermic animals represents both the energy cost of panting and the Q_{10} effect of the elevated body temperature. This increase in oxygen consumption is small relative to the 60% to 70% increments found in the dog (Males and Dampney 1975) and in the brown neck raven (Marder 1973a). It is, however, similar to that reported for the Bedouin fowl (Marder 1973b) and the sheep (Hales 1973b). The lower P_{CO_2} level represent a CO_2 washout during panting, in spite of the reduced tidal volume known to occur under those conditions (Frankel et al. 1962). Hypocapnia was not, however, accompanied by respiratory alkalosis, as indicated by the normal blood pH values, although panting is associated in various birds with such disturbance of the acid-base balance. This might be due either to differences between species in response (Calder and Schmidt-Nielsen 1968; Marder 1973b) or to the degree of hyperthermia.

The 14% increase in heart rate and the concomitant 10% reduction in arterial blood pressure are typical for hyperthermic fowls (Frankel et al. 1962; Whittow et al. 1964). Such response also prevails in the hyperthermic man, dog and sheep (Thauer 1965; Hales 1973a; Rowell 1974). Cardiac output as determined in 5 normothermic fowls, in which the microspheres were uniformly distributed to upper and lower body reference organs, was 178 $ml \cdot min^{-1} \cdot kg^{-1}$. This value is within the range of cardiac output values reported in other studies (Whittow et al. 1964; Boelkins et al. 1973, 1976). We could estimate the cardiac output in hyperthermic fowls to about 214 $ml \cdot min^{-1} \cdot kg^{-1}$, a 20% increment above the control state. A 27% increase in cardiac output was reported for fowls in which body temperature was brought to 43.4° C (Whittow et al. 1964), as compared to 42.9° C in this study. In terms of the change in cardiac output during heat stress, the fowl seems, therefore, to be in the intermediate range when its response is compared to the 2% increment reported in sheep (Hales 1973a), the 40% increment in dogs (Hales and Dampney 1975) and the 100% increment in man (Rowell 1974) under comparable body temperature elevations.

Blood Flow in Organs Active in Heat Dissipation. The insulative feather layer is not uniform: it is sparser over the ventral side of the main body and the wings (Lucas and Stettenheim 1972). It is significant that the vascular responses over the body correspond to the distribution of insulation: the increase in BF over the skin of the back was only two fold, while in the ventral side a 7-fold increase was found. This would also aid in the dissipation of heat on spreading of the wings, as birds do during heat stress, and probably assist in the warming of eggs during brooding. This adaptive distribution of the vascular response over the body is not found in the dog and sheep, in which only little if any increase in skin BF occurs over the main body during heat stress (Hales 1973a; Hales and Dampney 1975).

The comb and the wattles have an important role in the dissipation of heat in birds in which these organs are developed. During hyperthermia, BF to these organs was increased 4 and 2-fold, respectively. This increment is similar to the 2 – 2.5-fold increase in comb blood flow as determined by a drop counter method (Nolan et al. 1978). Van Handel-Hruska et al. (1977) in an abstract of their work mention that BF to these organs was higher in 32° C acclimated than in 21° C acclimated hens.

Blood flow to the upper respiratory tract – tongue, larynx and trachea – increased during hyperthermia to 320 – 430 % of the control levels. A similar increase in BF to the tongue was recorded in other panting animals like the dog (Ederstrom 1954; Kindermann and Pleschka 1973) and the sheep (Hales 1973a). The regression analyses indicated the increase in BF is proportional to the increment in respiratory frequency. A similar trend was found in the duck (C. Beck, personal communication). These data suggest that vasomotor adjustments are possibly involved in the maintenance of the evaporative capacity of the respiratory tract during panting.

Blood Flow Distribution to Inner Body Organs in Hyperthermia. A main feature of the results was that hyperthermia did not induce a uniform response in all the inner body organs. In the digestive system, a reduction in BF was evident; similar reductions were observed in unanaesthetized mammals (Hales 1973a; Hales and Dampney 1975). The non-significant changes in liver BF and the stability of kidney BF was similar to the observations in the dog under a comparable degree of hyperthermia (Hales and Dampney 1975). This observation should, however, be viewed with caution, considering that this might be partly due to microspheres evading the lower body organs via AVA and being trapped in the portal systems of the kidney and the liver.

Another feature of the data is the nonuniform response of organs within a system. This was true for the muscles, the reproductive system and the digestive system in which a gradient in the response to hyperthermia was evident along the tract. Hyperthermia did not significantly alter BF to the leg muscle, that to the pectoral muscle increased by only a minor degree, while that to the abdominal muscles increased 4-fold. These results are supported by studies which indicated small and inconsistent changes in nonrespiratory muscle BF in the hyperthermic man (Thauer 1965), dog (Hales and Dampney 1975) and sheep (Hales 1973b), as well as the evidence that muscle BF is unaffected by thermal stimulation of the hypothalamus or the spinal cord (Kullman et al. 1970). The different response of the abdominal muscle might be due to its active part in breathing in the fowl and the part played by metabolites released during muscle activity in the regulation of vasomotor function in this tissue (Rowell 1974).

Significant decreases in BF in the reproductive system occurring during heat stress have only recently been documented. Within the reproductive system, the uterus was the most affected by the stress of heat. Studies carried out were restricted to the mammalian uterus only. Roman-Ponce et al. (1978) showed that the vasodilatory effect of estrogen on the ovine uterus is reduced by the stress of heat. Oakes et al. (1976) indicated a synergistic effect of hyperthermia and respiratory alkalosis on uterine BF: their combined action reduced BF by 50 %, while hyperthermia by itself caused only a 25 % reduction. The implications of this reduction in BF on embryonal development were brought up by Leduc (1972), in a study in which a 46 % reduction in placental BF of rabbits was associated with embryonal deaths and increased incidence of impaired embryonal morphogenesis. This study first brought evidence for a significant reduction in BF to the larger ovarian follicles. Such reduction in BF might reduce the availability of gonadotropins to the follicles, as well as to reduce the outflow of ovarian steroids from the ovary to the systemic circulation. The latter possibility is supported by the lower plasma estrogens levels in fowls stressed by heat for a few hours (Wolfenson et al. 1979).

The marked reduction in tibial BF is of marked significance for the fowl, in which the temporary storage of Ca in the bone and its subsequent release during egg shell formation (Mueller 1976) would be dependent upon the rate of blood flow. BF in the cerebrum increased by 40 % during hyperthermia, contrasting the reduction in BF to this organ in mammals (Hales 1973c; Colton and Frankel 1972). In mammals, the response seems to depend on the hypocapnia accompanying the hyperthermal state, since in hyperthermic-normocapnic dogs BF increased by 45 % (Colton and Frankel 1972), similarly to the fowls in this experiment. It is also possible that the cerebral vascular system in the fowl is less sensitive to hypocapnia than that of the mammals.

Evidence for the effect of thermoregulatory function on the distribution of BF between the body periphery and the inner body organs was already brought in mammals in a number of studies in the last years. Spinal heating in cats and rabbits was shown to cause skin vasodilation and mesenteric vasoconstriction, concomitant with a reduction in skin sympathetic activity and its increase in the viscera, with reverse effects on spinal cooling (Walter et al. 1970). Similar results were observed on thermal stimulation of the hypothalamus or the skin in rabbits (Iriki et al. 1971; Riedel et al. 1972). These studies indicate that the

sympathetic control of vasomotor function is modified by the thermoregulatory system. The present study extends these characteristics to the fowl. The large variation in response between organs within a system does indicate that viewing the redistribution of BF as occurring between body periphery and between body core would be an oversimplification of the mechanisms involved.

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