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Thermoregulation in rapid growing broiler chickens is compromised by constraints on radiative and convective cooling performance.

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ABSTRACT

Broiler chickens are selected to undergo a rapid six-week hatch-to-slaughter growth phase to attain large body and muscle mass. Broilers have relatively high resting and locomotor metabolic costs suggesting that adaptive thermoregulatory mechanisms are required to dissipate excess heat. Using thermal imaging in the growing broiler we characterised the trajectory of radiative and convective cooling in still air across broiler development. Scaling of head, tarsus and toe surface area did not deviate from body mass$^{2/3}$ while torso area increased with positive allometry, body mass$^{0.82}$, reflecting increased feather coverage and/or disproportionate abdominal/thoracic growth. Despite relatively increased area, the body became less effective for heat transfer presumably due to increasing feather coverage. Conversely, the magnitude of heat exchange from the distal hindlimbs was improved in larger birds. Overall capacity to transfer heat by convection and radiation in still air was attenuated over development, since the proportion of resting metabolic rate accounted for decreased in standing and sitting postures. This physiological constraint could be ameliorated by increased latent heat transfer or provision of environmental ventilation, which we modelled according to industrial guidelines. Based on models, higher airspeeds coincided with improved convective cooling that assisted in maintaining the proportion of RMR accounted for by convective and radiative heat transfer. These data highlight the potentially adverse thermoregulatory effects of rapid growth rate and body mass increases, which may contribute to the increased sedentary resting and decreased locomotor behaviour observed in large broilers.

Key words: broiler, development, thermoregulation, air velocity, thermal imaging

1. INTRODUCTION

Modern broiler chickens are the product of ongoing artificial selection for rapid growth, high feed conversion efficiency and large meat yield. While highly desirable for efficient meat production, these characteristics are concomitant with health problems, such as cardiorespiratory disease (Wideman, et al., 2007) and leg pathologies (Bradshaw, et al., 2002). The lag between organ and skeletal development related to muscle growth are thought to drive the underlying health related issues (Havenstein, et al., 2003b; Schmidt, et al., 2009; Tickle, et al., 2014). Despite the physiological challenges that have accompanied selection for rapid growth, unlimited access to food to satisfy metabolic demand coupled with closely-controlled environmental conditions ensure that broiler production is profitable and sustained with only limited losses due to disease and premature mortality. The energy balance of broilers is different when compared to other galliform species, with resting metabolic rate (RMR) and the cost of locomotion unusually high across development (Tickle, et al., 2018). Resting posture in birds has a pronounced effect on the magnitude of RMR, and this effect is magnified as body mass increases (Tickle, et al., 2018). Particularly pertinent to broilers is that an increased cost of breathing may account for this observation since the metabolic requirements of respiratory muscles to power movements of the increasing heavy sternal mass are likely to parallel the sternal-weight gain (Tickle, Paxton, Rankin, Hutchinson and Codd, 2014; Tickle, et al., 2010).

The elevated energetic costs of normal physiological functions in the broiler indicate that dissipation of excess heat to the environment is likely to play an increasingly important role for maintaining normal body temperature. Development of large body size and breast muscles (Tickle, Paxton, Rankin, Hutchinson and Codd, 2014) and elevated metabolic rate (Tickle, Hutchinson and Codd, 2018) indicates that broilers may struggle to maintain thermoregulatory balance as they grow because the surface area available for heat exchange via convection, radiation and conduction is expected to increase with body mass$^{2/3}$ (Walsberg and King, 1978). In the commercial farming of broilers, careful control of environmental conditions is required to optimise broiler development, since growth rate and feed efficiency are affected by temperature (Deaton, et al., 1996; Deeb and Cahaner, 2002; Donkoh, 1989; May and Lott, 2000), relative humidity (Yahav, 2000; Yahav, et al., 1995) and airflow (May, et al., 2000; Simmons, et al., 2003; Yahav, et al., 2004; Yahav, et al., 2001). The importance of maintaining optimal environmental conditions is highlighted by the limited broiler energy budget (Tickle, Hutchinson and Codd, 2018), which gives minimal scope for increasing resting metabolic rate to conserve the energetic resources available for growth when thermoregulatory costs are increased. The capacity for maximal metabolic heat dissipation (Speakman and Krol, 2010) may therefore impose a limit on energy utilisation to prevent hyperthermia in broilers.

Previous studies have considered the contribution of thermoregulatory mechanisms in birds, highlighting the role of evaporative (Dawson, 1982), radiative (Greenberg, et al., 2012; Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004), convective (Giloh, et al., 2012) and conductive (Van Sant and Bakken, 2006) cooling. Here, we quantify the changing profile of two mechanisms of heat transfer (radiation and convection) under normal environmental conditions across a size range of broilers and consider the potentially significant effect of resting posture on thermal biology. We hypothesise that sensible heat loss becomes less effective in larger broilers, and that artificial airflow becomes an essential compensatory mechanism. Our data provides a novel perspective on the thermal challenges faced by developing broilers and underscores the coupled importance of physiological constraints and environmental airflow on energetics and behaviour.

2. METHODS

2.1 Animals

Commercial broilers (Cobb® 500) were obtained from a local supplier and housed in pens with *ad libitum* access to poultry pellets and water. Daily recordings of body mass (M_b) and gait (Kestin 1992) were made to monitor development and welfare thereby ensuring that only healthy birds were included in thermal imaging analysis. The sex ratio of hatched broiler chickens has a slight female bias (55% female, 45% male) (Zakaria and Omar, 2013). Experimental procedures and methods were carried out under ethical approval from the University of Manchester Ethics Committee in accordance with the Animal (Scientific Procedures) Act 1986, covered by a Home Office project licence (40/3549) held by Dr. Codd.

2.2 Thermal Imaging

Experiments were conducted on birds (N = 18) from 2 to 6 weeks old (body mass (M_b) range: 256g – 2903g). Single measurements were made using 6 birds whereas multiple (3 or fewer) measurements were conducted on 12 birds across the developmental period. Individual birds were removed from their housing pen and placed in an experimental set-up that consisted of an open-sided Perspex box (volume 61L) resting on a plastic floor. A FLIR i7 (FLIR Systems Inc., Wilsonville, OR, USA) thermal imaging camera (< 0.1°c precision; ± 2% accuracy) was used to photograph the lateral perspective of each bird resting in sitting and standing posture. Thermal images (Fig. 1) were recorded when the birds were seen to rest quietly in a particular posture (Tickle, Hutchinson and Codd, 2018). A portable combined temperature and relative humidity (RH) meter (± 0.1°c / 1% RH) was used to record ambient conditions during each trial. Temperature and humidity (Fig. 2) were controlled in line with industry guidelines (Cobb-Vantress® "Broiler Management Guide" revised 2012) and therefore assumed to fall within the thermoneutral zone for broilers (Donkoh, 1989; Meltzer, 1983). Air speed was not measured but assumed to be minimal because the birds were enclosed within a laboratory. Consequently, no measure of evaporative or conductive heat transfer was made in this study so an estimate of total heat transfer is not possible. Rather, the contribution of two principal thermoregulatory mechanisms under favourable environmental conditions are presented. Comparison of sensible heat loss with RMR allows an estimation of the magnitude of combined evaporative and conductive heat loss which we assume accounts for the remainder.

Linear measurements (mm) of the head, body, tarsus and toes 1-4 were taken after each trial, enabling calculation of surface area by assuming each segment's geometry was equivalent to three-dimensional shapes (Yahav, et al., 2005). The head was modelled as a sphere, the body (i.e. thorax and abdomen) as a prolate spheroid and the legs and toes as open-ended cylinders (to account for surface area only, and therefore disregarding the internal anatomy that would otherwise be included). Linear regression on log–transformed data was used to calculate scaling relationships for surface area over development.

2.3 Calculation of Heat Transfer

Thermal images were processed in the FLIR Tools program (version 5.11). Photographs were analysed by overlaying 2-dimensional shapes to each body component (e.g. an oval was fitted to the torso). The mean temperature within each shape was calculated in the FLIR Tools program. Metabolic heat loss (Watts, W) was estimated as the sum of radiative and convective heat transfer.

2.3.1 Calculated Radiative Heat Transfer

Radiative heat transfer (q_{rad}; W) from the bird to the environment was calculated for each body segment as:

$$q_{\mathrm{rad}} = A\sigma\varepsilon_{\mathrm{a}}\left(T_{\mathrm{b}}^{4} - T_{\mathrm{a}}^{4}\right) \quad (1)$$

where A is body segment surface area (m^2), σ is the Stefan-Boltzmann constant (relates radiative energy emittance to absolute temperature; 5.67×10^{-8} W m^{-2} K^{-1}), ε_a is emissivity of bird feathers (assumed as 0.95; (Ward, et al., 1999)), T_b is the segment mean surface temperature and T_a is ambient air temperature (K).

2.3.2 Modelled Convective Heat Transfer

A temperature gradient between the bird and surrounding air underlies the heat transferred by convection (q_{conv}; W) and can be modelled as:

$$q_{\mathrm{conv}} = Ah_{\mathrm{c}}(T_{\mathrm{b}} - T_{\mathrm{a}}) \quad (2)$$

where h_c is the convective heat transfer coefficient (W m^{-2} K^{-1}):

$$h_c = \mathrm{Nu}\frac{\mathrm{k}}{\mathrm{d}} \quad (3)$$

and Nu is the dimensionless Nusselt number, k is the thermal conductivity of air (W m^{-1} K^{-1}) and d is the characteristic dimension of each body segment (Mitchell, 1976). The Nusselt number can be considered a function of the dimensionless Reynolds (Re) and Prandtl (Pr) numbers:

$$\mathrm{Re} = \frac{\mathrm{ud}}{\mathrm{v}} \tag{4}$$

where *u* is airspeed ($\mathrm{ms^{-1}}$) and *v* is the kinematic viscosity of air ($\mathrm{m^2\ s^{-1}}$).

$$\mathrm{Pr} = \frac{\mathrm{v}}{\mathrm{k}} \tag{5}$$

Nu is determined according to Re and Pr as:

$$\mathrm{Nu} = \mathrm{d}\ (\mathrm{Pr} \times \mathrm{Re}) \tag{6}$$

Convective heat transfer was therefore calculated for each body segment based upon its specific geometry (Yahav, Shinder, Tanny and Cohen, 2005). Given the effective lack of air movement during imaging, heat loss was modelled for birds according to ventilatory guidelines produced for broiler farms rearing Cobb 500 broilers (Cobb-Vantress® "Broiler Management Guide" revised 2012). Implementation of airflow guidelines contributes to establishing environmental conditions that allow for optimal broiler production. Airspeed was modelled as 0.300, 0.500, 0.875 $\mathrm{ms^{-1}}$ for birds with measured body mass as expected for ages between 0-14, 15-21 and 22-28 days, respectively. A range of simulated airspeeds was implemented for older, heavier birds according to the suggested ventilation conditions (1.750-3.00 $\mathrm{ms^{-1}}$) provided in the Broiler Management Guide. Convective heat transfer was also calculated as by free convection, i.e. in still air. In this case, Nu is a function of the Grashof number (Gr):

$$\frac{\mathrm{Gr} = \mathrm{agd}^3\,(\mathrm{T_b} - \mathrm{T_a})}{\mathrm{v}^2} \tag{5}$$

where *a* is the coefficient of thermal expansion (K^{-1}) and *g* is acceleration due to gravity (9.81 m s^{-2}). The relationships between Nu, Gr and the geometry of body segments were taken into account when estimating convective heat exchange (Monteith and Unsworth, 1990; Morgan, 1975).

2.4 Resting metabolic rate

Comparable broiler RMR data (Tickle, Hutchinson and Codd, 2018) was transformed from $V\square_{\mathrm{CO2}}$ (ml min^{-1}) to metabolic power (W) using the thermal equivalent in Brody (1945), assuming a respiratory exchange ratio (RER) of 0.85. Scaling analyses were completed by fitting ordinary least-squares regression to log-transformed RMR, q_{rad} and q_{conv} data. Statistical analyses were completed in SPSS v.24 (IBM SPSS Statistics for Windows, Version 24.0.0.1 Armonk, NY: IBM Corp.) and PAST v.2.17c (Hammer, et al., 2001). Details of linear and polynomial regression equations and statistics are provided in the Supplementary Material.

3. RESULTS

3.1 Morphology

Head, tarsus and toe surface areas scaled geometrically, i.e. $M_b^{0.67}$ (Table 1). In contrast, body surface area developed with positive allometry ($M_b^{0.82}$) which was indicative of a disproportionate increase in thoracic and/or abdominal size and/or plumage volume over development. Regression on M_b (kg) indicated that the proportional surface area (M_b =

2.635*body + 80.002; $r^2 = 0.463$, $F = 23.268$, $P < 0.001$) accounted for by the body surface accounted for 80.6% in a 0.25kg bird rising to 87.5% in a 2.90kg bird (Supplementary Material). Therefore, proportion of overall surface area accounted for by unfeathered skin was reduced over development.

3.2 Heat loss

Mean toe surface temperature increased with body mass, body surface temperature decreased, and head and tarsus temperature were unchanged (Figs. 1, 2a & 2c). The difference between ambient and body surface temperature reduced as birds grew larger, while the inverse relationship was detected for head, tarsus and toes (Fig. 2b & 2d). Total sensible heat loss in still air decreased as a proportion of RMR over development (Fig. 3 & Table 2), indicating that convection and radiation were not adequate to maintain a neutral energy balance in the sitting bird in still air (Fig. 4a). In contrast, radiative and convective cooling in a standing posture was sufficient to dissipate total metabolic heat production until the birds weighed in excess of approximately 1.00kg (Fig. 4b). Developmental trajectories of radiative and convective heat loss were similar (comparison of regression slopes by ANCOVA: $F = 0.507$; $P = 0.480$) in the sitting and standing bird (Fig. 3c), although the magnitude of heat exchange was higher during standing (comparison of intercepts by ANCOVA: $F = 20.570$; $P < 0.001$).

Simulated air movement improved convective heat transfer in sitting (Fig. 4a) and standing birds (Fig. 4b). Comparison of the scaling relationship between body mass and total sensible heat transfer indicated that the magnitude of heat loss increases with airspeed and allows the proportion of sensible heat transfer to remain constant over development (Table 2). In still air, heat transfer scales with negative allometry indicating that the risk of heat stress increases as birds grow.

4. DISCUSSION

In this study, we have identified how convective and radiative cooling mechanisms contribute to heat exchange in the broiler over development, and the potentially important thermoregulatory role of posture. Our hypothesis that heavier birds have impaired radiative and convective cooling mechanisms was supported by comparison of thermal imaging and respirometry data, and posture appears to exert a determining role in the magnitude of heat loss. Large body size coupled with a high resting metabolic rate present a significant challenge to the thermal physiology of the modern broiler and this restriction on adequate heat loss may constrain other functions including locomotor activity.

There was a change in the spatial distribution of surface temperature (Cangar, et al., 2008) over development (Figs. 1 & 3). As birds grew larger, body surface temperature decreased while toe temperature increased (Figs. 3). In accordance with earlier research (Cangar, Aerts, Buyse and Berckmans, 2008) and regardless of resting posture, the disparity between ambient and surface temperature reduced for the body while the difference increased for head, tarsus and toes, indicating a switch in the relative importance of thermoregulatory surfaces over development. Sensible heat loss in still air was inadequate to maintain adequate thermoregulation over development (Fig. 4), consistent with a reduction in proportional surface area (Table 1) and increased feathering to provide greater thermal insulation in older birds (Herreid and Kessel, 1967). Postural-dependent thermoregulation was inferred because sitting contributes to reduced heat loss (Fig. 4a) when compared to standing (Fig. 4b), a finding consistent with previous reports of RMR in birds (Tickle, Hutchinson and Codd, 2018; Tickle, et al., 2012; van Kampen, 1976). It is striking that resting in a sitting position is used for proportionately longer periods of the day given that heavier birds, which are potentially subject to greater thermal stress, tend to sit for longer than lighter birds (Bokkers and Koene, 2003; Tickle, Hutchinson and Codd, 2018). A number of factors, including leg pathologies (Paxton, et al., 2014) and restriction on daily metabolic rate (Tickle, Hutchinson and Codd, 2018) are likely to determine resting posture, but a limit on heat dissipation by convection and radiation due to morphological changes may constrain overall energy expenditure so that heavier broilers are unable to undergo exertion, or else risk hyperthermia (Speakman and Krol, 2010; Tickle, Hutchinson and Codd, 2018), especially if the cooling capacity of other heat exchange mechanisms is insufficient. Specific guidelines for ventilation in commercial production facilities (Cobb-Vantress® "Broiler Management Guide" revised 2012) highlight the necessity of applying engineering solutions to this biological problem. Older, heavy broilers are unable to dissipate heat at the required rate in still air using convection and radiation alone (Figs. 4 & 5) and require formation of convection currents to ensure adequate thermoregulation and weight-gain performance. Elevated mortality due to high ambient temperature coupled with inadequate ventilation (Knezacek, et al., 2010; Warriss, et al., 2005) illustrates the critical function of airflow to thermoregulation in large broilers. An unknown variable in this study is the contribution of latent heat transfer, which is expected to increase in importance when convection and radiation become less effective (Richards, 1970). Evaporative cooling via panting can be used to supplement other thermoregulatory mechanisms when broilers are placed under considerable heat stress (Borges, et al., 2004) and is therefore highly likely to have occurred in the broilers used in this study. While we did not observe panting/gular flutter during experiments, the possibility of increased evaporative cooling cannot be dismissed; rather, it is likely that this process was progressively upregulated in larger birds due to the greater disparity between RMR and measured heat transfer in still air (Fig.4). It is important to note that for optimal body mass gain a significant contribution of evaporative cooling should be avoided in broilers due to the energetic expenditure associated with panting that may reduce the efficiency of heat transfer (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004) Interestingly, in light of recent findings we speculate that this important function may be compromised in broilers due to the relatively slow development of musculoskeletal components of the respiratory system. A relatively reduced muscle mass in larger birds indicates that the power available to maintain increased respiratory rate during panting may be reduced over development (Tickle and Codd, 2009; Tickle, Paxton, Rankin, Hutchinson and Codd, 2014). Our results show that environmental ventilation to improve convective cooling is necessary for heat dissipation (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004), becoming more significant as the broilers reach slaughter-weight of approximately 2.5 – 3.0kg (Fig. 5). In line with existing data (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004), the magnitude of convective heat transfer is related to airspeed (Fig. 5) thereby enabling the overall proportion of RMR accounted for by sensible heat loss to remain effectively constant (at least in sitting birds, Fig. 5a) over development, under controlled conditions (Fig. 5). Interestingly, airflow alone did not prevent a reduction in the relative contribution of sensible heat transfer during standing in the largest broilers (Fig. 5b) indicating that an alternative thermoregulatory strategy was necessary e.g. evaporative cooling (Borges et al., 2004). This finding corresponds to previous reports of reduced activity in larger broilers (Bokkers and Koene, 2003; Tickle, Hutchinson and Codd, 2018) and provides evidence for a thermoregulatory constraint on posture and locomotion.

The contribution to sensible heat loss from each body segment varied across development. As expected, there was a proportional decrease in the heat transfer from head, body and tarsus relative to body mass over development (Table 2), consistent with a reduction in relative surface area available for thermoregulation (Table 1). However, toe q_{conv} increased with positive allometry (Table 2), indicating that, in still air, cooling via the toes is important for heat transfer and may partially compensate for the less effective cooling from other body segments. Analysis of the scaling relationship between sensible heat loss and body surface area indicated a reducing magnitude of sensible heat loss via the head and body over development, while cooling via the tarsus and toes increased at a faster rate than surface area (Table 3), highlighting the importance of the distal hindlimb as a conduit for heat transfer (Macleod and Hocking, 1993; Steen and Steen, 1965). The negatively allometric relationship between surface area and heat loss from the head and body is potentially due to increasing feather coverage providing better surface insulation (Wolf and Walsberg, 2000), and highlights the reduction in thermoregulatory capacity via sensible heat transfer from these relatively large anatomical components as the birds grow.

An improvement in convective cooling with airspeed suggests that there is potential for an adverse effect on thermoregulation as birds grow and effective stocking density increases. High stocking density is associated with increased body and surface temperatures and relatively poor broiler performance (Abudabos, et al., 2013), which may be due in part to an increased thermoregulatory burden. Birds become more closely spaced with increasing body size potentially causing a reduction in circulating airflow and therefore compromising the efficacy of convective heat transfer. Behavioural changes, including a shift in favoured resting posture (Bokkers and Koene, 2003; Tickle, Hutchinson and Codd, 2018) may therefore be used by broilers to balance metabolic heat production and dissipation.

Our analyses considered the effects of simulated rather than experimentally modified ventilation, so no consideration was given to the effect of airspeed on radiative heat transfer, although no significant effect on radiative cooling performance was expected in light of existing work showing this mechanism to be insensitive to airflow (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004). Furthermore, our assumption that surface temperature was unaffected by ventilation is a potential source of error since relatively small changes (<10%) in leg surface temperature are related to air velocity up to 3.1ms^{-1} in broilers (Furlan, et al., 2000). Nevertheless, our data confirm previous reports (Yahav, Shinder, Tanny and Cohen, 2005; Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004) that identified the significance of convective and radiative thermoregulatory mechanisms in broilers. Following the end of experiments, thermal imaging often revealed localised heat transfer via conduction to the substrate (i.e. elevated surface temperature of substrate), but we were unable to quantify the magnitude of this transfer because broiler surface area in contact with the ground proved difficult to measure accurately. While heat transfer by conduction contributed to broiler thermoregulation in our experiments (Gerken, et al., 2006), the substrates (e.g. wood shavings, rice husks etc.) on which broilers are routinely reared are unlikely to confer a favourable surface on account of low thermal conductivity, meaning that any heat conduction is minimal. Despite the unknown components of evaporative and conductive heat transfer , broiler sensible heat loss in still air accounts for between 52-100% of RMR measured during standing (Tickle, Hutchinson and Codd, 2018). Clearly, a margin of error is implicit in our calculation of sensible heat loss since addition of unmeasured latent and conductive heat transfer would result in total heat exchange in excess of RMR (Fig. 4). Measurement of RMR while birds underwent thermal imaging may have reduced the level of this error because broilers with seemingly impossible sensible heat values greater than 100% RMR potentially had a relatively elevated RMR compared to expected values (Tickle, Hutchinson and Codd, 2018). Nevertheless, a comparable study in canaries (*Serinus canaria*) quantified sensible heat loss in a standing posture as 77% of RMR (Ward and Slater, 2005), highlighting that despite considerable disparity in M_b (canary $M_{b:}$ 21.5±1.5g) and morphology, sensible heat loss in birds is the main thermoregulatory mechanism under normal conditions. Interestingly, broilers with relatively low M_b can transfer a greater proportion of total metabolic heat production via sensible heat loss when compared to the canary, and this is likely a consequence of incomplete feather development (Wolf and Walsberg, 2000).

The data presented in this paper highlight the effectiveness of thermal imaging techniques for understanding animal behaviour and the relationship with the environment. Using this approach, we have presented evidence for a thermoregulatory constraint on broiler physiology and this may be a determining factor for reducing activity levels over development.

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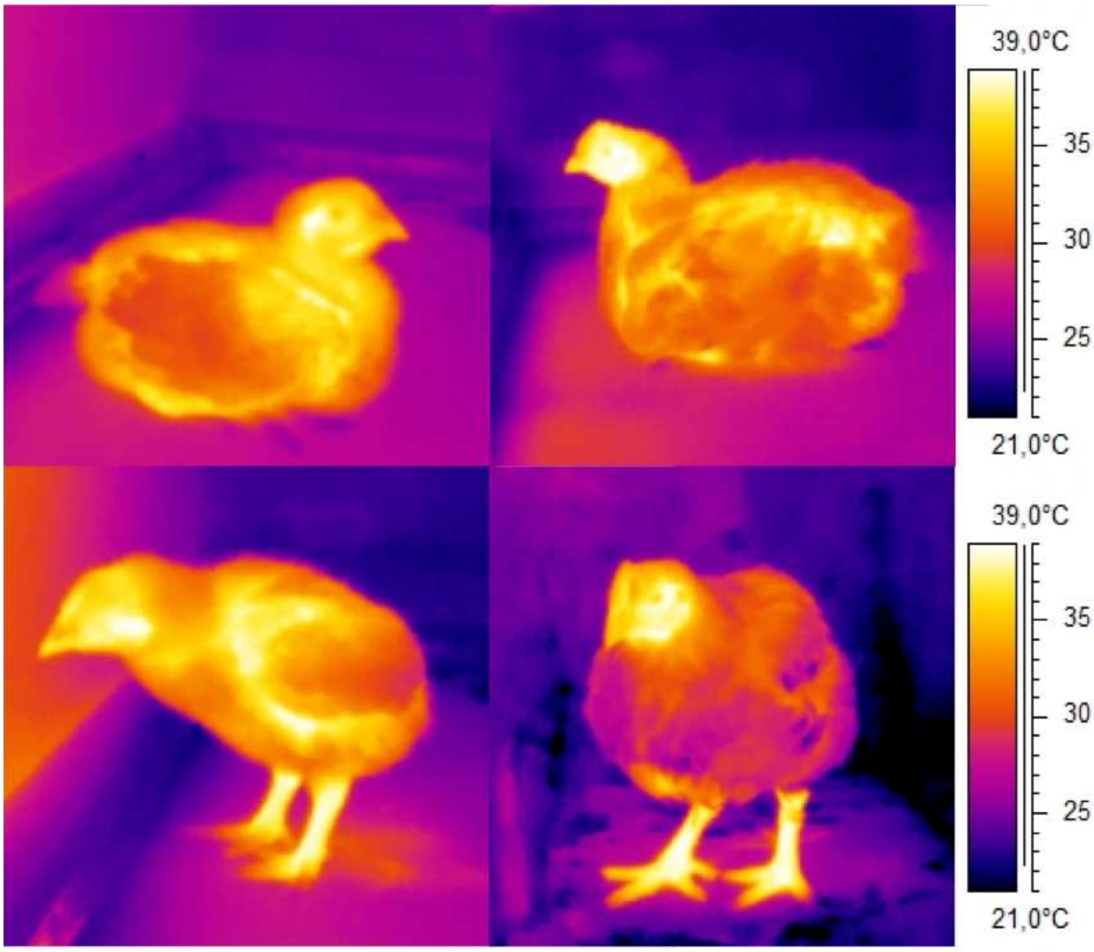
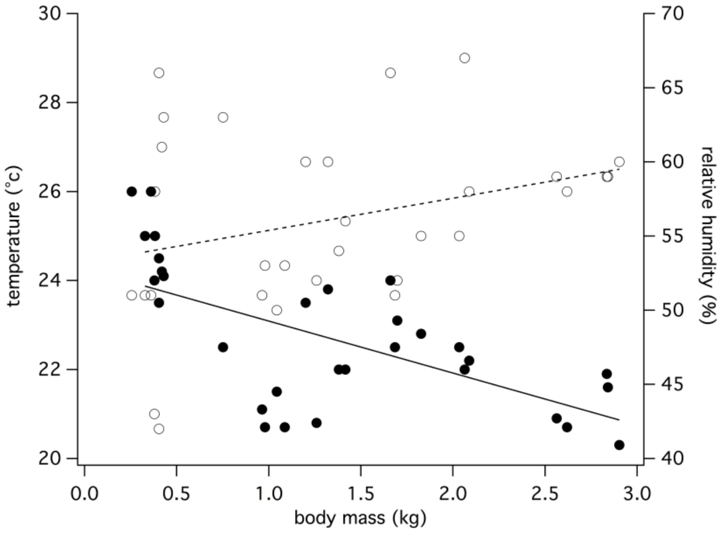
Figure 1: Representative thermal images of low and high body mass broilers.



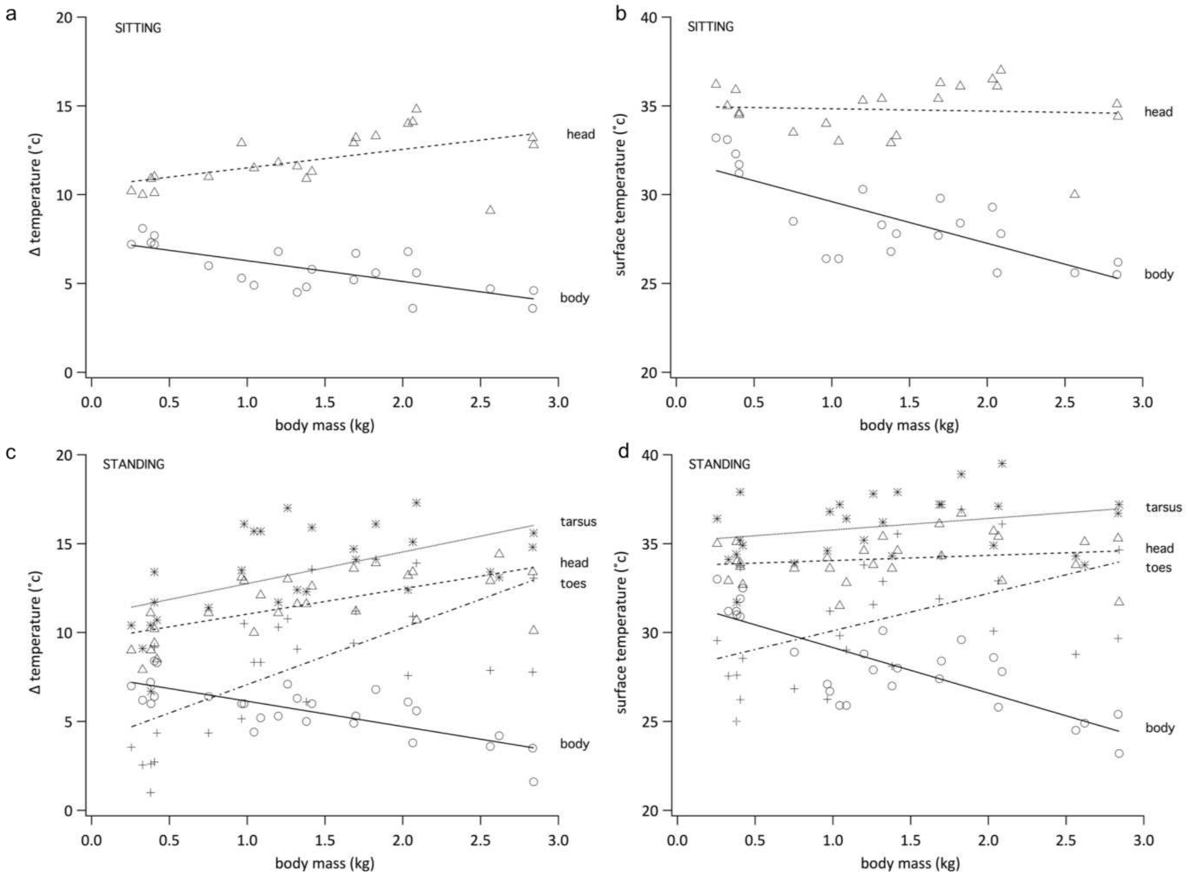
Typical thermal images of broilers in standing and sitting postures. Compare the high surface temperature of the smaller (0.26kg) bird (a, b) with a larger (2.0kg) broiler (c, d) that has better feather insulation. Ambient temperature/relative humidity at time of imaging were (a & b: 26.0°c / 51%; c & d: 22.0°c / 55%).

Figure 2: Ambient conditions during thermal imaging.



Ambient temperature during thermal imaging was reduced over the growing period (y = -1.272x+24.461; F = 23.209; R^2 = 0.445; $P < 0.001$) while there was a simultaneous non-significant trend for increasing relative humidity (y = 2.309x + 52.935; F = 3.319; R^2 =0.103; P = 0.079).

Figure 3: Body surface temperature in the growing broiler



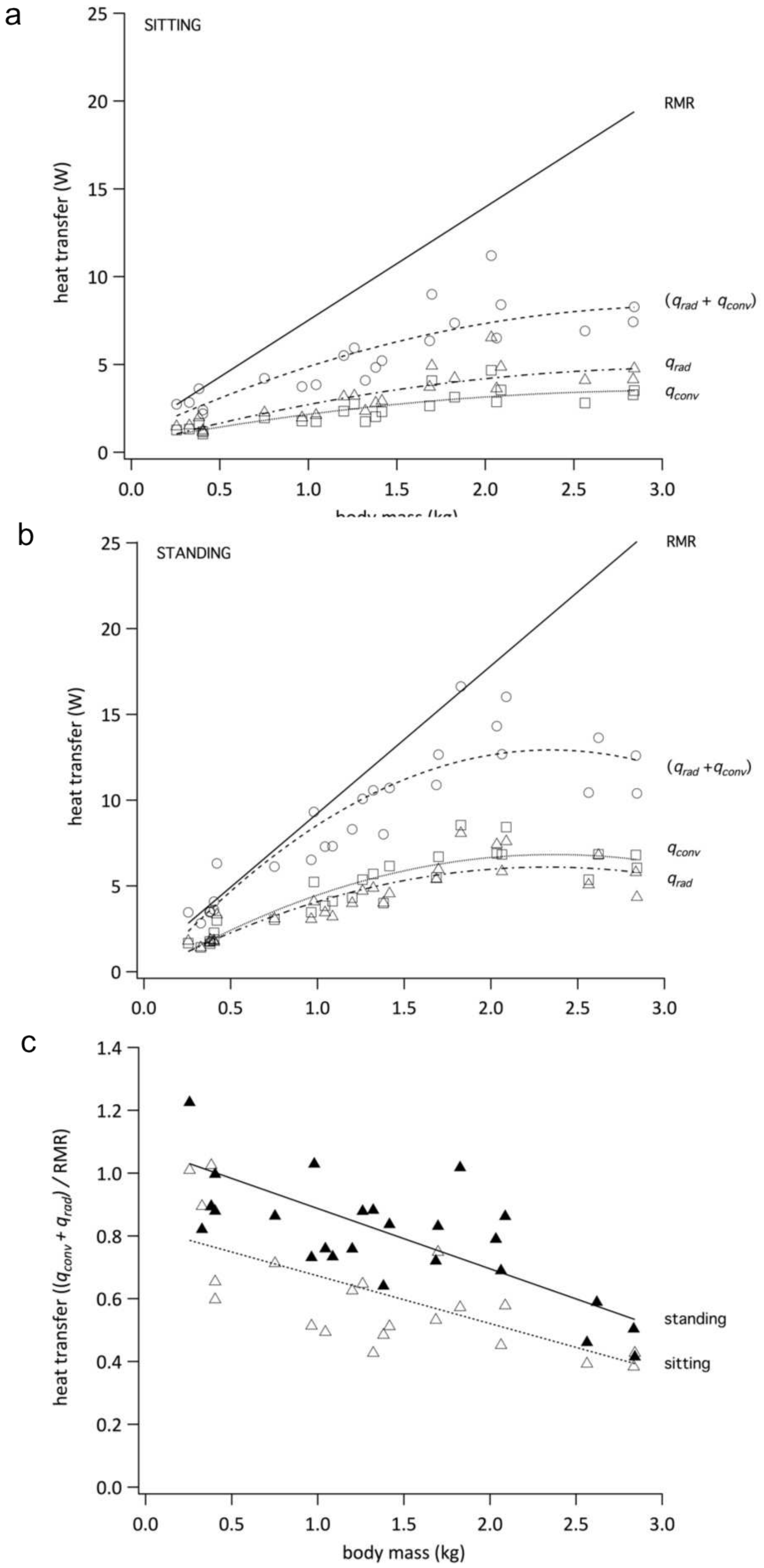
Surface temperature and difference between ambient and surface temperature (Δ temperature) of the growing broiler in sitting (a, c) and standing (b, d) postures. Symbols denote distinct body segments:

circle/solid line: **body** (*surface temperature*: sitting: P < 0.001; standing: P < 0.001; *Δ temperature*: sitting: P < 0.001; standing: P < 0.001)

triangle/dashed line: **head** (*surface temperature*: sitting: P = 0.765; standing: P = 0.350; *Δ temperature*: sitting: P = 0.009; standing: P < 0.001)

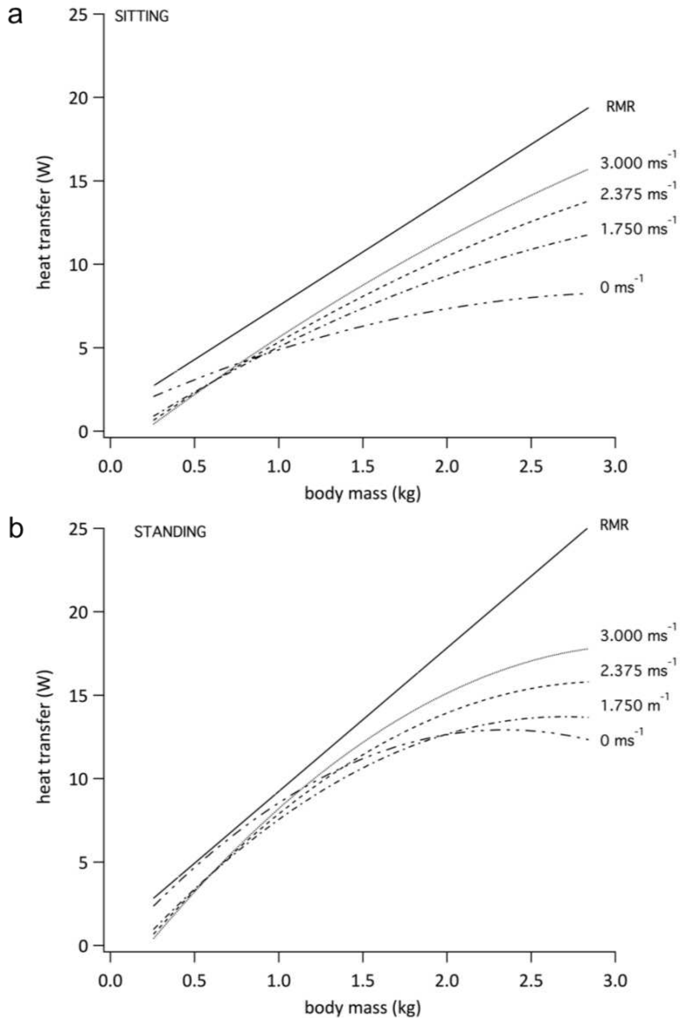
asterisk/dotted line : **tarsus** (*surface temperature*: standing: P = 0.143 *Δ temperature*: standing: P = 0.002) cross/dot-dash line: **combined toes** (*surface temperature*: standing: $P = 0.010$; Δ *temperature*: standing: $P < 0.001$)

Figure 4: Convective and radiative heat transfer over development



The contribution of total radiative (triangles; dot-dash line) and convective (crosses; dotted line) cooling in the sitting (a) and standing (b) broiler. Polynomial curves ($P < 0.001$) are plotted for radiative (triangles; dot-dash line), convective (crosses; dotted line) and combined heat transfer (circles; dashed line). Metabolic rate for broilers as measured using respirometry (Tickle et al., 2018) is plotted as the solid line. Sensible heat loss in still air as a proportion of RMR across development (c) highlights the decreasing contribution over development *of* $q_{rad}+q_{conv}$ in standing (filled triangles, solid line: $R^2 = 0.492$; $P < 0.001$) and sitting (open triangles, dashed line: y = $R^2 = 0.428$; $P = 0.001$). Each marker represents an individual measurement

Figure 5: Modelled heat loss with increasing airspeed



Sensible heat loss ($q_{rad} + q_{conv}$) from sitting (a) and standing (b) birds in still air (dot-dot-dash line) and under simulated airflow conditions. Estimated sensible heat transfer from broilers older than 28 days (>1.524kg) is shown for airspeeds of 1.750 (dot-dash line)), 2.375 (dashed line) and 3.000 ms^{-1} (dotted line). All polynomial fits were significant ($P < 0.001$). RMR is also shown (solid line; sitting: $y = 6.452*M_b +1.059$; standing: $y = 8.6074*M_b + 0.6187$).

	m	*c*	*95% CI*	*R^2*	*F*	*P*
Head	3.686	0.644	0.512 - 0.775	0.781	100.129	< 0.001
Torso	4.869	0.824	0.734 - 0.915	0.925	347.49	< 0.001
Tarsus	3.626	0.653	0.569 - 0.737	0.901	253.92	< 0.001
Toe1	2.800	0.595	0.505 - 0.684	0.869	184.984	< 0.001
Toe2	3.072	0.628	0.542 - 0.714	0.888	222.385	< 0.001
Toe3	3.32	0.651	0.575 - 0.728	0.916	304.416	< 0.001
Toe4	3.100	0.574	0.476 - 0.671	0.833	145.59	< 0.001
Sum of toes	3.716	0.620	0.559 - 0.682	0.938	426.423	< 0.001

Table 1: Development of body segment surface areas (mm^2) in proportion to body mass (kg) as described by regression analysis performed on log-transformed data. Equations are in the form $y = mx^c$

			m	*c*	*95% CI*	*R^2*	*F*	*P*
Sitting	*qconv*	Head	0.399	0.710	0.512 - 0.909	0.747	56.201	< 0.001
		Body	0.224	0.436	0.294 - 0.578	0.685	41.225	< 0.001
	qrad	Head	0.787	0.427	0.230 - 0.624	0.521	20.653	< 0.001
		Body	0.389	0.601	0.460 - 0.741	0.809	80.480	< 0.001
Standing	*qconv*	Head	-0.416	0.757	0.614 - 0.900	0.819	118.852	< 0.001
		Body	0.201	0.351	0.157 - 0.544	0.544	13.91	0.001
		Tarsus	0.040	0.843	0.700 - 0.986	0.856	148.154	< 0.001
		Toes	-0.221	1.416	1.087 - 1.745	0.759	78.753	< 0.001
	qrad	Head	-0.808	0.327	0.149 - 0.506	0.364	14.283	0.001
		Body	0.369	0.528	0.352 - 0.704	0.605	38.277	< 0.001
		Tarsus	-0.485	0.841	0.703 - 0.980	0.862	156.256	< 0.001
		Toes	-0.736	1.350	1.074 - 1.626	0.802	101.455	< 0.001

Table 2: Developmental change in magnitude of heat transfer (W) with body mass (kg) over development. Regression ($y = mx^c$)was performed on log-transformed data.

			m	*c*	*95% CI*	R^2	*F*	*P*
Sitting	q_{conv}	Head	2.009	1.041	0.931 - 1.152	0.953	389.223	< 0.001
		Body	0.819	0.523	0.382 - 0.664	0.760	60.236	< 0.001
	q_{rad}	Head	0.833	0.701	0.551 - 0.852	0.834	95.387	< 0.001
		Body	1.204	0.717	0.596 - 0.838	0.889	152.772	< 0.001
Standing	q_{conv}	Head	2.117	1.096	0.964 - 1.228	0.921	291.756	< 0.001
		Body	0.703	0.444	0.242 - 0.647	0.449	20.365	< 0.001
		Tarsus	3.063	1.275	1.111 - 1.438	0.912	258.574	< 0.001
		Toes	4.246	1.943	1.434 - 2.451	0.712	61.915	< 0.001
	q_{rad}	Head	0.503	0.568	0.370 - 0.766	0.583	34.961	< 0.001
		Body	1.107	0.653	0.486 - 0.820	0.723	65.152	< 0.001
		Tarsus	2.568	1.287	1.155 - 1.420	0.941	401.263	< 0.001
		Toes	3.555	1.866	1.440 - 2.293	0.764	81.078	< 0.001

Table 3: Developmental change in magnitude of heat transfer (W) with surface area (m^2) over development. Regression ($y = mx^c$) was performed on log-transformed data. Heat transfer from the tarsus and toes increases at a greater rate than surface area (95% CI does not overlap isometry, i.e. $c = 1$). In contrast, the head (q_{rad}) and body (q_{conv} and q_{rad}) become less effective conduits for sensible heat transfer as surface area increases.