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4 1 **Thermoregulation in rapid growing broiler chickens is compromised by constraints on**  
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6 2 **radiative and convective cooling performance.**  
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63 26 ABSTRACT  
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68 28 Broiler chickens are selected to undergo a rapid six-week hatch-to-slaughter growth  
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70 29 phase to attain large body and muscle mass. Broilers have relatively high resting and locomotor  
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72 30 metabolic costs suggesting that adaptive thermoregulatory mechanisms are required to  
73  
74 31 dissipate excess heat. Using thermal imaging in the growing broiler we characterised the  
75  
76 32 trajectory of radiative and convective cooling in still air across broiler development. Scaling of  
77  
78 33 head, tarsus and toe surface area did not deviate from body mass<sup>2/3</sup> while torso area increased  
79  
80 34 with positive allometry, body mass<sup>0.82</sup>, reflecting increased feather coverage and/or  
81  
82 35 disproportionate abdominal/thoracic growth. Despite relatively increased area, the body  
83  
84 36 became less effective for heat transfer presumably due to increasing feather coverage.  
85  
86 37 Conversely, the magnitude of heat exchange from the distal hindlimbs was improved in larger  
87  
88 38 birds. Overall capacity to transfer heat by convection and radiation in still air was attenuated  
89  
90 39 over development, since the proportion of resting metabolic rate accounted for decreased in  
91  
92 40 standing and sitting postures. This physiological constraint could be ameliorated by increased  
93  
94 41 latent heat transfer or provision of environmental ventilation, which we modelled according to  
95  
96 42 industrial guidelines. Based on models, higher airspeeds coincided with improved convective  
97  
98 43 cooling that assisted in maintaining the proportion of RMR accounted for by convective and  
99  
100 44 radiative heat transfer. These data highlight the potentially adverse thermoregulatory effects of  
101  
102 45 rapid growth rate and body mass increases, which may contribute to the increased sedentary  
103  
104 46 resting and decreased locomotor behaviour observed in large broilers.  
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108 47  
109  
110 48 Key words: broiler, development, thermoregulation, air velocity, thermal imaging  
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123 51 1. INTRODUCTION  
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128 53 Modern broiler chickens are the product of ongoing artificial selection for rapid growth,  
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130 54 high feed conversion efficiency and large meat yield. While highly desirable for efficient meat  
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132 55 production, these characteristics are concomitant with health problems, such as  
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134 56 cardiorespiratory disease (Wideman, et al., 2007) and leg pathologies (Bradshaw, et al., 2002).  
135  
136 57 The lag between organ and skeletal development related to muscle growth are thought to drive  
137  
138 58 the underlying health related issues (Havenstein, et al., 2003b; Schmidt, et al., 2009; Tickle, et  
139  
140 59 al., 2014). Despite the physiological challenges that have accompanied selection for rapid  
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142 60 growth, unlimited access to food to satisfy metabolic demand coupled with closely-controlled  
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144 61 environmental conditions ensure that broiler production is profitable and sustained with only  
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146 62 limited losses due to disease and premature mortality. The energy balance of broilers is  
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148 63 different when compared to other galliform species, with resting metabolic rate (RMR) and the  
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150 64 cost of locomotion unusually high across development (Tickle, et al., 2018). Resting posture  
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152 65 in birds has a pronounced effect on the magnitude of RMR, and this effect is magnified as body  
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154 66 mass increases (Tickle, et al., 2018). Particularly pertinent to broilers is that an increased cost  
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156 67 of breathing may account for this observation since the metabolic requirements of respiratory  
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158 68 muscles to power movements of the increasing heavy sternal mass are likely to parallel the  
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160 69 sternal-weight gain (Tickle, Paxton, Rankin, Hutchinson and Codd, 2014; Tickle, et al., 2010).  
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162  
163 70 The elevated energetic costs of normal physiological functions in the broiler indicate  
164  
165 71 that dissipation of excess heat to the environment is likely to play an increasingly important  
166  
167 72 role for maintaining normal body temperature. Development of large body size and breast  
168  
169 73 muscles (Tickle, Paxton, Rankin, Hutchinson and Codd, 2014) and elevated metabolic rate  
170  
171 74 (Tickle, Hutchinson and Codd, 2018) indicates that broilers may struggle to maintain  
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173 75 thermoregulatory balance as they grow because the surface area available for heat exchange  
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183 76 via convection, radiation and conduction is expected to increase with body mass<sup>2/3</sup> (Walsberg  
184  
185 77 and King, 1978). In the commercial farming of broilers, careful control of environmental  
186  
187 78 conditions is required to optimise broiler development, since growth rate and feed efficiency  
188  
189 79 are affected by temperature (Deaton, et al., 1996; Deeb and Cahaner, 2002; Donkoh, 1989;  
190  
191 80 May and Lott, 2000), relative humidity (Yahav, 2000; Yahav, et al., 1995) and airflow (May,  
192  
193 81 et al., 2000; Simmons, et al., 2003; Yahav, et al., 2004; Yahav, et al., 2001). The importance  
194  
195 82 of maintaining optimal environmental conditions is highlighted by the limited broiler energy  
196  
197 83 budget (Tickle, Hutchinson and Codd, 2018), which gives minimal scope for increasing resting  
198  
199 84 metabolic rate to conserve the energetic resources available for growth when thermoregulatory  
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201 85 costs are increased. The capacity for maximal metabolic heat dissipation (Speakman and Krol,  
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203 86 2010) may therefore impose a limit on energy utilisation to prevent hyperthermia in broilers.  
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207 87 Previous studies have considered the contribution of thermoregulatory mechanisms in  
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209 88 birds, highlighting the role of evaporative (Dawson, 1982), radiative (Greenberg, et al., 2012;  
210  
211 89 Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004), convective (Giloh, et al., 2012)  
212  
213 90 and conductive (Van Sant and Bakken, 2006) cooling. Here, we quantify the changing profile  
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215 91 of two mechanisms of heat transfer (radiation and convection) under normal environmental  
216  
217 92 conditions across a size range of broilers and consider the potentially significant effect of  
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219 93 resting posture on thermal biology. We hypothesise that sensible heat loss becomes less  
220  
221 94 effective in larger broilers, and that artificial airflow becomes an essential compensatory  
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223 95 mechanism. Our data provides a novel perspective on the thermal challenges faced by  
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225 96 developing broilers and underscores the coupled importance of physiological constraints and  
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227 97 environmental airflow on energetics and behaviour.  
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## 231 232 99 2. METHODS 233 234 235 100

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243 101 2.1 Animals  
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245 102  
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247 103 Commercial broilers (Cobb® 500) were obtained from a local supplier and housed in  
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249 pens with *ad libitum* access to poultry pellets and water. Daily recordings of body mass ( $M_b$ )  
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251 and gait (Kestin 1992) were made to monitor development and welfare thereby ensuring that  
252 105  
253 only healthy birds were included in thermal imaging analysis. The sex ratio of hatched broiler  
254 106  
255 chickens has a slight female bias (55% female, 45% male) (Zakaria and Omar, 2013).  
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257 Experimental procedures and methods were carried out under ethical approval from the  
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259 University of Manchester Ethics Committee in accordance with the Animal (Scientific  
260 109  
261 Procedures) Act 1986, covered by a Home Office project licence (40/3549) held by Dr. Codd.  
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266 112 2.2 Thermal Imaging  
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271 114 Experiments were conducted on birds (N = 18) from 2 to 6 weeks old (body mass ( $M_b$ )  
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273 115 range: 256g – 2903g). Single measurements were made using 6 birds whereas multiple (3 or  
274  
275 116 fewer) measurements were conducted on 12 birds across the developmental period. Individual  
276  
277 117 birds were removed from their housing pen and placed in an experimental set-up that consisted  
278  
279 118 of an open-sided Perspex box (volume 61L) resting on a plastic floor. A FLIR i7 (FLIR Systems  
280  
281 119 Inc., Wilsonville, OR, USA) thermal imaging camera (< 0.1°C precision; ± 2% accuracy) was  
282  
283 120 used to photograph the lateral perspective of each bird resting in sitting and standing posture.  
284  
285 121 Thermal images (Fig. 1) were recorded when the birds were seen to rest quietly in a particular  
286  
287 122 posture (Tickle, Hutchinson and Codd, 2018). A portable combined temperature and relative  
288  
289 123 humidity (RH) meter (± 0.1°C / 1% RH) was used to record ambient conditions during each  
290  
291 124 trial. Temperature and humidity (Fig. 2) were controlled in line with industry guidelines (Cobb-  
292  
293 125 Vantress® “Broiler Management Guide” revised 2012) and therefore assumed to fall within  
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301 |  
302  
303 126 the thermoneutral zone for broilers (Donkoh, 1989; Meltzer, 1983). Air speed was not  
304  
305 127 measured but assumed to be minimal because the birds were enclosed within a laboratory.  
306  
307 128 Consequently, no measure of evaporative or conductive heat transfer was made in this study  
308  
309 129 so an estimate of total heat transfer is not possible. Rather, the contribution of two principal  
310  
311 130 thermoregulatory mechanisms under favourable environmental conditions are presented.  
312  
313 131 Comparison of sensible heat loss with RMR allows an estimation of the magnitude of combined  
314  
315 132 evaporative and conductive heat loss which we assume accounts for the remainder.  
316  
317

318 133 Linear measurements (mm) of the head, body, tarsus and toes 1-4 were taken after each  
319  
320 134 trial, enabling calculation of surface area by assuming each segment's geometry was equivalent  
321  
322 135 to three-dimensional shapes (Yahav, et al., 2005). The head was modelled as a sphere, the body  
323  
324 136 (i.e. thorax and abdomen) as a prolate spheroid and the legs and toes as open-ended cylinders  
325  
326 137 (to account for surface area only, and therefore disregarding the internal anatomy that would  
327  
328 138 otherwise be included). Linear regression on log-transformed data was used to calculate  
329  
330 139 scaling relationships for surface area over development.  
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333 140

### 335 141 2.3 Calculation of Heat Transfer

337 142

339 143 Thermal images were processed in the FLIR Tools program (version 5.11). Photographs were  
340  
341 144 analysed by overlaying 2-dimensional shapes to each body component (e.g. an oval was fitted  
342  
343 145 to the torso). The mean temperature within each shape was calculated in the FLIR Tools  
344  
345 146 program. Metabolic heat loss (Watts, W) was estimated as the sum of radiative and convective  
346  
347 147 heat transfer.  
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350 148

#### 352 149 2.3.1 Calculated Radiative Heat Transfer

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363 151 Radiative heat transfer ( $q_{rad}$ ; W) from the bird to the environment was calculated for each  
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365 152 body segment as:

$$367 \quad 153 \quad 368 \quad 154 \quad 369 \quad 154 \quad 370 \quad 154 \quad 371 \quad 154 \quad 372 \quad 155 \quad 373 \quad 155 \quad 374 \quad 156 \quad 375 \quad 156 \quad 376 \quad 157 \quad 377 \quad 157 \quad 378 \quad 158 \quad 379 \quad 158 \quad 380 \quad 159 \quad 381 \quad 159 \quad 382 \quad 160 \quad 383 \quad 160 \quad 384 \quad 161 \quad 385 \quad 161 \quad 386 \quad 162 \quad 387 \quad 162 \quad 388 \quad 163 \quad 389 \quad 163 \quad 390 \quad 164 \quad 391 \quad 164 \quad 392 \quad 165 \quad 393 \quad 165 \quad 394 \quad 166 \quad 395 \quad 166 \quad 396 \quad 166 \quad 397 \quad 167 \quad 398 \quad 167 \quad 399 \quad 168 \quad 400 \quad 168 \quad 401 \quad 169 \quad 402 \quad 169 \quad 403 \quad 170 \quad 404 \quad 170 \quad 405 \quad 171 \quad 406 \quad 171 \quad 407 \quad 171 \quad 408 \quad 172 \quad 409 \quad 172 \quad 410 \quad 173 \quad 411 \quad 173 \quad 412 \quad 174 \quad 413 \quad 174 \quad 414 \quad 174 \quad 415 \quad 174 \quad 416 \quad 174 \quad 417 \quad 174 \quad 418 \quad 174 \quad 419 \quad 174 \quad 420 \quad 174$$
$$q_{rad} = A\sigma\epsilon_a(T_b^4 - T_a^4) \quad (1)$$

374 156 where  $A$  is body segment surface area ( $m^2$ ),  $\sigma$  is the Stefan-Boltzmann constant (relates  
375 156 radiative energy emittance to absolute temperature;  $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-1}$ ),  $\epsilon_a$  is emissivity of  
376 157 bird feathers (assumed as 0.95; (Ward, et al., 1999)),  $T_b$  is the segment mean surface  
377 157 temperature and  $T_a$  is ambient air temperature (K).

### 385 161 2.3.2 Modelled Convective Heat Transfer

389 163 A temperature gradient between the bird and surrounding air underlies the heat transferred by  
390 164 convection ( $q_{conv}$ ; W) and can be modelled as:

$$395 \quad 166 \quad 396 \quad 166 \quad 397 \quad 167 \quad 398 \quad 167 \quad 399 \quad 168 \quad 400 \quad 168 \quad 401 \quad 169 \quad 402 \quad 169 \quad 403 \quad 170 \quad 404 \quad 170 \quad 405 \quad 171 \quad 406 \quad 171 \quad 407 \quad 171 \quad 408 \quad 172 \quad 409 \quad 172 \quad 410 \quad 173 \quad 411 \quad 173 \quad 412 \quad 174 \quad 413 \quad 174 \quad 414 \quad 174 \quad 415 \quad 174 \quad 416 \quad 174 \quad 417 \quad 174 \quad 418 \quad 174 \quad 419 \quad 174 \quad 420 \quad 174$$
$$q_{conv} = Ah_c(T_b - T_a) \quad (2)$$

402 169 where  $h_c$  is the convective heat transfer coefficient ( $\text{W m}^{-2} \text{ K}^{-1}$ ):

$$406 \quad 171 \quad 407 \quad 171 \quad 408 \quad 172 \quad 409 \quad 172 \quad 410 \quad 173 \quad 411 \quad 173 \quad 412 \quad 174 \quad 413 \quad 174 \quad 414 \quad 174 \quad 415 \quad 174 \quad 416 \quad 174 \quad 417 \quad 174 \quad 418 \quad 174 \quad 419 \quad 174 \quad 420 \quad 174$$
$$h_c = \text{Nu} \frac{k}{d} \quad (3)$$

411 173 and  $\text{Nu}$  is the dimensionless Nusselt number,  $k$  is the thermal conductivity of air ( $\text{W m}^{-1} \text{ K}^{-1}$ )  
412 174 and  $d$  is the characteristic dimension of each body segment (Mitchell, 1976). The Nusselt

421 |  
422  
423 175 number can be considered a function of the dimensionless Reynolds (Re) and Prandtl (Pr)  
424  
425 176 numbers:

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430 178 
$$\text{Re} = \frac{ud}{\nu} \quad (4)$$
  
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432 179  
433  
434 180 where  $u$  is airspeed ( $\text{ms}^{-1}$ ) and  $\nu$  is the kinematic viscosity of air ( $\text{m}^2 \text{s}^{-1}$ ).  
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437 181  
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439 182 
$$\text{Pr} = \frac{\nu}{k} \quad (5)$$
  
440

441 183  
442  
443 184 Nu is determined according to Re and Pr as:

445 185  
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447  
448 186 
$$\text{Nu} = d (\text{Pr} \times \text{Re}) \quad (6)$$
  
449

450 187  
451  
452 188 Convective heat transfer was therefore calculated for each body segment based upon its  
453  
454 189 specific geometry (Yahav, Shinder, Tanny and Cohen, 2005). Given the effective lack of air  
455  
456 190 movement during imaging, heat loss was modelled for birds according to ventilatory guidelines  
457  
458 191 produced for broiler farms rearing Cobb 500 broilers (Cobb-Vantress® “Broiler Management  
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460 192 Guide” revised 2012). Implementation of airflow guidelines contributes to establishing  
461  
462 193 environmental conditions that allow for optimal broiler production. Airspeed was modelled as  
463  
464 194 0.300, 0.500, 0.875  $\text{ms}^{-1}$  for birds with measured body mass as expected for ages between 0-  
465  
466 195 14, 15-21 and 22-28 days, respectively. A range of simulated airspeeds was implemented for  
467  
468 196 older, heavier birds according to the suggested ventilation conditions (1.750-3.00  $\text{ms}^{-1}$ )  
469  
470 197 provided in the Broiler Management Guide. Convective heat transfer was also calculated as by  
471  
472 198 free convection, i.e. in still air. In this case, Nu is a function of the Grashof number (Gr):  
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475  
476 199

$$\text{Gr} = \frac{\text{agd}^3 (\text{T}_b - \text{T}_a)}{\nu^2} \quad (5)$$

where  $a$  is the coefficient of thermal expansion ( $\text{K}^{-1}$ ) and  $g$  is acceleration due to gravity ( $9.81 \text{ m s}^{-2}$ ). The relationships between  $\text{Nu}$ ,  $\text{Gr}$  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  $V_{\text{CO}_2}$  ( $\text{ml min}^{-1}$ ) 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,  $q_{\text{rad}}$  and  $q_{\text{conv}}$  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 ( $M_b =$

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542  
543 225  $2.635 \cdot \text{body} + 80.002$ ;  $r^2 = 0.463$ ,  $F = 23.268$ ,  $P < 0.001$ ) accounted for by the body surface  
544  
545 226 accounted for 80.6% in a 0.25kg bird rising to 87.5% in a 2.90kg bird (Supplementary Material).  
546  
547 227 Therefore, proportion of overall surface area accounted for by unfeathered skin was reduced  
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549 228 over development.  
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### 553 230 3.2 Heat loss

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558 232 Mean toe surface temperature increased with body mass, body surface temperature  
559  
560 233 decreased, and head and tarsus temperature were unchanged (Figs. 1, 2a & 2c). The difference  
561  
562 234 between ambient and body surface temperature reduced as birds grew larger, while the inverse  
563  
564 235 relationship was detected for head, tarsus and toes (Fig. 2b & 2d). Total sensible heat loss in  
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566 236 still air decreased as a proportion of RMR over development (Fig. 3 & Table 2), indicating that  
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568 237 convection and radiation were not adequate to maintain a neutral energy balance in the sitting  
569  
570 238 bird in still air (Fig. 4a). In contrast, radiative and convective cooling in a standing posture was  
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572 239 sufficient to dissipate total metabolic heat production until the birds weighed in excess of  
573  
574 240 approximately 1.00kg (Fig. 4b). Developmental trajectories of radiative and convective heat  
575  
576 241 loss were similar (comparison of regression slopes by ANCOVA:  $F = 0.507$ ;  $P = 0.480$ ) in the  
577  
578 242 sitting and standing bird (Fig. 3c), although the magnitude of heat exchange was higher during  
579  
580 243 standing (comparison of intercepts by ANCOVA:  $F = 20.570$ ;  $P < 0.001$ ).

581  
582  
583 244 Simulated air movement improved convective heat transfer in sitting (Fig. 4a) and  
584  
585 245 standing birds (Fig. 4b). Comparison of the scaling relationship between body mass and total  
586  
587 246 sensible heat transfer indicated that the magnitude of heat loss increases with airspeed and  
588  
589 247 allows the proportion of sensible heat transfer to remain constant over development (Table 2).  
590  
591 248 In still air, heat transfer scales with negative allometry indicating that the risk of heat stress  
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593 249 increases as birds grow.  
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#### 4. DISCUSSION

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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.

261

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

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662  
663 275 to greater thermal stress, tend to sit for longer than lighter birds (Bokkers and Koene, 2003;  
664  
665 276 Tickle, Hutchinson and Codd, 2018). A number of factors, including leg pathologies (Paxton,  
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667  
668 277 et al., 2014) and restriction on daily metabolic rate (Tickle, Hutchinson and Codd, 2018) are  
669  
670 278 likely to determine resting posture, but a limit on heat dissipation by convection and radiation  
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672 279 due to morphological changes may constrain overall energy expenditure so that heavier broilers  
673  
674 280 are unable to undergo exertion, or else risk hyperthermia (Speakman and Krol, 2010; Tickle,  
675  
676 281 Hutchinson and Codd, 2018), especially if the cooling capacity of other heat exchange  
677  
678 282 mechanisms is insufficient. Specific guidelines for ventilation in commercial production  
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680 283 facilities (Cobb-Vantress® “Broiler Management Guide” revised 2012) highlight the necessity  
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682 284 of applying engineering solutions to this biological problem. Older, heavy broilers are unable  
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684  
685 285 to dissipate heat at the required rate in still air using convection and radiation alone (Figs. 4 &  
686  
687 286 5) and require formation of convection currents to ensure adequate thermoregulation and  
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689 287 weight-gain performance. Elevated mortality due to high ambient temperature coupled with  
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691 288 inadequate ventilation (Knezacek, et al., 2010; Warriss, et al., 2005) illustrates the critical  
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693 289 function of airflow to thermoregulation in large broilers. An unknown variable in this study is  
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695 290 the contribution of latent heat transfer, which is expected to increase in importance when  
696  
697 291 convection and radiation become less effective (Richards, 1970). Evaporative cooling via  
698  
699 292 panting can be used to supplement other thermoregulatory mechanisms when broilers are  
700  
701  
702 293 placed under considerable heat stress (Borges, et al., 2004) and is therefore highly likely to  
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704 294 have occurred in the broilers used in this study. While we did not observe panting/gular flutter  
705  
706 295 during experiments, the possibility of increased evaporative cooling cannot be dismissed;  
707  
708 296 rather, it is likely that this process was progressively upregulated in larger birds due to the  
709  
710 297 greater disparity between RMR and measured heat transfer in still air (Fig.4). It is important to  
711  
712 298 note that for optimal body mass gain a significant contribution of evaporative cooling should  
713  
714 299 be avoided in broilers due to the energetic expenditure associated with panting that may reduce  
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723 300 the efficiency of heat transfer (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004)  
724  
725 301 Interestingly, in light of recent findings we speculate that this important function may be  
726  
727 302 compromised in broilers due to the relatively slow development of musculoskeletal  
728  
729 303 components of the respiratory system. A relatively reduced muscle mass in larger birds  
730  
731 304 indicates that the power available to maintain increased respiratory rate during panting may be  
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733 305 reduced over development (Tickle and Codd, 2009; Tickle, Paxton, Rankin, Hutchinson and  
734  
735 306 Codd, 2014). Our results show that environmental ventilation to improve convective cooling  
736  
737 307 is necessary for heat dissipation (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004),  
738  
739 308 becoming more significant as the broilers reach slaughter-weight of approximately 2.5 – 3.0kg  
740  
741 309 (Fig. 5). In line with existing data (Yahav, Straschnow, Luger, Shinder, Tanny and Cohen,  
742  
743 310 2004), the magnitude of convective heat transfer is related to airspeed (Fig. 5) thereby enabling  
744  
745 311 the overall proportion of RMR accounted for by sensible heat loss to remain effectively  
746  
747 312 constant (at least in sitting birds, Fig. 5a) over development, under controlled conditions (Fig.  
748  
749 313 5). Interestingly, airflow alone did not prevent a reduction in the relative contribution of  
750  
751 314 sensible heat transfer during standing in the largest broilers (Fig. 5b) indicating that an  
752  
753 315 alternative thermoregulatory strategy was necessary e.g. evaporative cooling (Borges et al.,  
754  
755 316 2004). This finding corresponds to previous reports of reduced activity in larger broilers  
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757 317 (Bokkers and Koene, 2003; Tickle, Hutchinson and Codd, 2018) and provides evidence for a  
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759 318 thermoregulatory constraint on posture and locomotion.

760  
761 319 The contribution to sensible heat loss from each body segment varied across  
762  
763 320 development. As expected, there was a proportional decrease in the heat transfer from head,  
764  
765 321 body and tarsus relative to body mass over development (Table 2), consistent with a reduction  
766  
767 322 in relative surface area available for thermoregulation (Table 1). However, toe  $q_{conv}$  increased  
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769 323 with positive allometry (Table 2), indicating that, in still air, cooling via the toes is important  
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771 324 for heat transfer and may partially compensate for the less effective cooling from other body  
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783 325 segments. Analysis of the scaling relationship between sensible heat loss and body surface area  
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785 326 indicated a reducing magnitude of sensible heat loss via the head and body over development,  
786  
787 327 while cooling via the tarsus and toes increased at a faster rate than surface area (Table 3),  
788  
789 328 highlighting the importance of the distal hindlimb as a conduit for heat transfer (Macleod and  
790  
791 329 Hocking, 1993; Steen and Steen, 1965). The negatively allometric relationship between surface  
792  
793 330 area and heat loss from the head and body is potentially due to increasing feather coverage  
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795 331 providing better surface insulation (Wolf and Walsberg, 2000), and highlights the reduction in  
796  
797 332 thermoregulatory capacity via sensible heat transfer from these relatively large anatomical  
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799 333 components as the birds grow.  
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802 334 An improvement in convective cooling with airspeed suggests that there is potential for  
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804 335 an adverse effect on thermoregulation as birds grow and effective stocking density increases.  
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806 336 High stocking density is associated with increased body and surface temperatures and relatively  
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808 337 poor broiler performance (Abudabos, et al., 2013), which may be due in part to an increased  
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810 338 thermoregulatory burden. Birds become more closely spaced with increasing body size  
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812 339 potentially causing a reduction in circulating airflow and therefore compromising the efficacy  
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814 340 of convective heat transfer. Behavioural changes, including a shift in favoured resting posture  
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816 341 (Bokkers and Koene, 2003; Tickle, Hutchinson and Codd, 2018) may therefore be used by  
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818 342 broilers to balance metabolic heat production and dissipation.  
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821 343 Our analyses considered the effects of simulated rather than experimentally modified  
822  
823 344 ventilation, so no consideration was given to the effect of airspeed on radiative heat transfer,  
824  
825 345 although no significant effect on radiative cooling performance was expected in light of  
826  
827 346 existing work showing this mechanism to be insensitive to airflow (Yahav, Straschnow, Luger,  
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829 347 Shinder, Tanny and Cohen, 2004). Furthermore, our assumption that surface temperature was  
830  
831 348 unaffected by ventilation is a potential source of error since relatively small changes (<10%)  
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833 349 in leg surface temperature are related to air velocity up to  $3.1\text{ms}^{-1}$  in broilers (Furlan, et al.,  
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842  
843 350 2000). Nevertheless, our data confirm previous reports (Yahav, Shinder, Tanny and Cohen,  
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845 351 2005; Yahav, Straschnow, Luger, Shinder, Tanny and Cohen, 2004) that identified the  
846  
847 352 significance of convective and radiative thermoregulatory mechanisms in broilers. Following  
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849 353 the end of experiments, thermal imaging often revealed localised heat transfer via conduction  
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851 354 to the substrate (i.e. elevated surface temperature of substrate), but we were unable to quantify  
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853 355 the magnitude of this transfer because broiler surface area in contact with the ground proved  
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855 356 difficult to measure accurately. While heat transfer by conduction contributed to broiler  
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857 357 thermoregulation in our experiments (Gerken, et al., 2006), the substrates (e.g. wood shavings,  
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859 358 rice husks etc.) on which broilers are routinely reared are unlikely to confer a favourable  
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861 359 surface on account of low thermal conductivity, meaning that any heat conduction is minimal.  
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863 360 Despite the unknown components of evaporative and conductive heat transfer, broiler sensible  
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865 361 heat loss in still air accounts for between 52-100% of RMR measured during standing (Tickle,  
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867 362 Hutchinson and Codd, 2018). Clearly, a margin of error is implicit in our calculation of sensible  
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869 363 heat loss since addition of unmeasured latent and conductive heat transfer would result in total  
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871 364 heat exchange in excess of RMR (Fig. 4). Measurement of RMR while birds underwent thermal  
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873 365 imaging may have reduced the level of this error because broilers with seemingly impossible  
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875 366 sensible heat values greater than 100% RMR potentially had a relatively elevated RMR  
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877 367 compared to expected values (Tickle, Hutchinson and Codd, 2018). Nevertheless, a  
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879 368 comparable study in canaries (*Serinus canaria*) quantified sensible heat loss in a standing  
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881 369 posture as 77% of RMR (Ward and Slater, 2005), highlighting that despite considerable  
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883 370 disparity in  $M_b$  (canary  $M_b$ :  $21.5 \pm 1.5$ g) and morphology, sensible heat loss in birds is the main  
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885 371 thermoregulatory mechanism under normal conditions. Interestingly, broilers with relatively  
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887 372 low  $M_b$  can transfer a greater proportion of total metabolic heat production via sensible heat  
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889 373 loss when compared to the canary, and this is likely a consequence of incomplete feather  
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891 374 development (Wolf and Walsberg, 2000).  
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903 375 The data presented in this paper highlight the effectiveness of thermal imaging  
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905 376 techniques for understanding animal behaviour and the relationship with the environment.  
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907 377 Using this approach, we have presented evidence for a thermoregulatory constraint on broiler  
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909 378 physiology and this may be a determining factor for reducing activity levels over development.  
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## 912 379 913 914 380 5. ACKNOWLEDGEMENTS 915

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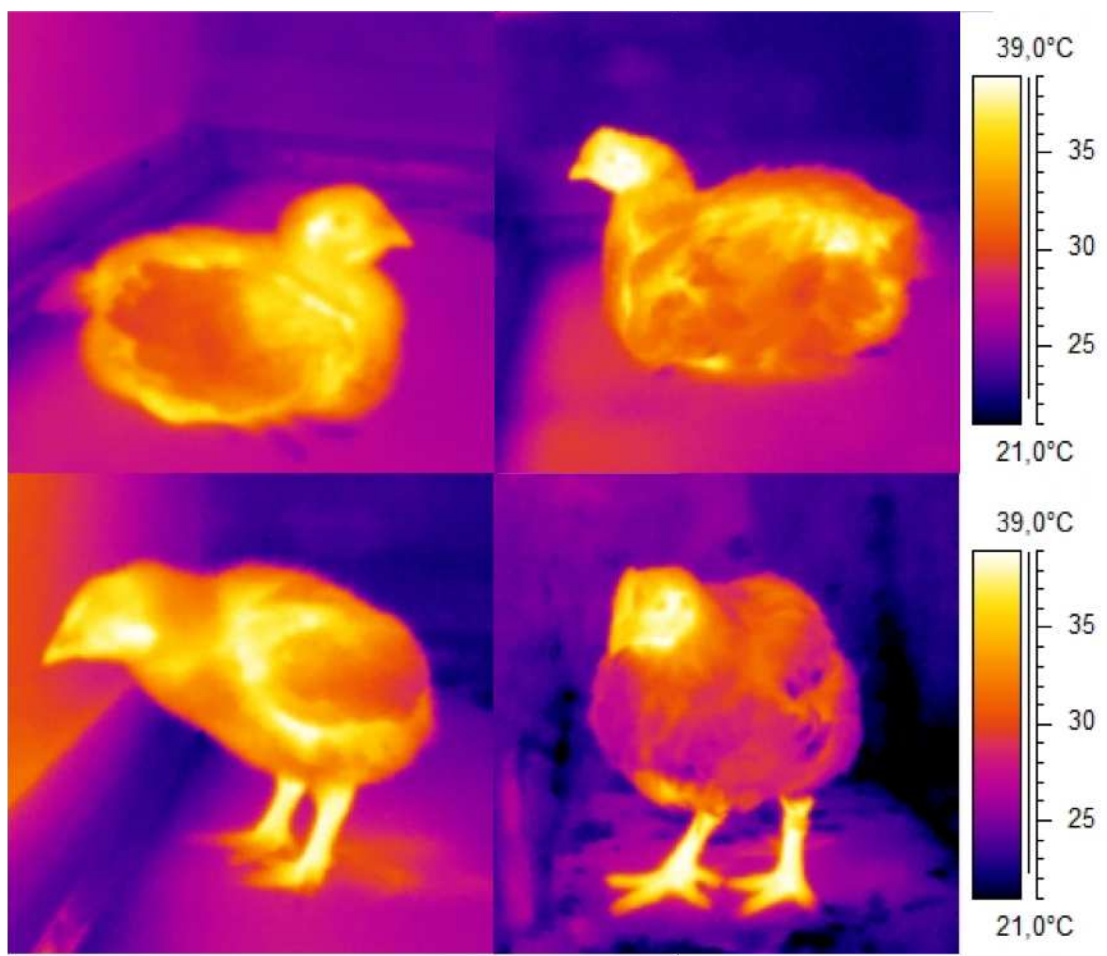
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508 Figure 1: Representative thermal images of low and high body mass broilers.  
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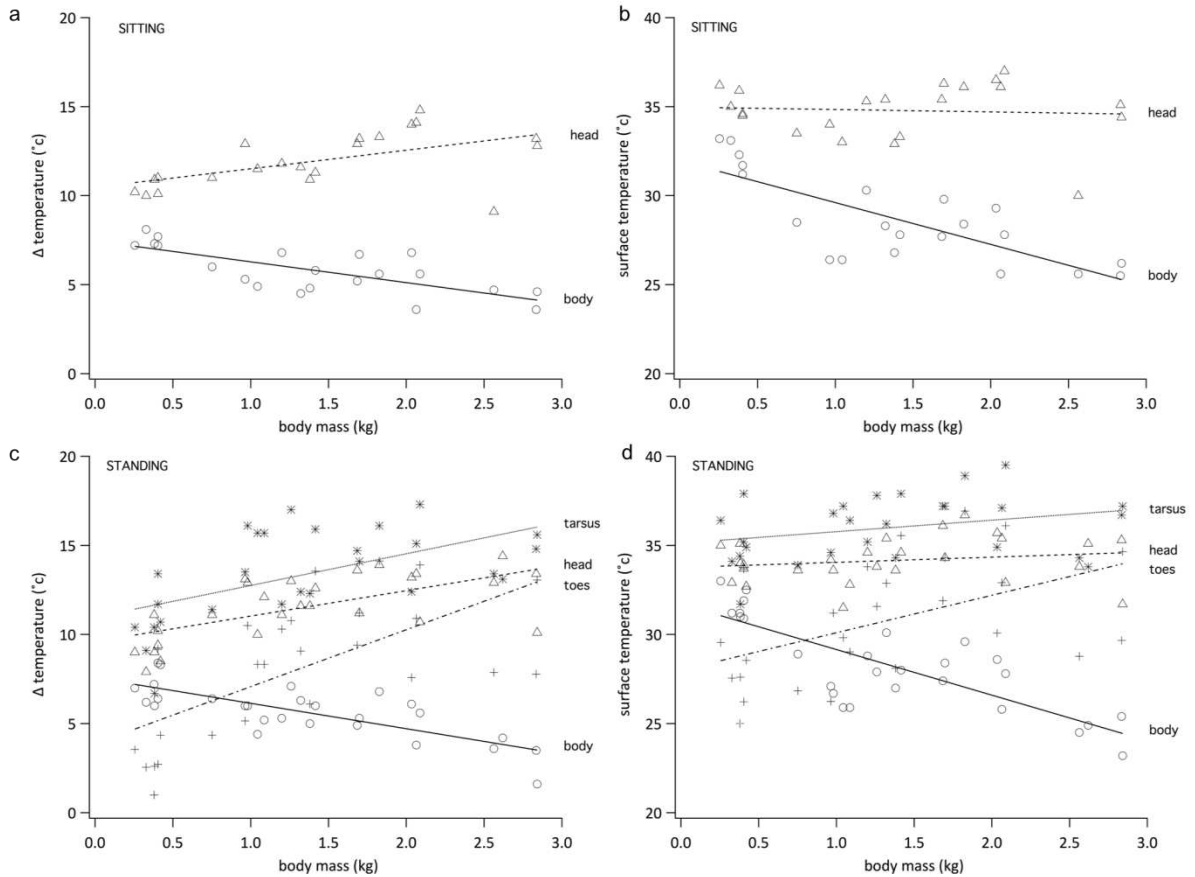
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511 Typical thermal images of broilers in standing and sitting postures. Compare the high surface  
512 temperature of the smaller (0.26kg) bird (a, b) with a larger (2.0kg) broiler (c, d) that has  
513 better feather insulation. Ambient temperature/relative humidity at time of imaging were (a &  
514 b: 26.0°C / 51%; c & d: 22.0°C / 55%).



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Figure 3: Body surface temperature in the growing broiler



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525 Surface temperature and difference between ambient and surface temperature ( $\Delta$  temperature)

526 of the growing broiler in sitting (a, c) and standing (b, d) postures. Symbols denote distinct

527 body segments:

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529 circle/solid line: **body** (*surface temperature*: sitting:  $P < 0.001$ ; standing:  $P < 0.001$ ;  $\Delta$

530 *temperature*: sitting:  $P < 0.001$ ; standing:  $P < 0.001$ )

531

532 triangle/dashed line: **head** (*surface temperature*: sitting:  $P = 0.765$ ; standing:  $P = 0.350$ ;  $\Delta$

533 *temperature*: sitting:  $P = 0.009$ ; standing:  $P < 0.001$ )

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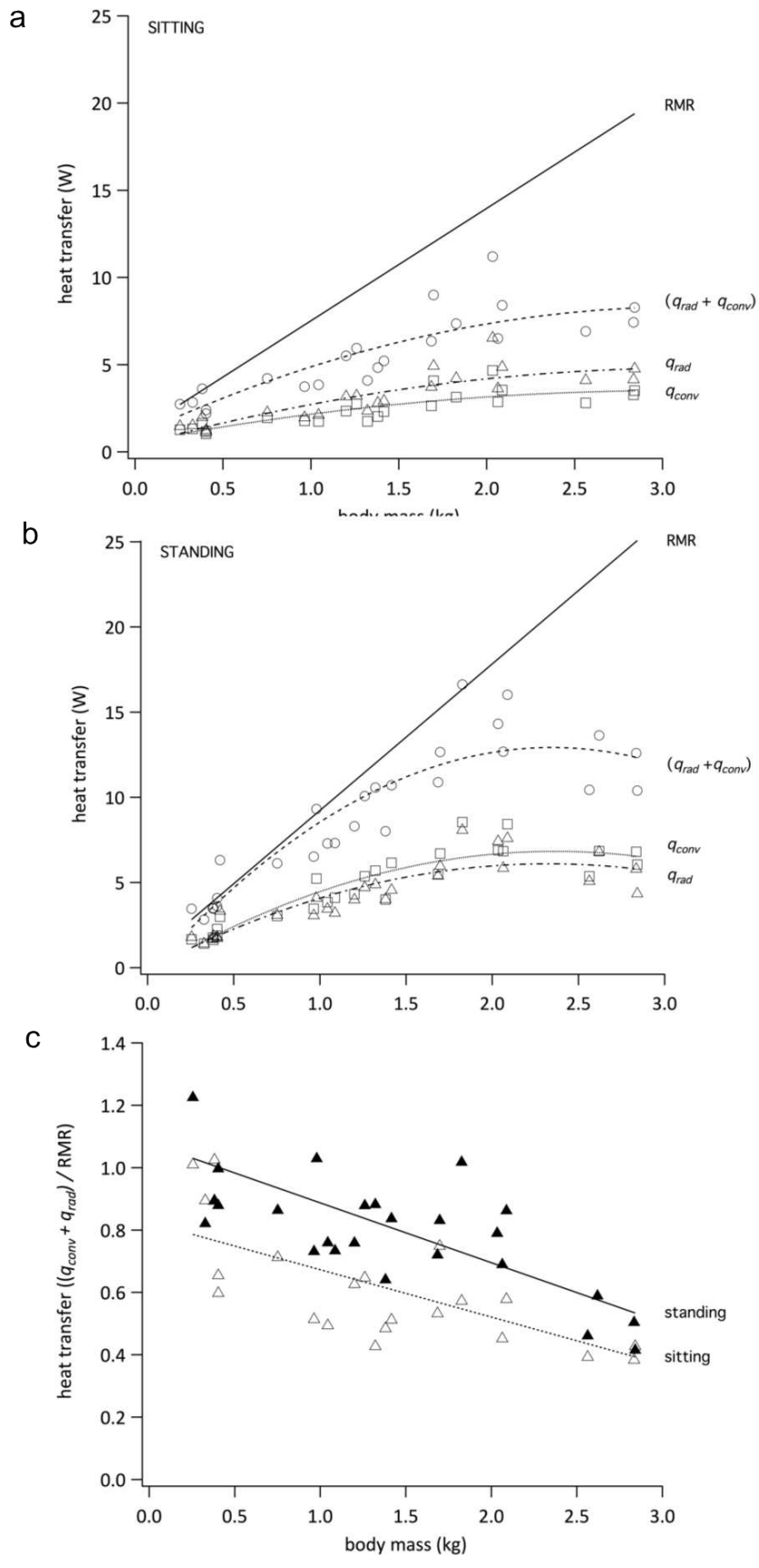
535 asterisk/dotted line : **tarsus** (*surface temperature*: standing:  $P = 0.143$   $\Delta$ *temperature*: standing:

536  $P = 0.002$ )

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1326 538 cross/dot-dash line: **combined toes** (*surface temperature*: standing:  $P = 0.010$ ;  $\Delta$   
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1328 539 *temperature*: standing:  $P < 0.001$ )  
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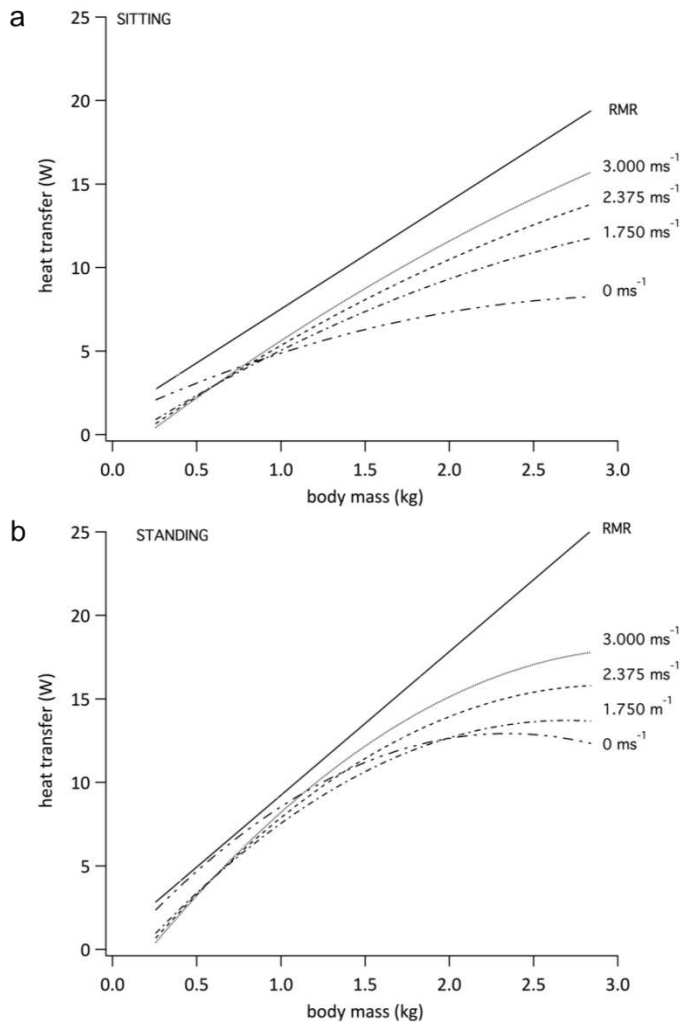
540 Figure 4: Convective and radiative heat transfer over development



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1443 543 The contribution of total radiative (triangles; dot-dash line) and convective (crosses; dotted line)  
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1445 544 cooling in the sitting (a) and standing (b) broiler. Polynomial curves ( $P < 0.001$ ) are plotted for  
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1447 radiative (triangles; dot-dash line), convective (crosses; dotted line) and combined heat transfer  
1448 545  
1449 (circles; dashed line). Metabolic rate for broilers as measured using respirometry (Tickle et al.,  
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1451 2018) is plotted as the solid line. Sensible heat loss in still air as a proportion of RMR across  
1452 547  
1453 development (c) highlights the decreasing contribution over development of  $q_{rad}+q_{conv}$  in  
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1455 standing (filled triangles, solid line:  $R^2 = 0.492$ ;  $P < 0.001$ ) and sitting (open triangles, dashed  
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1457 line:  $y = R^2 = 0.428$ ;  $P = 0.001$ ). Each marker represents an individual measurement  
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 1503 551 Figure 5: Modelled heat loss with increasing airspeed  
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 1538 554 Sensible heat loss ( $q_{rad} + q_{conv}$ ) from sitting (a) and standing (b) birds in still air (dot-dot-dash  
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 1540 555 line) and under simulated airflow conditions. Estimated sensible heat transfer from broilers  
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 1542 556 older than 28 days ( $>1.524\text{kg}$ ) is shown for airspeeds of 1.750 (dot-dash line), 2.375 (dashed  
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 1544 557 line) and  $3.000\text{ ms}^{-1}$  (dotted line). All polynomial fits were significant ( $P < 0.001$ ). RMR is also  
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 1546 558 shown (solid line; sitting:  $y = 6.452 * M_b + 1.059$ ; standing:  $y = 8.6074 * M_b + 0.6187$ ).  
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	<i>m</i>	<i>c</i>	95% CI	<i>R</i> <sup>2</sup>	<i>F</i>	<i>P</i>
<i>Head</i>	3.686	0.644	0.512 - 0.775	0.781	100.129	< 0.001
<i>Torso</i>	4.869	0.824	0.734 - 0.915	0.925	347.49	< 0.001
<i>Tarsus</i>	3.626	0.653	0.569 - 0.737	0.901	253.92	< 0.001
<i>Toe1</i>	2.800	0.595	0.505 - 0.684	0.869	184.984	< 0.001
<i>Toe2</i>	3.072	0.628	0.542 - 0.714	0.888	222.385	< 0.001
<i>Toe3</i>	3.32	0.651	0.575 - 0.728	0.916	304.416	< 0.001
<i>Toe4</i>	3.100	0.574	0.476 - 0.671	0.833	145.59	< 0.001
<i>Sum of toes</i>	3.716	0.620	0.559 - 0.682	0.938	426.423	< 0.001

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

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

			<i>m</i>	<i>c</i>	95% CI	<i>R</i> <sup>2</sup>	<i>F</i>	<i>P</i>
Sitting	<i>q<sub>conv</sub></i>	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
	<i>q<sub>rad</sub></i>	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	<i>q<sub>conv</sub></i>	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
	<i>q<sub>rad</sub></i>	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<sup>2</sup>) 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.