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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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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

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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).
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136 57 The lag between organ and skeletal development related to muscle growth are thought to drive
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138 58 the underlying health related issues (Havenstein, et al., 2003b; Schmidt, et al., 2009; Tickle, et
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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
147
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
159
160 69 sternal-weight gain (Tickle, Paxton, Rankin, Hutchinson and Codd, 2014; Tickle, et al., 2010).

161
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
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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^{2/3} (Walsberg
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185 77 and King, 1978). In the commercial farming of broilers, careful control of environmental
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187 78 conditions is required to optimise broiler development, since growth rate and feed efficiency
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189 79 are affected by temperature (Deaton, et al., 1996; Deeb and Cahaner, 2002; Donkoh, 1989;
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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
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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,
202
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;
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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
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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 99 2. METHODS

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243 101 2.1 Animals
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247 103 Commercial broilers (Cobb® 500) were obtained from a local supplier and housed in
248
249 pens with *ad libitum* access to poultry pellets and water. Daily recordings of body mass (M_b)
250 104 and gait (Kestin 1992) were made to monitor development and welfare thereby ensuring that
251
252 105 only healthy birds were included in thermal imaging analysis. The sex ratio of hatched broiler
253
254 106 chickens has a slight female bias (55% female, 45% male) (Zakaria and Omar, 2013).
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256 107 Experimental procedures and methods were carried out under ethical approval from the
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258 108 University of Manchester Ethics Committee in accordance with the Animal (Scientific
259
260 109 Procedures) Act 1986, covered by a Home Office project licence (40/3549) held by Dr. Codd.
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267 112 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-
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293 125 Vantress® “Broiler Management Guide” revised 2012) and therefore assumed to fall within
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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.
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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
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330 139 scaling relationships for surface area over development.
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335 141 2.3 Calculation of Heat Transfer

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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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352 149 2.3.1 Calculated Radiative Heat Transfer

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362
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:

$$367 \quad 153 \quad 368 \quad 154 \quad 369 \quad 155 \quad 370 \quad 156 \quad 371 \quad 157 \quad 372 \quad 158 \quad 373 \quad 159 \quad 374 \quad 160 \quad 375 \quad 161 \quad 376 \quad 162 \quad 377 \quad 163 \quad 378 \quad 164 \quad 379 \quad 165 \quad 380 \quad 166 \quad 381 \quad 167 \quad 382 \quad 168 \quad 383 \quad 169 \quad 384 \quad 170 \quad 385 \quad 171 \quad 386 \quad 172 \quad 387 \quad 173 \quad 388 \quad 174 \quad 389 \quad 175 \quad 390 \quad 176 \quad 391 \quad 177 \quad 392 \quad 178 \quad 393 \quad 179 \quad 394 \quad 180 \quad 395 \quad 181 \quad 396 \quad 182 \quad 397 \quad 183 \quad 398 \quad 184 \quad 399 \quad 185 \quad 400 \quad 186 \quad 401 \quad 187 \quad 402 \quad 188 \quad 403 \quad 189 \quad 404 \quad 190 \quad 405 \quad 191 \quad 406 \quad 192 \quad 407 \quad 193 \quad 408 \quad 194 \quad 409 \quad 195 \quad 410 \quad 196 \quad 411 \quad 197 \quad 412 \quad 198 \quad 413 \quad 199 \quad 414 \quad 200 \quad 415 \quad 201 \quad 416 \quad 202 \quad 417 \quad 203 \quad 418 \quad 204 \quad 419 \quad 205 \quad 420$$
$$q_{rad} = A\sigma\epsilon_a(T_b^4 - T_a^4) \quad (1)$$

374 156 where A is body segment surface area (m^2), σ is the Stefan-Boltzmann constant (relates
375 157 radiative energy emittance to absolute temperature; $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-1}$), ϵ_a is emissivity of
376 158 bird feathers (assumed as 0.95; (Ward, et al., 1999)), T_b is the segment mean surface
377 159 temperature and T_a is ambient air temperature (K).

385 161 2.3.2 Modelled Convective Heat Transfer

387 162
388
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:

$$393 \quad 165 \quad 394 \quad 166 \quad 395 \quad 167 \quad 396 \quad 168 \quad 397 \quad 169 \quad 398 \quad 170 \quad 399 \quad 171 \quad 400 \quad 172 \quad 401 \quad 173 \quad 402 \quad 174 \quad 403 \quad 175 \quad 404 \quad 176 \quad 405 \quad 177 \quad 406 \quad 178 \quad 407 \quad 179 \quad 408 \quad 180 \quad 409 \quad 181 \quad 410 \quad 182 \quad 411 \quad 183 \quad 412 \quad 184 \quad 413 \quad 185 \quad 414 \quad 186 \quad 415 \quad 187 \quad 416 \quad 188 \quad 417 \quad 189 \quad 418 \quad 190 \quad 419 \quad 191 \quad 420$$
$$q_{conv} = Ah_c(T_b - T_a) \quad (2)$$

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

$$406 \quad 171 \quad 407 \quad 172 \quad 408 \quad 173 \quad 409 \quad 174 \quad 410 \quad 175 \quad 411 \quad 176 \quad 412 \quad 177 \quad 413 \quad 178 \quad 414 \quad 179 \quad 415 \quad 180 \quad 416 \quad 181 \quad 417 \quad 182 \quad 418 \quad 183 \quad 419 \quad 184 \quad 420$$
$$h_c = \text{Nu} \frac{k}{d} \quad (3)$$

411 173 and 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

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

$$430 \quad 178 \quad \text{Re} = \frac{ud}{\nu} \quad (4)$$

432 179

434 180 where u is airspeed (ms^{-1}) and ν is the kinematic viscosity of air ($\text{m}^2 \text{s}^{-1}$).

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$$439 \quad 182 \quad \text{Pr} = \frac{\nu}{k} \quad (5)$$

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

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

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452 188 Convective heat transfer was therefore calculated for each body segment based upon its
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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
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462 193 environmental conditions that allow for optimal broiler production. Airspeed was modelled as
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464 194 0.300, 0.500, 0.875 ms^{-1} for birds with measured body mass as expected for ages between 0-
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466 195 14, 15-21 and 22-28 days, respectively. A range of simulated airspeeds was implemented for
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468 196 older, heavier birds according to the suggested ventilation conditions (1.750-3.00 ms^{-1})
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470 197 provided in the Broiler Management Guide. Convective heat transfer was also calculated as by
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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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474 199

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

where a is the coefficient of thermal expansion (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_{CO_2} (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 ($M_b =$

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225 2.635*body + 80.002; $r^2 = 0.463$, $F = 23.268$, $P < 0.001$) accounted for by the body surface
226 accounted for 80.6% in a 0.25kg bird rising to 87.5% in a 2.90kg bird (Supplementary Material).
227 Therefore, proportion of overall surface area accounted for by unfeathered skin was reduced
228 over development.

230 3.2 Heat loss

231
232 Mean toe surface temperature increased with body mass, body surface temperature
233 decreased, and head and tarsus temperature were unchanged (Figs. 1, 2a & 2c). The difference
234 between ambient and body surface temperature reduced as birds grew larger, while the inverse
235 relationship was detected for head, tarsus and toes (Fig. 2b & 2d). Total sensible heat loss in
236 still air decreased as a proportion of RMR over development (Fig. 3 & Table 2), indicating that
237 convection and radiation were not adequate to maintain a neutral energy balance in the sitting
238 bird in still air (Fig. 4a). In contrast, radiative and convective cooling in a standing posture was
239 sufficient to dissipate total metabolic heat production until the birds weighed in excess of
240 approximately 1.00kg (Fig. 4b). Developmental trajectories of radiative and convective heat
241 loss were similar (comparison of regression slopes by ANCOVA: $F = 0.507$; $P = 0.480$) in the
242 sitting and standing bird (Fig. 3c), although the magnitude of heat exchange was higher during
243 standing (comparison of intercepts by ANCOVA: $F = 20.570$; $P < 0.001$).

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

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605 251 4. DISCUSSION
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610 253 In this study, we have identified how convective and radiative cooling mechanisms
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612 254 contribute to heat exchange in the broiler over development, and the potentially important
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614 255 thermoregulatory role of posture. Our hypothesis that heavier birds have impaired radiative
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616 256 and convective cooling mechanisms was supported by comparison of thermal imaging and
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618 257 respirometry data, and posture appears to exert a determining role in the magnitude of heat
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620 258 loss. Large body size coupled with a high resting metabolic rate present a significant challenge
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622 259 to the thermal physiology of the modern broiler and this restriction on adequate heat loss may
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624 260 constrain other functions including locomotor activity.
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626
627 261 There was a change in the spatial distribution of surface temperature (Cangar, et al.,
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629 262 2008) over development (Figs. 1 & 3). As birds grew larger, body surface temperature
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631 263 decreased while toe temperature increased (Figs. 3). In accordance with earlier research
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633 264 (Cangar, Aerts, Buyse and Berckmans, 2008) and regardless of resting posture, the disparity
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635 265 between ambient and surface temperature reduced for the body while the difference increased
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637 266 for head, tarsus and toes, indicating a switch in the relative importance of thermoregulatory
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639 267 surfaces over development. Sensible heat loss in still air was inadequate to maintain adequate
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641 268 thermoregulation over development (Fig. 4), consistent with a reduction in proportional surface
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643 269 area (Table 1) and increased feathering to provide greater thermal insulation in older birds
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645 270 (Herreid and Kessel, 1967). Postural-dependent thermoregulation was inferred because sitting
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647 271 contributes to reduced heat loss (Fig. 4a) when compared to standing (Fig. 4b), a finding
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649 272 consistent with previous reports of RMR in birds (Tickle, Hutchinson and Codd, 2018; Tickle,
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651 273 et al., 2012; van Kampen, 1976). It is striking that resting in a sitting position is used for
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653 274 proportionately longer periods of the day given that heavier birds, which are potentially subject
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663 275 to greater thermal stress, tend to sit for longer than lighter birds (Bokkers and Koene, 2003;
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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
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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
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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
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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
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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
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710 297 greater disparity between RMR and measured heat transfer in still air (Fig.4). It is important to
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712 298 note that for optimal body mass gain a significant contribution of evaporative cooling should
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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)
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725 301 Interestingly, in light of recent findings we speculate that this important function may be
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727 302 compromised in broilers due to the relatively slow development of musculoskeletal
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729 303 components of the respiratory system. A relatively reduced muscle mass in larger birds
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731 304 indicates that the power available to maintain increased respiratory rate during panting may be
732
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),
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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.
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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
756
757 317 (Bokkers and Koene, 2003; Tickle, Hutchinson and Codd, 2018) and provides evidence for a
758
759 318 thermoregulatory constraint on posture and locomotion.

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761
762 319 The contribution to sensible heat loss from each body segment varied across
763
764 320 development. As expected, there was a proportional decrease in the heat transfer from head,
765
766 321 body and tarsus relative to body mass over development (Table 2), consistent with a reduction
767
768 322 in relative surface area available for thermoregulation (Table 1). However, toe q_{conv} increased
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770 323 with positive allometry (Table 2), indicating that, in still air, cooling via the toes is important
771
772 324 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,
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787 327 while cooling via the tarsus and toes increased at a faster rate than surface area (Table 3),
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789 328 highlighting the importance of the distal hindlimb as a conduit for heat transfer (Macleod and
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791 329 Hocking, 1993; Steen and Steen, 1965). The negatively allometric relationship between surface
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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
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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
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823 344 ventilation, so no consideration was given to the effect of airspeed on radiative heat transfer,
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825 345 although no significant effect on radiative cooling performance was expected in light of
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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
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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 3.1ms^{-1} in broilers (Furlan, et al.,
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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 ± 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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912 379 913 380 5. ACKNOWLEDGEMENTS

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920 384 and Biological Sciences Research Council (Grant No: BB/I021116/1).
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926 386 6. REFERENCES

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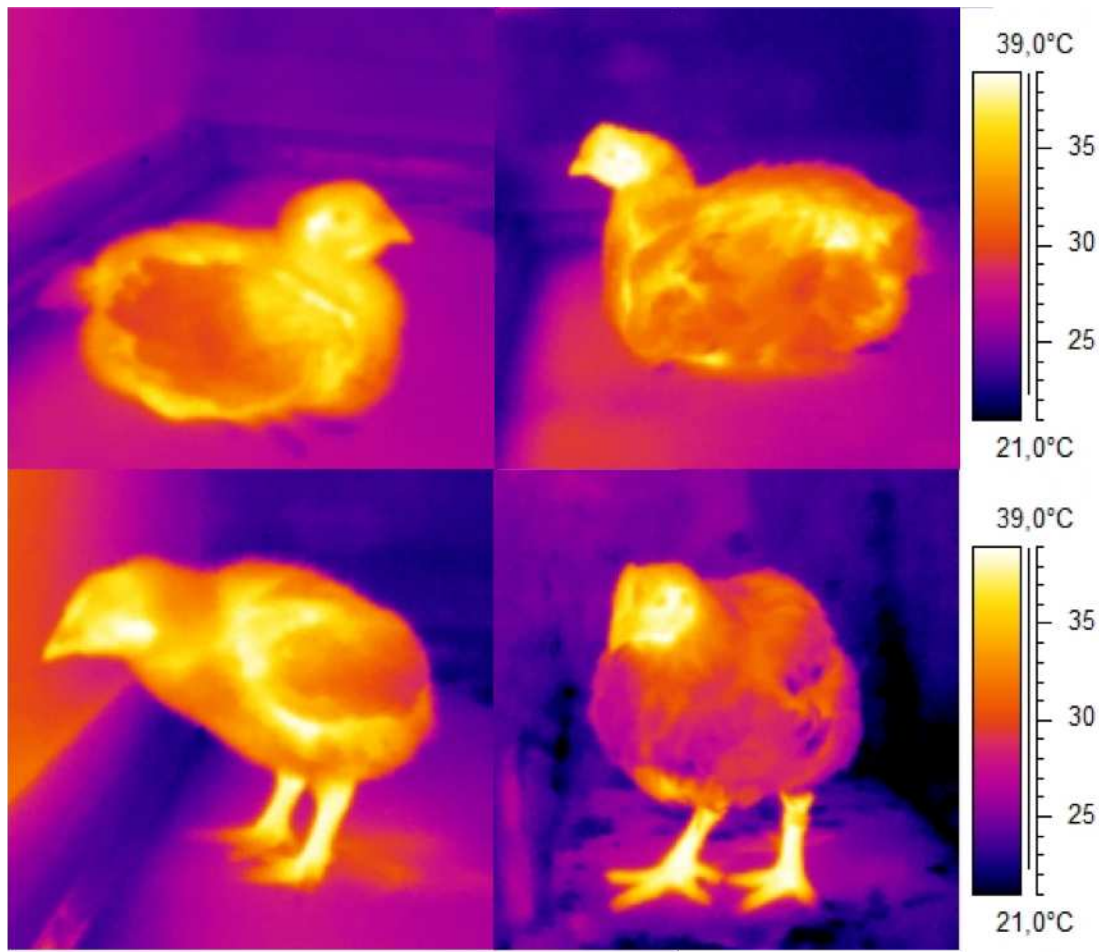
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Figure 1: Representative thermal images of low and high body mass broilers.

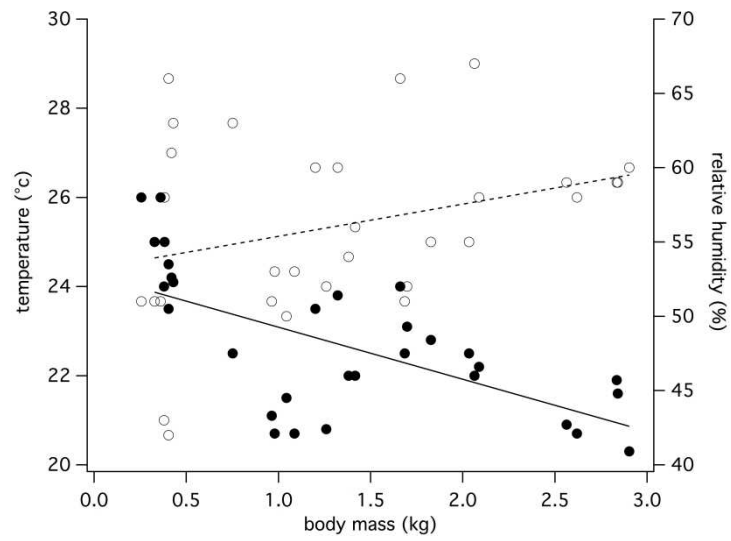


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511 Typical thermal images of broilers in standing and sitting postures. Compare the high surface
512 temperature of the smaller (0.26kg) bird (a, b) with a larger (2.0kg) broiler (c, d) that has
513 better feather insulation. Ambient temperature/relative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

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515 Figure 2: Ambient conditions during thermal imaging.



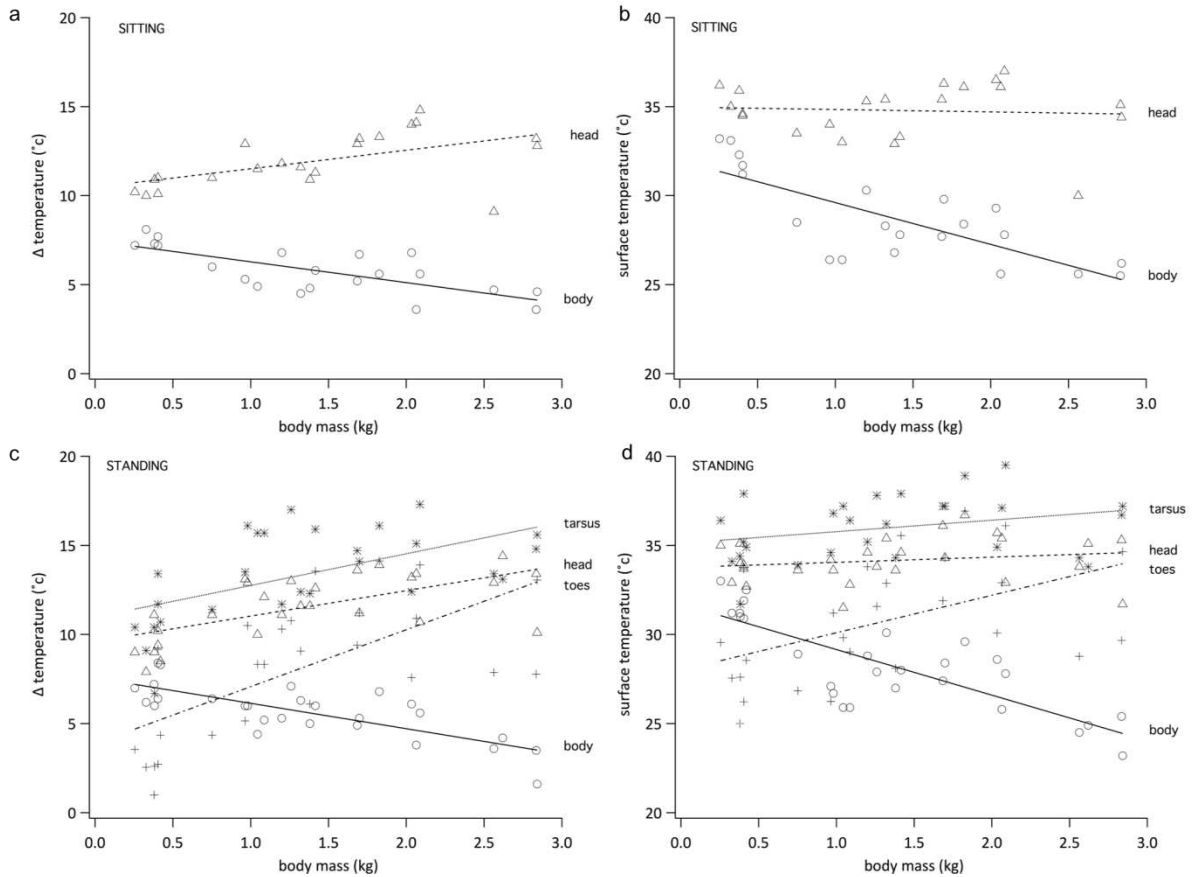
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517 Ambient temperature during thermal imaging was reduced over the growing period ($y = -$
518 $1.272x + 24.461$; $F = 23.209$; $R^2 = 0.445$; $P < 0.001$) while there was a simultaneous non-
519 significant trend for increasing relative humidity ($y = 2.309x + 52.935$; $F = 3.319$; $R^2 = 0.103$;
520 $P = 0.079$).

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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 (Δ 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: $P < 0.001$; Δ

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

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

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

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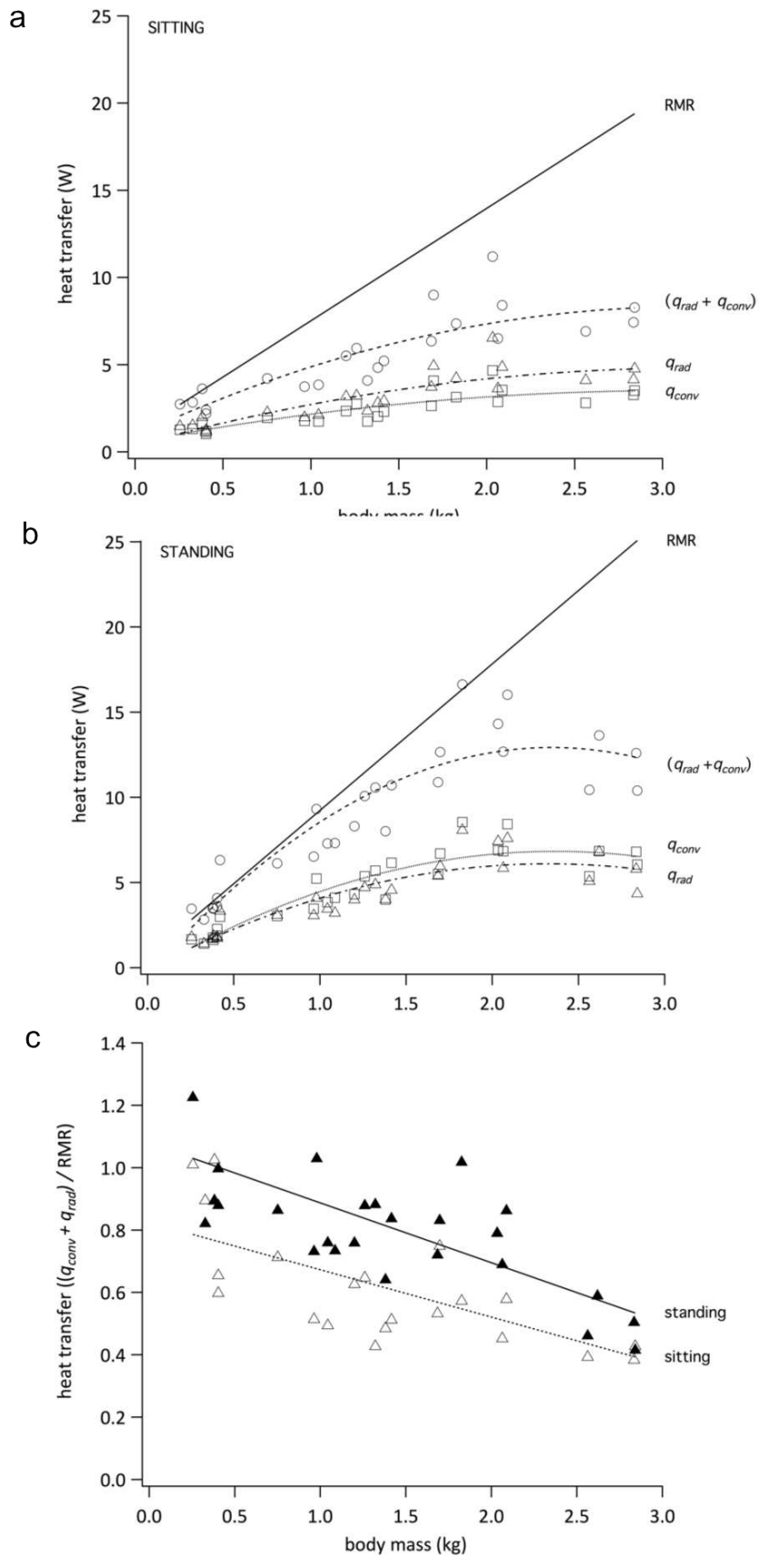
535 asterisk/dotted line : **tarsus** (*surface temperature*: standing: $P = 0.143$ Δ *temperature*: standing:

536 $P = 0.002$)

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1326 538 cross/dot-dash line: **combined toes** (*surface temperature*: standing: $P = 0.010$; Δ
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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



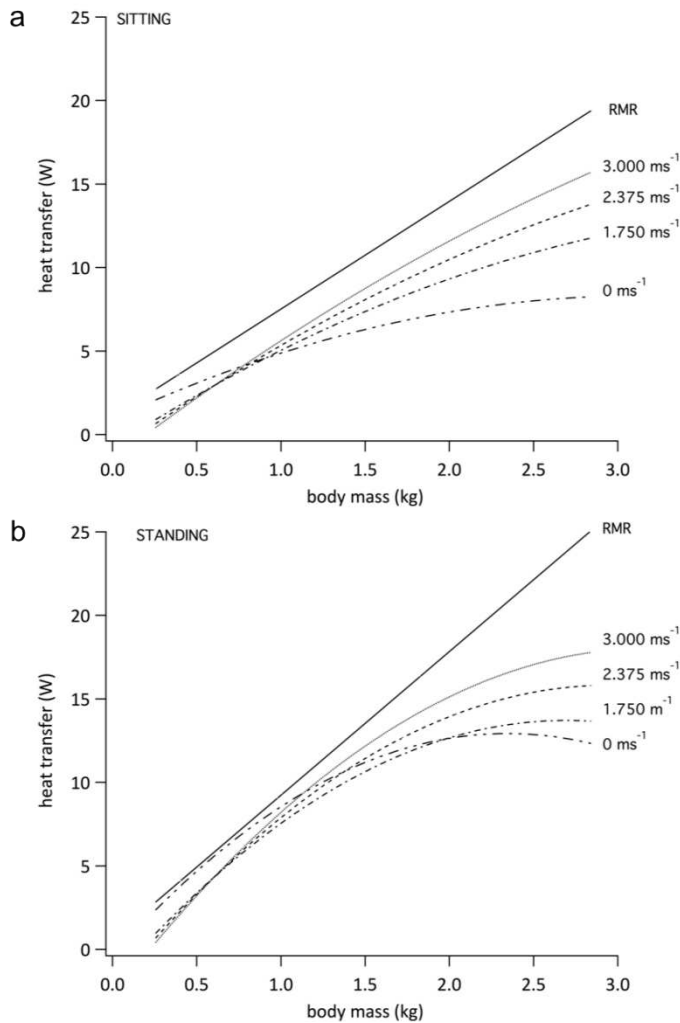
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543 The contribution of total radiative (triangles; dot-dash line) and convective (crosses; dotted line)
544 cooling in the sitting (a) and standing (b) broiler. Polynomial curves ($P < 0.001$) are plotted for
545 radiative (triangles; dot-dash line), convective (crosses; dotted line) and combined heat transfer
546 (circles; dashed line). Metabolic rate for broilers as measured using respirometry (Tickle et al.,
547 2018) is plotted as the solid line. Sensible heat loss in still air as a proportion of RMR across
548 development (c) highlights the decreasing contribution over development of $q_{rad}+q_{conv}$ in
549 standing (filled triangles, solid line: $R^2 = 0.492$; $P < 0.001$) and sitting (open triangles, dashed
550 line: $y = R^2 = 0.428$; $P = 0.001$). Each marker represents an individual measurement

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551 Figure 5: Modelled heat loss with increasing airspeed



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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 ($>1.524\text{kg}$) 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: $y = 8.6074 * M_b + 0.6187$).

	<i>m</i>	<i>c</i>	95% CI	<i>R</i> ²	<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 (mm²) 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> ²	<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> ²	<i>F</i>	<i>P</i>
<i>Sitting</i>	<i>q_{conv}</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_{rad}</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
<i>Standing</i>	<i>q_{conv}</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_{rad}</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 (m²) 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.