The relationship between personality and basal metabolic rate in Red Junglefowl (*Gallus gallus*)

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Sammanfattning/Abstract:
‘Animal personality’ refers to individual behavioural differences that are consistent over time and context. Physiological constraints are suggested to underlie this constraint in behavioural plasticity. As energy is required for physiological processes that generate behaviour, energy metabolism could be a proximate explanation for personality. Currently, the most coherent framework linking behaviour, metabolism and life history-traitis is still poorly tested empirically, and studies are showing contradicting results. Therefore, I here aim to explore this relationship further by investigating the relationship between basal metabolic rate (BMR) and personality in Red Junglefowl (Gallus gallus). Birds used had known responses in personality assays, and their metabolic rates were measured by determining oxygen consumption in standardized conditions throughout the night using an open respirometry system. BMR was negatively correlated with time spent foraging, and positively correlated with time spent being vigilant. Considering foraging an ‘activity’ (due to its energy-demand), my results support the allocation model, a model that assumes that an animal has a fixed amount of energy, thus that an energetic trade-off occur between competing energy requiring processes such as BMR and activity. Hence, an animal with low BMR has more energy to spend on activity. However, I do not consider vigilance as an energy-demanding activity; hence this relationship cannot be interpreted in this framework. Taken together, my results show a relationship between personality and BMR, although their relationship still needs further investigation to understand the causality and consequences of it.
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1 Abstract

‘Animal personality’ refers to individual behavioural differences that are consistent over time and context. Physiological constraints are suggested to underlie this constraint in behavioural plasticity. As energy is required for physiological processes that generate behaviour, energy metabolism could be a proximate explanation for personality. Currently, the most coherent framework linking behaviour, metabolism and life history-trait is still poorly tested empirically, and studies are showing contradicting results. Therefore, I here aim to explore this relationship further by investigating the relationship between basal metabolic rate (BMR) and personality in Red Junglefowl (*Gallus gallus*). Birds used had known responses in personality assays, and their metabolic rates were measured by determining oxygen consumption in standardized conditions throughout the night using an open respirometry system. BMR was negatively correlated with time spent foraging, and positively correlated with time spent being vigilant. Considering foraging an ‘activity’ (due to its energy-demand), my results support the allocation model, a model that assumes that an animal has a fixed amount of energy, thus that an energetic trade-off occur between competing energy requiring processes such as BMR and activity. Hence, an animal with low BMR has more energy to spend on activity. However, I do not consider vigilance as an energy-demanding activity; hence this relationship cannot be interpreted in this framework. Taken together, my results show a relationship between personality and BMR, although their relationship still needs further investigation to understand the causality and consequences of it.

2 Introduction

Traditionally, behaviours were considered to be highly plastic and an individual was therefore predicted to be able to perform the optimal behaviours for any given situation (Sih et al. 2004). However, it is now becoming clear that individuals of the same population may perform different behaviours in the same situation, or similar behaviour in different situations (Stamps 2007). This observation implies that there are limitations to the behavioural plasticity of individuals (Sih et al. 2004). This has been termed ‘animal personality’ and refers to individual behavioural differences that are consistent over time and/or context (Gosling 2001, Sih et al. 2004, Reale et al. 2007, Biro and Stamps 2010). Recent studies have observed animal personalities in a wide range of species including mammals, birds, fish, reptiles, amphibians, molluscs, spiders, cephalopods and arthropods (reviewed by Gosling 2001, Stamps 2007). When investigating variation in animal personality, the most commonly observed behavioural traits are boldness/shyness,
aggressiveness, exploration, activity and sociability (Gosling 2001, Reale et al. 2007, Biro and Stamps 2008, Careau et al. 2008). Empirical studies indicate that these behavioural traits are positively related to food intake, productivity and other life-history traits (Biro and Stamps 2008). Correlations among behavioural traits might also exist, for example; an individual expressing high aggressiveness might also be bolder, more exploratory and active (Sih et al. 2004, Biro and Stamps 2008).

According to Careau and co-workers (2008), physiological constraints may underlie consistent individual differences in behaviour (i.e. personality). Energy metabolism could be a proximate explanation for personality, since energy is required for the physiological processes that generate behaviours (Biro and Stamps 2010). Careau and Garland (2012) suggests a link between energy metabolism and personality, and link these to the proactive-reactive life-history continuum, also termed as variation in individuals’ ‘pace of life’. Individuals within a population can vary in their life-history strategies (Dall et al. 2004, Biro and Stamps 2008). Studies on birds and mammals suggests that a proactive individual is characterised as bold, with higher levels of activity and aggressiveness, while a reactive individual is shyer, with low activity and aggressiveness (Careau et al. 2008, Reale et al. 2010). A proactive individual is therefore predicted to have a fast pace of life and is further expected to live a short life with high growth rate and be highly fecund (Biro and Stamps 2010). A proactive strategy is suggested to require a higher metabolic rate than a reactive life strategy (Careau et al. 2008). The higher energy requirement may generate a positive relationship between a proactive strategy and resting metabolic rate (Reale et al. 2010). A survey by Biro and Stamps (2010) shows a positive correlation between metabolic rate and proactive behaviour in birds, fish, mammals, crustaceans and insects. Several studies support these findings (Careau et al. 2011, Martins et al. 2011, Killen et al. 2011), while others fail to find such a relationship (Kane et al. 2008, Lantova et al. 2011). According to Careau and Garland (2012), the positive relationship between metabolic rate and personality is only weakly supported on an individual level. For example, earlier studies on birds show that resting metabolic rate is reduced when increasing the energy invested in activity (Deerenberg et al. 1998, Wikelski et al. 1999). Contrary, Mathot and co-workers (2009) showed a positive correlation between basal metabolic rate and foraging behaviour in birds. Therefore, the currently most coherent framework that links behaviour, metabolism and life history-traits (i.e. the idea that individuals differ in their pace of life) still need to be further investigated empirically as studies so far have given inconclusive results of the predicted relationship. The here presented study therefore aimed to explore this relationship further by
investigating if there are correlations between basal metabolic rate and personality traits in Red Junglefowl (*Gallus gallus*).

3 Materials and methods

3.1 Animals and management

The animals used in this study were adult Red Junglefowl (ca. 1 year of age), 17 hens and 16 roosters with known behavioural scores in personality assays, according to the methods used in Thorpe (2013). The birds were housed at Linköping University’s chicken facility at Vreta Naturbruksgymnasium. 7-5 hours before each trial when oxygen consumption was measured (see below), birds were transported to Linköping University where the trials were performed. Each trial started in the afternoon and lasted throughout the night. In the morning when the trial was complete, birds were transported back to Vreta animal facility. During the time the birds were housed at the university, they were kept in an indoor enclosure (140 x 70 cm) with wood shavings and *ad libitum* access to food and water.

3.2 Metabolic rate measurements

Metabolic rate is measured by an animal’s O$_2$-consumption or CO$_2$-production per unit of time (Careau et al. 2008). To determine the birds’ basal metabolic rate (BMR), their O$_2$-consumption was measured. The experimental set-up for the metabolic measurement used in the current study was an open respirometry system with an air pump pushing air through four respiration chambers (CurTec) that were placed in a thermostatic chamber (type 3001, Rubarth ® apparate GmbH). This allowed me to measure simultaneously four individuals per trial. Two types of chambers were used: 10 L for hens (diameter of 274 mm and a height of 283 mm), 15 L for roosters (diameter of 274 mm and with a height of 327 mm) due to the larger size of the male birds. The flow of air through the chambers was set to 2-2.5 L/min. The air flow through the chambers was measured with a multichannel flow measurement system (FB8, Sable Systems Inc.). The system was set to collect sequential outflow samples for three minutes in each chamber and a baseline, which resulted in a cycle of 15 minutes throughout the 16 hours each bird was tested. The baseline is a measurement of the O$_2$-concentration in the air before going into the chambers. The air from the chambers and baseline was analysed with a gas analysis system FOXBOX (Sable Systems Inc.). Before the air entered the gas analysis system, it passed through a drying column (60 ml) with Drierite (Hammond Drierite) to eliminate moisture from the incoming air. Temperature sensors (iButton, type DS1921L;
Maxim/Dallas Semiconductor Corp.) were placed in the chambers to monitor the temperature inside the chambers during the trials. A temperature sensor was also placed inside the thermostatic chamber to measure and enable me to account for incubator temperature. Each bird was measured once since the individual differences in BMR are assumed to be consistent (Biro and Stamps 2010).

Resting and basal metabolic rate are the most common methods when studying energy metabolism in vertebrates (Careau et al. 2008). Basal metabolic rate is defined as the metabolic rate in the thermoneutral zone when an adult individual is inactive, post-absorptive and non-reproductive (McNab 1997). Resting metabolic rate (RMR) is a slightly less strict measurement as the individual does not need to be post-absorptive (Careau et al. 2008). The metabolic measurement in this study will be considered as basal metabolic rate (BMR) because the birds were post-absorptive, as they did not have access to food and water while inside the thermostatic chamber for 16 hours. The birds, however, will be in their reproductive cycle as it is more or less ‘chronic’ in domesticated species, and the birds used were kept on 12:12 light: dark cycles, simulating the breeding season.

3.3 Morphological measurement

Before a trial started, the comb length and comb height of each individual was measured, as well as the tarsal length (all measured in mm by the use of a digital calliper). These measurements were taken to investigate their potential relationship with variation in BMR. Tarsal length is a measure of how large the bird is, as a more conservative complement to the actual weight, which may change over short intervals for various reasons. Comb size is commonly used as a surrogate measure for variation in levels of reproductive hormones (Eitan et al. 1998).

BMR is affected by body mass; an animal with higher body mass is expected to have a higher BMR (McNab 2008). To account for the individuals’ mass-differences, the birds’ weight (in grams) was noted before and after each trial to be able to calculate the mass-specific BMR of individuals. The chambers’ weights were also noted before and after each trial to determine how much of the birds’ weight losses were due to defecation.

3.3.1 Plumage scoring

The hens varied greatly in their plumage cover; some had complete coverage and some were very feather-pecked. This may affect the metabolic rate of individuals due to that plucked individuals do not have
the same amount of insulation as hens with full plumage. The lack of insulation may thus result in a higher BMR value because of the extra metabolic effort needed to maintain a normal, stable body temperature. I therefore scored the plumage of all hens in categories 1 – 4 in a descendent scale where 1 was scored as having full, or close to full plumage, and 4 being almost completely plucked on the neck, back and wings.

3.4 Behavioural responses

Different behavioural responses were recorded in personality assays when the birds were younger, at 34 and 40 weeks of age. These observations were conducted by Hanne Thorpe as part of her master thesis (Thorpe 2013). In a novel arena test, just after being introduced to the arena, ‘latency to walk’ was recorded as a measure of nervousness, and ‘number of movements’ in the arena was used as a measure of activity. Variation in ‘vigilance’ and ‘foraging’ among individuals were quantified by the time a bird spent being alert or foraging, respectively. A novel object test was used to quantify variation in neophobia by recording ‘latency to first head movement’ and ‘latency to stand’ in a tonic immobility test, were used as two measures of fearfulness. In a startle test, the ‘instant response’ and ‘vigilance’ after the simulated predator attack had occurred were used as measures of how the birds handle stressful situations. See Thorpe (2013) for further details on the behavioural responses recorded.

3.5 Calculations and statistical analysis

Variation in O₂-consumption per unit of time of each individual (VO₂) was calculated using a customised LabView programme and based on the values of each individual from the in- and out-respirometer oxygen concentrations and air flow used. The program averaged the oxygen concentrations from the last minute in each respirometer in every 15 minute cycle. This way, a full trial of 16 h provided 64 measurements of metabolic rate for each individual. To get the basal metabolic rate of an individual, mean values were calculated from the four lowest consecutive values for each individual. This represents the hour where each individual had the lowest metabolic rate during the night and is here used as the individuals’ basal metabolic rate. These basal metabolic rate values can, after adjusting for mass-differences, be interpreted as metabolic rate in ml of O₂ h⁻¹ g⁻¹. To obtain the mass-specific BMR, the individual metabolic rate values were divided by the individual’s weight after completion of a trial, id est at a time when the gastrointestinal tracts would be almost empty.
Variation in BMR explained by sex was investigated using a Mann-Whitney U test. To investigate how variation in the plumage scoring of hens might relate to variation in BMR, a one-way ANOVA was used. Categories 2 and 3 were pooled due to low sample sizes. Category 1 was referred to as ‘full plumage’, category 2 and 3 as ‘intermediate’ and category 4 as ‘plucked’.

To compare behavioural responses and BMR independent of the observed sex differences, sex-centred mass-specific BMR was calculated for all individuals. This was done by calculating the mean mass-specific BMR for each sex and subtracting this mean from each individual mass-specific BMR.

The behavioural responses used to correlate with the BMR values of individuals, were from the same individuals, but from when it was at an age of 40 weeks (Thorpe 2013). To determine which behaviours where more consistent within individuals, and to further correlate with metabolic rate, each behaviour was correlated within individuals between responses obtained at 34 and 40 weeks of age, by the use of Spearman rank correlations. Those behaviours that had the highest correlation coefficient between the two were the most interesting to investigate, since this showed consistency in behaviours suggesting that there is an underlying constraint (e.g. BMR).

Correlations between mass-specific BMR and the morphological measures comb length, comb height and tarsal length were analysed though independent Pearson correlations.

Spearman rank correlations were conducted in Statistica 10, all other analyses were conducted in Minitab 16.

4 Results

4.1 Sex differences and plumage score

There was a great difference in mass-specific BMR between the sexes; roosters had a lower BMR compared to hens (mean ± standard error (SE); roosters, 0.610 ± 0.085 ml of O$_2$ h$^{-1}$ g$^{-1}$; hens; 0.818 ± 0.145 ml of O$_2$ h$^{-1}$ g$^{-1}$, P < 0.01). In addition, hens had a larger intra-sex individual variation in their mass-specific BMR in comparison to the roosters (range minimum to maximum: hens, 0.637 - 1.153 ml of O$_2$ h$^{-1}$ g$^{-1}$; roosters, 0.488 - 0.844 ml of O$_2$ h$^{-1}$ g$^{-1}$). This larger range in mass-specific BMR of hens could in principle be explained by the larger spread in plumage variation among the hens, compares to among the roosters (where all had full plumage). Indeed, I found that hens that were plucked had a
significantly higher mass-specific BMR than hens of full or intermediate plumage (Figure 1, $F = 7.90$, $P < 0.01$).

![Figure 1](image_url)

Figure 1. Mass-specific BMR among Red Junglefowl hens of different plumage scores (mean ± SE; full plumage: 0.728 ± 0.069, intermediate: 0.735 ± 0.091, plucked: 0.940 ± 0.133; full plumage; N=5, intermediate; N=5, plucked; N=7).

Due to the significant differences between plucked hens and hens with full or intermediate plumage, the plucked hens were removed from the data when comparing variation in mass-specific BMR between the sexes. Removing these hens from the data elucidated sex differences in BMR without the values being affected by the thermoregulatory effects that the lack of insulation may have had. This sex comparison again showed that roosters had a significantly lower mass-specific BMR than hens (Figure 2, $U = 155.0$, $P < 0.01$).
Figure 2. Mass-specific basal metabolic rate (mean ± SE; roosters: 0.604 ± 0.021 ml of O₂ h⁻¹ g⁻¹; hens: 0.732 ± 0.076 ml of O₂ h⁻¹ g⁻¹) in female and male Red Junglefowl after the removal of feather pecked hens from the data. N=16 for roosters and N=10 for hens.

4.2 Relationships between variation in behaviour and BMR

The behavioural response assays involved four different types of tests (novel arena, novel object, startle and tonic immobility) with a number of different behaviours observed in each test. Some of these behavioural responses showed consistency over time, but most did not (Table 1, see Thorpe 2013 for further details).
Table 1. Behavioural responses of Red Junglefowl, correlated between responses obtained at 34 and 40 weeks of age. Behaviours with an R-value above 0.35 showed moderate to high consistency.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Novel Arena tests</strong></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.29</td>
</tr>
<tr>
<td>Foraging</td>
<td>0.32</td>
</tr>
<tr>
<td>Latency to non freeze</td>
<td>0.15</td>
</tr>
<tr>
<td>Latency to walk</td>
<td>-0.15</td>
</tr>
<tr>
<td>Number of vocalisations</td>
<td>0.22</td>
</tr>
<tr>
<td>Activity</td>
<td>0.44</td>
</tr>
<tr>
<td><strong>Novel Object tests</strong></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.31</td>
</tr>
<tr>
<td>Foraging</td>
<td>0.33</td>
</tr>
<tr>
<td>Activity</td>
<td>0.05</td>
</tr>
<tr>
<td><strong>Startle tests</strong></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.37</td>
</tr>
<tr>
<td>Instant response</td>
<td>0.37</td>
</tr>
<tr>
<td><strong>Tonic immobility</strong></td>
<td></td>
</tr>
<tr>
<td>Latency to first head movement</td>
<td>0.10</td>
</tr>
<tr>
<td>Latency to stand</td>
<td>0.58</td>
</tr>
</tbody>
</table>

Time spent foraging was negatively correlated with sex-centred mass-specific BMR (Figure 3, R = -0.53, P < 0.01), while time spent being vigilant was positively correlated with this measure of variation in BMR (Figure 4, R = 0.42, P = 0.01).
Figure 3. Correlation between time spent foraging during novel arena test and sex-centred mass-specific basal metabolic rate in Red Junglefowl.

Figure 4. Correlation between time spent being vigilant during novel arena test and sex-centred mass-specific basal metabolic rate in Red Junglefowl.

When looking at the sexes separately, roosters and hens show similar patterns in foraging and vigilance (Figure 5 and 6).
Figure 5. The relationship between time spent foraging during novel arena test and basal metabolic rate in Red Junglefowl. Roosters = black diamonds, hens =open diamonds.

Figure 6. The relationship between time spent being vigilant during novel arena test and basal metabolic rate in Red Junglefowl. Roosters = black diamonds, hens =open diamonds.
Variation in foraging and vigilance among individuals was strongly, negatively correlated ($R = -0.90$, $P < 0.05$) explaining the opposing relationships between the two behaviours and variation in BMR.

For other behaviours investigated, the relationship with sex-centred mass-specific BMR were non-existing or weak (Table 2).

Table 2. Correlations between behavioural responses and sex-centred mass-specific BMR in Red Junglefowl. (Correlations that show a significant relationship between sex-centred mass-specific BMR and behavioural responses are marked with an asterisk *.)

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>R</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Novel Arena tests</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.42</td>
<td>0.01*</td>
</tr>
<tr>
<td>Foraging</td>
<td>-0.53</td>
<td>0.001*</td>
</tr>
<tr>
<td>Latency to non-freeze</td>
<td>-0.05</td>
<td>0.80</td>
</tr>
<tr>
<td>Latency to walk</td>
<td>0.16</td>
<td>0.37</td>
</tr>
<tr>
<td>Number of vocalisations</td>
<td>0.05</td>
<td>0.79</td>
</tr>
<tr>
<td>Activity</td>
<td>0.05</td>
<td>0.80</td>
</tr>
<tr>
<td><strong>Novel Object tests</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.42</td>
<td>0.02*</td>
</tr>
<tr>
<td>Foraging</td>
<td>-0.42</td>
<td>0.01*</td>
</tr>
<tr>
<td>Activity</td>
<td>-0.03</td>
<td>0.87</td>
</tr>
<tr>
<td><strong>Startle tests</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vigilance</td>
<td>0.30</td>
<td>0.09</td>
</tr>
<tr>
<td>Instant response</td>
<td>-0.05</td>
<td>0.79</td>
</tr>
<tr>
<td><strong>Tonic Immobility tests</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latency to first head movement</td>
<td>-0.26</td>
<td>0.14</td>
</tr>
<tr>
<td>Latency to stand</td>
<td>-0.08</td>
<td>0.66</td>
</tr>
</tbody>
</table>

4.3 Weight loss, tarsal length and comb size

The mean body weight of the roosters after they were taken out of the chambers was $1190.0 \pm 70.3$ g (mean ± SE). Thus they had lost on average $4.1 \pm 1.2$ % of their weight from before the trial started. Out of
this weight loss, approximately 40% was due to defecation. This means that the roosters lost 2.3 ± 0.5% of their body weight during the 16 h trial. The mean body weight of the hens after they were taken out of the chambers was 796.2 ± 94.9 g. They had lost on average 6.9 ± 2.5% of their weight from before the trial started. Out of this weight loss approximately 50% was due to defecation. This means that the hens had lost an average of 3.3 ± 1.8% of their body weight during the 16 h trial.

There were large differences in comb length, comb height and tarsal length between the sexes (Table 3). However, in neither sex were any of these trait related to variation in mass-specific BMR (hens, R = 0.02, P = 0.94; roosters, R = 0.03, P = 0.92; comb length: hens, R = -0.13, P = 0.63; roosters, R = -0.41, P = 0.12; comb height: hens, R = 0.07, P = 0.937; roosters, R = -0.28, P = 0.30). No morphological measures showed any relationship with BMR (Rs < 0.2, P > 0.2).

Table 3. Variation in morphological measures of Red Junglefowl roosters and hens. (Values are given as mean ± standard error).

<table>
<thead>
<tr>
<th></th>
<th>Comb length (mm)</th>
<th>Comb height (mm)</th>
<th>Tarsal length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Roosters</strong></td>
<td>90.7 ± 6.7</td>
<td>49.8 ± 6.0</td>
<td>72.2 ± 3.1</td>
</tr>
<tr>
<td><strong>Hens</strong></td>
<td>34.2 ± 5.8</td>
<td>15.6 ± 3.7</td>
<td>60.2 ± 3.2</td>
</tr>
</tbody>
</table>

5 Discussion

This study found that hens have a higher mass-specific BMR than roosters, but also that certain behavioural responses scored in personality assays correlated with variation in BMR combined for the two sexes.

A reason for the hens’ higher BMR compared to the roosters could be due to egg production. When an egg is produced, new cells are formed and this is a metabolically costly process. According to Wolfenson and co-workers (1978), a laying hen produces an egg weighing 50-70 g during a short laying cycle. Out of the egg’s weight, 25-35 g of albumen and 5-6 g of shell are produced during this short period. Out of the hen’s body weight, this daily production is equivalent to 1.5% (Wolfenson et al. 1978). Empirical studies have shown that metabolic rate is increased during the production of eggs (Nilsson and Råberg 2001, Vezina et al. 2006). The increase in metabolic rate during egg laying is individual and
varies between 16-27% (Vezina et al. 2006), but is proportional to egg size; it is more costly to produce a larger egg and maintain larger oviducts (Nilsson and Råberg 2001). Thus, the metabolic cost of egg production may be a contributing factor to the hens’ overall higher mass-specific BMR in comparison to the roosters. Previous studies on Red Junglefowl have also shown that roosters have a lower BMR than hens, in support of the findings in my study (Hammond et al. 2000).

Recent studies show that feather pecked hens consume more food than less feather pecked hens (Su et al. 2006, de Haas et al. 2010). The increased food consumption is thought to be the consequence of an increase in heat production, which is effected by various factors such as BMR, plumage cover and physical activity (Su et al. 2006). This indicates that a feather pecked hen with low plumage-cover has less insulation and therefore must increase its’ BMR to increase the heat production, which increases the energy requirement and therefore also food consumption. This is, in some ways, in contradiction to the findings of my study, which show that feather pecked hens forage less than hens with full plumage. On the other hand, my study supports the findings that feather pecked hens have a higher BMR than hens with full plumage and that this indicates that the higher BMR of the feather pecked hens is due to lack of insulation.

No morphological measures showed any link to variation in mass-specific BMR, suggesting that only mass was of importance in explaining variation in metabolic rate.

Not all behaviours showed a significant relationship with BMR; some of these behaviours were not correlated between 34 and 40 weeks of age, thus no relationships were predicted with BMR.

Careau and co-workers (2008) hypothesised two different mechanistic models of how variation in BMR and activity may be related, within individuals. The models are called ‘the performance model’ and ‘the allocation model’ (Careau et al. 2008). The idea for the performance model comes from aerobic-capacity model for evolution of endothermy and suggests that an increased activity level leads to an increase in maximal aerobic metabolic rate, which in turn leads to an increase in RMR/BMR (Careau et al. 2008, Nespolo et al. 2011, Careau and Garland 2012). This means that the performance model predicts a positive relationship between BMR and activity because an individual with higher BMR is able to support a higher activity level (Careau et al. 2008, Careau and Garland 2012). In contrast to the performance model, the allocation model assumes that an animal has a fixed amount of energy (Careau et al. 2008, Careau and Garland 2012). This means that an energetic trade-off
must occur between competing energy requiring processes such as BMR and activity. The trade-off that occurs means that the allocation model predicts a negative relationship between BMR and activity (Careau et al. 2008, Careau and Garland 2012). Ergo, an animal with low BMR has more energy to spend on being active. Both the performance model and the allocation model are supported by the literature (see references in Careau et al. 2008, Careau and Garland 2012).

In the discussion of personality and variation in metabolic rate by Careau and co-workers, activity is defined as an individual’s physical activity in terms of muscular movement leading to locomotion (Reale et al. 2007, Careau and Garland 2012). I therefore consider foraging as recorded in the birds I measured metabolic rate on, as activity, since the birds move around in their search for food (thus performed physical activity leading to locomotion). The results from my study show that sex-centred mass-specific BMR and foraging are negatively correlated, which means that my results support the allocation model. The birds with high BMR have less energy to spend on foraging because of the energetic trade-off and therefore spend less time on food search. On the other hand, the birds with low BMR have more energy to allocate to other energy-demanding activities such as foraging and can therefore spend more time searching for food. My study also showed a positive relationship between sex-centred mass-specific BMR and how much time a bird spent being vigilant. However, I do not consider vigilance as an energy-demanding activity, hence; it cannot be applied to these models. Although, this positive relationship was expected; birds that spend more time foraging spend less time being vigilant and vice versa. As suggested by Sih and co-workers (2004) and later by Biro and Stamps (2008), correlations among behavioural traits typically exist. An individual that is considered to be active and spends a lot of time foraging might then be expected to spend less time being vigilant and by extension, this individual may be considered as bolder, compared to an individual that spend more time being vigilant and less time searching for food. As predicted by the allocation model, this bolder, more active individual has a lower BMR. Due to the energetic trade-off, this individual has more energy to allocate to other energy demanding processes, which is why the individual is more active. Of course, this relationship can be turned on its head as well; an individual that spends less time foraging and more time being vigilant may be considered as shyer and less active. This shyer, less active individual has a high BMR, which is why it has less energy to spend on activity, since activity is an energy demanding process.

Although this study has contributed to determining the relationship between personality traits and BMR, more empirical studies are still
needed to fully understand the relationship between behaviour, metabolism and life history-trait.

6 Conclusion

My findings show that there is a correlation between basal metabolic rate and personality traits in Red Junglefowl. This correlation suggests that there may be physiological constraints underlying behavioural plasticity. However, the nature of this relationship needs to be investigated further for us to better understand the underlying mechanism of variation in animal personality.

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