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Fluctuating asymmetry, a marker of poor growth quality, is associated with adult male metabolic rate

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Abstract

Objectives: Life history theory, a branch of evolutionary theory, predicts the existence of trade-offs in energetic allocation between competing physiological functions. The core metabolic cost of self-maintenance, measured by resting metabolic rate (RMR), represents a large component of human daily energy expenditure. Despite strong selective pressures for energetic frugality and high observed inter-individual variation in RMR, the link between RMR and energetic allocation to life-history traits remains understudied in humans.

Materials: In a sample of 105 ($m = 57$, $f = 48$), we investigated the relationship between adult RMR and investment in growth quality, as measured by fluctuating asymmetry (FA).

Results: Measurement of RMR and FA in university rowers revealed a significant positive correlation amongst males ($n = 57$, $r = 0.344$, $p = 0.005$, 1-tailed; standardized 95% CI, 0.090 to 0.598). Convincing evidence for a correlation among females was not found ($n = 48$, $r = 0.142$, $p = 0.169$, 1-tailed, standardized 95% CI, -0.152 to 0.435).

Discussion: The data suggest that low-quality asymmetrical growth is associated with later-life metabolic inefficiencies in males. Energetic investment in processes (likely concerning the stress-response) unrelated to growth during childhood may thereby trade-off against adult metabolic efficiency. We suggest that the presence of a relationship between RMR and FA in males but not females may be explained by the additional metabolic strain associated with larger body size and increased male muscularity, which may amplify the inefficiencies arising from low-quality growth.

KEYWORDS

energetics, fluctuating asymmetry, growth, life history theory, metabolism

1 | INTRODUCTION

1.1 | Life history theory and metabolic rate

Life history theory seeks to characterize the competitive allocation of limited resources between competing physiological functions

throughout the lifespan (Leonard, 2012; Stearns, 1989, 1992; Zera & Harshman, 2001). In the absence of increased energy availability, a life history strategy involving a greater allocation of energy toward one trait necessitates reduced investment in others (Cody, 1966). The significant fitness consequences of such allocation patterns have led to strong selective pressures encouraging the effective capture and

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appropriate distribution of energy between functions (Leonard & Ulijaszek, 2002; Ulijaszek, 1995; Wells et al., 2017).

Resting metabolic rate (RMR) describes the sum of the specific energy expenditures of individual body organs and tissues at rest (Shirley et al., 2019). RMR represents a significant portion of an individual's daily energy budget, comprising around 50% of daily energy expenditure on average in mammals in general, and on average ~60%–70% for humans living in contemporary Western society (Black et al., 1996; Ravussin et al., 1986). Given strong selective pressures for energetic efficiency and frugality (i.e., performing a given physiological process at a lower metabolic cost), it is perhaps surprising that RMR appears to be highly variable both between and within populations in vertebrates (Careau et al., 2008; O'Steen & Janzen, 1999; Steyermark & Spotila, 2001; White & Seymour, 2004; Wikelski et al., 2010), including humans (Ferraro & Ravussin, 1992; Ravussin et al., 1986). High interindividual variation, coupled with low levels of day-to-day intraindividual variability (Haugen et al., 2003), provides a natural experiment to consider the relationship between RMR and other life-history traits.

The study of the energetics of life-history strategies has generated two distinct theories describing the relationship between RMR and life history variation. The first considers RMR as a cost of maintenance, consuming a large portion of an individual's daily energy budget. This theory stems from the “compensation hypothesis” (or principle of allocation) and describes negative trade-offs between RMR and traits such as growth, reproduction, and storage (Cody, 1966; Longman, Prall, et al., 2017; Reznick et al., 2000; Roff, 1992; Stearns, 1992; Zera & Harshman, 2001). Allocating less RMR may therefore free energy for use by other physiological processes (Mitton, 1993). Conversely, the “increased intake” hypothesis (or biosynthesis theory) (McNab, 1980, 1986) posits RMR to be an indicator of total potential energy turnover, and is thereby representative of energy input rather than output. Individuals with high RMR may be considered to have a larger metabolic “engine,” capable of generating higher levels of energy to achieve higher rates of biosynthesis. The increased intake hypothesis describes positive relationships between RMR and energetic investment in other physiological processes (Martin, 1983b).

Research investigating the relationship between RMR and a range of fitness-related traits in non-human species has been inconclusive (Burton et al., 2011). For example, a positive relationship was reported between RMR and reproductive fitness in bank voles (*Myodes glareolus*) (Boratyński & Koteja, 2010), while no association was found with reproductive senescence in great tits (*Parus major*) (Bouwhuis et al., 2011). Studies considering survival are similarly inconclusive, with investigations identifying positive (Jackson et al., 2001), negative (Álvarez & Nicieza, 2005; Artacho & Nespolo, 2009; Bochdanský et al., 2005; Jackson et al., 2001; Larivée et al., 2010), variable (Boratyński et al., 2010; Boratyński & Koteja, 2009) and no (Bouwhuis et al., 2011) associations.

1.2 | Growth quality and fluctuating asymmetry

Looking beyond reproduction, we now consider another life history function—growth. The energetic cost of growth represents a

significant energy investment in the life history of an individual (Hill & Kaplan, 1999), and may therefore interact with RMR. Two dimensions of growth may be considered—growth *rate* and growth *quality*.

A positive relationship is evident between metabolic rate and growth across generations. In humans, maternal basal metabolic rate (BMR) determines the extent of energetic allocation toward fetal growth during pregnancy (Wells, 2018). This is consistent with mammals in general, where maternal BMR represents a constraint on fetal growth, such that mothers with higher BMRs give birth to babies with larger body size and brain size (Martin, 1983a). However, studies considering the association between RMR and growth rate within the life-course of individuals have been inconclusive, although food availability appears to be an important mediator. In non-human species, laboratory studies providing food ad libitum tend to report positive correlations whereby individuals with higher RMR grow faster (thus supporting the increased intake hypothesis) (Nespolo & Franco, 2007; Yamamoto et al., 1998). Under such conditions, animals may have evolved a larger metabolic capacity to process food more quickly, and generate higher rates of energy output to meet physiological demands (Biro & Stamps, 2010). In contrast, in their native, food-restricted habitat, brown trout (*Salmo trutta*) (Álvarez & Nicieza, 2005) and snapping turtles (*Chelydra serpentina*) (Steyermark, 2002) exhibit negative correlations between RMR and growth (thus supporting the compensation hypothesis). Sea bass with high RMR also loses mass more quickly when fasting (Killen et al., 2011). This may reflect a strong selection for energetic frugality arising in habitats with limited energy availability (Harshman et al., 1999; Mueller & Diamond, 2001). Consequently, individuals with more efficient metabolisms and lower RMRs may be better suited to survive conditions of energetic stress (Álvarez & Nicieza, 2005; Wells, 2018).

A second dimension of energetic investment in growth concerns growth *quality*. Here, we consider growth quality in terms of the degree of symmetry. Growth quality can be measured via fluctuating asymmetry (FA), defined as “random deviation from perfect bilateral symmetry in a morphological straight for which differences between the right and left sides have a mean of zero and are normally distributed” (Watson & Thornhill, 1994). Since the same genetic code is responsible for both sides of any bilateral trait, the two structures represent independent replicates of the same developmental events. The degree of asymmetry is thereby informative of the propensity of an individual's growth to deviate from the genetically programmed outcome (Nilsson, 1994). Stressors such as infection by parasites (Møller, 1992), growth drive (Wells et al., 2006), mutations (Parsons, 1992), noise (Gest et al., 1986) and high living density impose competing demands on the energy budget, and act to increase FA (Møller et al., 1995). FA is of interest to a range of academic disciplines because it allows investigation of an individual's ability to achieve stable development of a genotype into a phenotype under given environmental conditions (Gangestad et al., 1994; Klingenberg, 2003; Møller, 1990; Palmer & Strobeck, 1986; Palmer & Strobeck, 1992; Thornhill & Gangestad, 1993; Thornhill & Møller, 1997; Van Dongen, 2006).

The extent of human fluctuating asymmetry varies during development. FA has been shown to decrease until aged 10 years (Hope

et al., 2013; Wilson & Manning, 1996), with a possible increase from 11 to 15 years (Wilson & Manning, 1996), before decreasing again and reaching a steady level around 18 years. Wilson and Manning (1996) suggest that the relationship between FA and age reflects the influence of growth rate (rapid growth may induce the development of FA) on growth quality as described in the equation:

$$P_g + P_r = A - (R_m + R_r)$$

Where P_g and P_r represent the production of growth and structures associated with reproduction, A is absorbed energy, R_m is the metabolic cost of maintenance, and R_r is the cost of other activities (Bayne & Newell, 1983). The imposition of environmental stress may reduce A or increase R_r , leading to a reduction of P_g and an increase in FA.

It is worth noting that similar developmental FA patterns were not observed in Jamaican children, suggesting that differences in environmental and ethnicity may play a role (Trivers et al., 1999).

This study sought to investigate the association between RMR and growth quality, as measured by fluctuating asymmetry. By

employing a larger sample size (an increase from $n = 30$ to $n = 105$) and more modern methods (a metabolic cart as opposed to a Douglas bag), we will build upon the work of Manning et al. (1997) who previously observed a positive relationship between FA and RMR in human adult males ($n = 30$, $p = 0.035$) but not in females ($n = 30$, $p = 0.19$).

The increased intake hypothesis predicts that an increased RMR allows the diversion of a greater amount of energy toward growth. This would be evidenced here by a positive association between RMR and growth quality, which generates a negative correlation between RMR and FA (Figure 1a below). In contrast, a positive correlation between RMR and FA could be interpreted in two ways. Firstly, a positive relationship between RMR and FA could be considered support for the compensation hypothesis, which predicts that RMR competes with growth for energetic allocation (Figure 1b below). Alternatively, a positive association could reflect later-life metabolic inefficiencies arising from previous low-quality asymmetrical growth (Figure 1c below). Energetic allocation toward growth may be reduced by, for example, high-pathogen environments necessitating energetic diversion toward immune function (Urlacher et al., 2018).

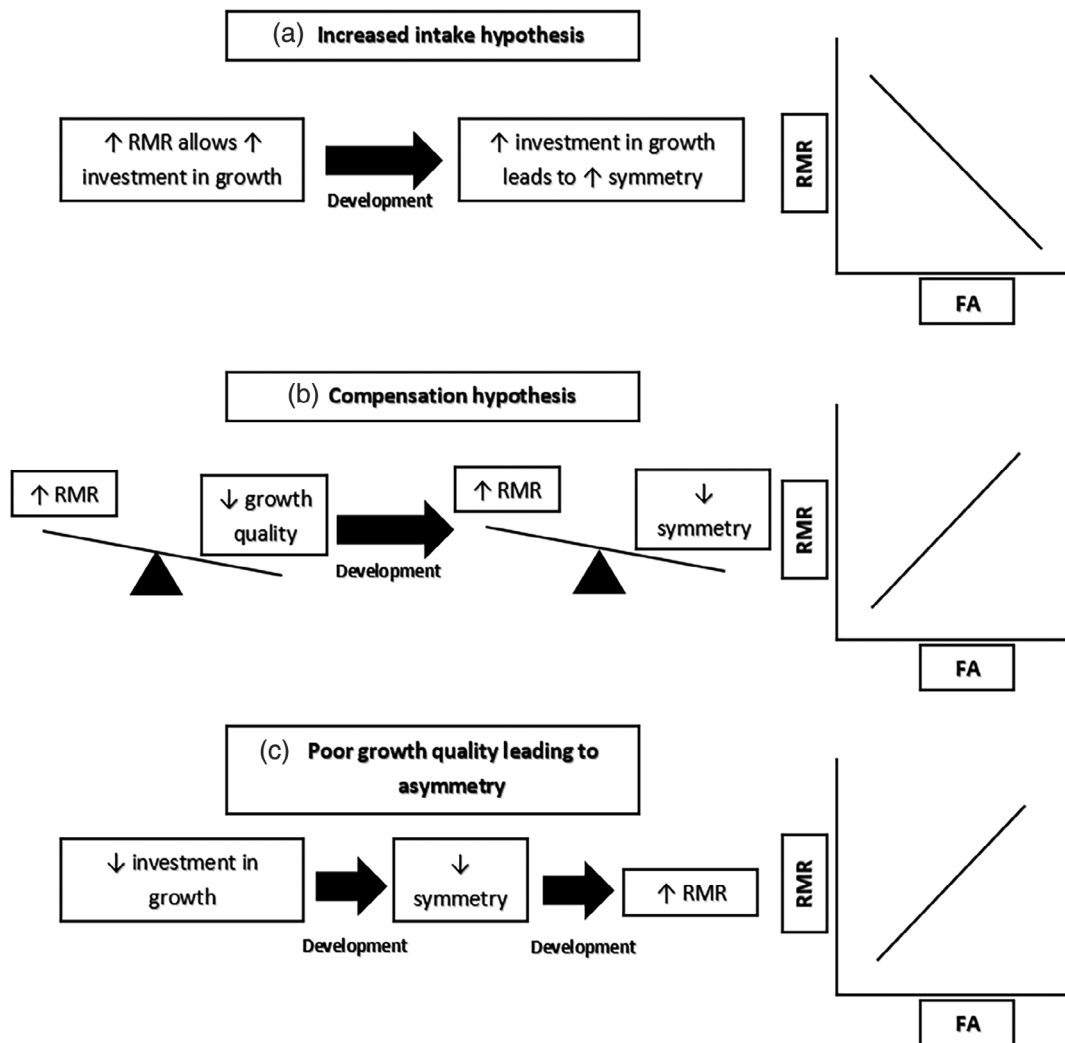


FIGURE 1 Conceptual diagram showing (a) the increased intake hypothesis, (b) the compensation hypothesis, with increased RMR potentially being induced by a genetic stressor, and (c) later-life metabolic inefficiencies arising from previous low-quality asymmetrical growth

TABLE 1 Sample descriptive characteristics

	Male (n = 57)			Female (n = 48)			Ln transformed % difference
	Mean	SD	Range	Mean	SD	Range	
Height (cm)	187.2	9.1	167.1–203.8	172.7	6.2	161.0–186.4	8.0***
Mass (kg)	83.4	8.8	63.8–106.6	68.3	9.4	54.2–87.8	20.3***
Age	23.6	3.9	18–35	24.3	4.4	18–35	2.5
Years rowed	5.1	4.0	0.25–16.0	5.3	3.6	0.5–17.0	18.1
RMR (kJ/day)	8185	1408	5631–11,380	6882	1293	3950–11,165	17.6***
Composite FA	1.95	0.66	0.59–3.48	1.82	0.66	0.77–3.93	6.6

* $p < 0.05$.** $p < 0.01$.*** $p < 0.001$.**TABLE 2** Male correlation matrix (n = 57)

	CFA	RMR	Height	Mass	Age
CFA	-				
RMR	0.344*	-			
Height	-0.042	0.135	-		
Mass	-0.035	0.208	0.708**	-	
Age	0.080	-0.048	0.240	-0.138	-

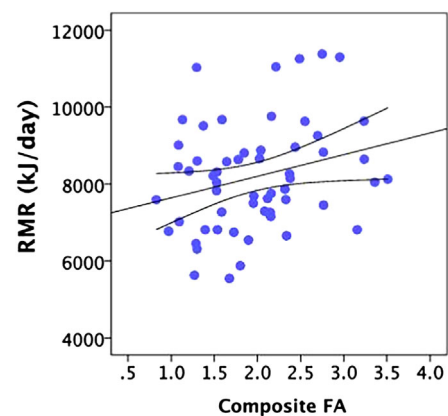
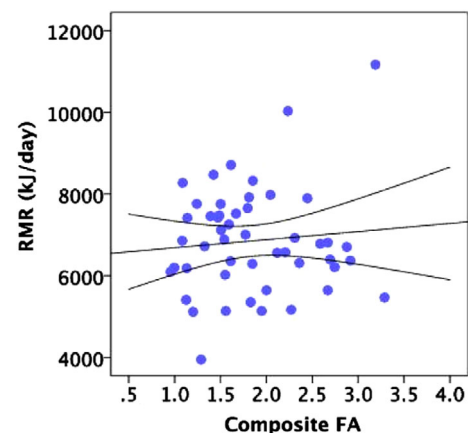
* $p < 0.05$.** $p < 0.01$.**TABLE 3** Female correlation matrix (n = 48)

	CFA	RMR	Height	Mass	Age
CFA	-				
RMR	0.142	-			
Height	0.019	0.294*	-		
Mass	0.125	-0.426**	0.559**	-	
Age	-0.107	0.227	-0.084	-0.101	-

* $p < 0.05$.** $p < 0.01$.

Asymmetry has been linked to energetic efficiency in a range of species. For example, the introduction of asymmetry to the tail feathers of barn swallows (*Hirundo rustica*) increases both the power required for low-speed flight and the energy cost of straight-line flight (Barbosa et al., 2003; Møller & Swaddle, 1997; Norberg, 1994; Thomas, 1993). In humans, it has been suggested that fluctuating asymmetry in external traits are indicative of internal developmental instability, which in turn generates energetic inefficiencies (Longman et al., 2011). The above scenarios can be visually represented in the conceptual diagram below in Figure 1.

Based on the preponderance of literature describing energetic trade-offs, including our own previous work (Longman, Prall, et al., 2017; Longman, Stock, & Wells, 2017), we hypothesized a positive relationship between RMR and FA in this study. We expect this positive association to be indicative of later-life metabolic inefficiencies resulting from low-quality growth during development (Figure 1c).

**FIGURE 2** Scatter plot of male RMR and CFA**FIGURE 3** Scatter plot of female RMR and CFA

The energetic costs of growth decrease rapidly during infancy (Wells & Davies, 1998), and despite a rise during the adolescent growth spurt (Bogin, 1999a; Bogin, 1999b; Dwyer, 1981), they rarely exceed 10% of the total daily energy budget (Dwyer, 1981). Although, as previously mentioned, there is evidence relating environmental

stressors to increased FA, we propose that it is unlikely that a high RMR in early life would act to constrain the quality of growth. Furthermore, the adult RMR data collected here do not directly describe the participant's RMR during childhood growth, which may then act to influence growth quality. Consequently, we predict that the data will support the hypothesis that early-life low-quality asymmetrical growth results in later-life metabolic inefficiencies.

Sex differences in body composition may lead to differential relationships between RMR and FA in males and females. In contrast to many animal species, humans exhibit significant sexual dimorphism in both height and body composition. Males are ~7% taller (Gustafsson & Lindenfors, 2004), and tend to have increased bone mineral content (Maynard et al., 1998) as well as greater lean mass (Welle et al., 2008) and lower fat mass relative to body weight (Wells, 2007) relative to women. As well as contributing to differential thermoregulatory challenges during prolonged physical activity (Longman et al., 2019, 2020), sex differences in body composition have energetic implications. Skeletal muscle mass is a metabolically expensive tissue, accounting for ~20% of human male basal metabolic rate (Elias, 1992), and a larger portion of whole-body energy expenditure upon activation (McArdle et al., 2001). As resting muscle metabolism has been shown to contribute to interindividual variation in RMR (Zurlo et al., 1990), males thereby experience greater constraint acting on the amount of energy available for competing physiological processes such as growth. We further hypothesize that the increased metabolic burden associated with greater male lean mass will lead to a more pronounced relationship between RMR and FA in male participants.

2 | MATERIALS AND METHODS

The participants were 57 male and 48 female student rowers from the University of Cambridge, and testing being carried out in Cambridge, UK. Ethical approval was granted by the University of Cambridge Human Biology Research Ethics Committee.

RMR was measured in accordance following standard procedure (Compher et al., 2006) using a Cortex Metalyzer 3b under controlled conditions (29% humidity and 18°C). The system was calibrated according to manufacturer specifications. Participants were tested in the morning under the following conditions: no food for 5 h, no alcohol for 2 h, no nicotine for 2 h, no caffeine for 4 h, no moderate exercise for 2 h, and no vigorous exercise for 14 h.

Participants' height and mass were measured using a stadiometer (Seca, Hamburg, Germany, accurate to the nearest 0.1 cm) and scales (also Seca, accurate to 0.1 kg) (Cameron, 1984, 2004; Gordon et al., 1988). Seven bilaterally symmetrical traits were selected given their previous use in the literature, high repeatability, and resistance to the effects of mechanical loading. These traits were: lengths of all four fingers, wrist width, ankle width, and foot length. Finger measurements were taken from the center of the digit crease proximal to the palm to the fingertip using Mitutoyo Vernier calipers accurate to 0.01 mm (Longman et al., 2011;

Manning & Chamberlain, 1993; Voracek et al., 2007; Wells et al., 2006). Wrist widths were measured between the medial and lateral aspects of the ulna styloid (Wilmore et al., 1988). The ankle width was measured as the maximum distance between the most medial extension of the medial malleolus and the most lateral extension of the lateral malleolus was recorded (Wilmore et al., 1988). Foot length was measured from the most posterior aspect of the heel to the tip of the big toe (Wells et al., 2006).

All symmetry measurements were taken blind (i.e., the measurer was unable to see the caliper digital display) twice, with the mean average of the two being used for analysis. The relative FA for each trait was calculated per participant by subtracting the mean of the left from the mean of the right measurement and dividing this value by the mean of the left and right measurements (Palmer & Strobeck, 1992). The modulus of this value was then used to obtain a composite FA score for each participant, found by summing the relative FA values for each trait and dividing by seven as follows (Trivers et al., 1999):

$$\text{Composite FA} = \{ \sum | R_i - L_i | / [(0.5 (R_i - L_i))] \} / 7$$

This composite FA (CFA) value was then used in analysis with RMR. Composite FA is thought to be a better indicator of an individual's growth quality than any single trait (Leung & Forbes, 1997; Livshits & Kobylansky, 1989; Thornhill & Gangestad, 1999). As in (Longman et al., 2011), the repeatability measures of the metrics contributing to CFA were high, ranging from $r = 0.991$ to 0.998 .

2.1 | Statistical analysis

2.1.1 | SPSS v25 was used for all analyses, with a significance benchmark of 0.05

Independent samples *t* tests were used to compare natural log transformations of male and female descriptive statistics. Correlations between composite FA, RMR, height, body mass, and age were evaluated using Pearson's Product Moment Correlations. Scatter plots with errors were made to visualize the relationship between the exposure variable, composite FA, and the outcome variable, RMR. Finally, a multiple linear regression model was used.

3 | RESULTS

3.1 | Sample characteristics

There was no significant difference between the age of the male and female participants (male $M = 23.6$, $SD = 3.95$; Female $M = 24.3$, $SD = 4.39$; $t[103] = -0.828$, $p = 0.410$). The cohort exhibited sexual dimorphism, with the largest differences being observed in body mass (females 20.32% lighter) and RMR (males 17.59% greater).

A description of the male and female cohorts is given in Table 1.

3.2 | Correlation analyses

Both male and female participants exhibited a significant positive correlation between height and mass (Male $r = 0.708$, $p < 0.001$; Female $r = 0.559$, $p < 0.001$). Female RMR was significantly positively associated with height ($r = 0.294$, $p = 0.043$) and mass ($r = 0.426$, $p = 0.003$). The male subsample did not exhibit positive associations between these variables. RMR was significantly positively correlated with composite FA in the male subsample ($r = 0.344$, $p < 0.001$) but not the female subsample ($r = 0.142$, $p = 0.169$). See Tables 2 and 3 for male and female correlation matrices.

3.3 | RMR and fluctuating asymmetry

3.3.1 | Males

Regression analysis revealed a significant positive correlation between RMR and CFA ($n = 57$, $r = 0.344$, $r^2 = 0.118$, $p = 0.009$, 1-tailed; standardized 95% CI, 0.090 to 0.598). See Figure 2 below.

3.3.2 | Females

Regression analysis revealed no significant correlation between RMR and CFA ($n = 48$, $r = 0.142$, $r^2 = 0.020$, $p = 0.169$, 1-tailed; standardized 95% CI, -0.152 to 0.435). See Figure 3 below.

In a multiple linear regression model, both CFA and sex were significant predictors of RMR, total $r^2 = 0.227$. RMR was 1233 kJ/day (95%CI -1752 , -712 , $p < 0.001$) lower in females than males, and increased by 525 kJ/day (95%CI 133, 918) for each unit increase in CFA score.

and/or efficiently, and thus generate higher levels of energy output to support costly physiological processes (Biro & Stamps, 2010). However, the positive relationship between adult RMR and growth quality predicted by the biosynthesis theory was not evident in this study. Furthermore, this data cannot provide direct support for the principle of allocation ("compensation" hypothesis), as the measures of RMR were taken in adulthood. Instead, the positive relationship described by our data supports the concept that poor-quality asymmetric growth leads to metabolic inefficiencies later in life. This is consistent with previous work, identifying deleterious metabolic consequences of structural asymmetry (Barbosa et al., 2003; Møller & Swaddle, 1997; Norberg, 1994; Thomas, 1993). To date, it is unclear whether measured asymmetry in external traits leads to inefficiencies because (a) the body is also asymmetry internally (e.g., blood vessel diameter on both sides of the body) or (b) the body is poorly constructed in other ways (e.g., leaky valves). Infant or adolescent energetic investment in processes other than high-quality, symmetrical growth (such as allocating energy to immune or other stress responses) can thereby be considered to trade-off against later life metabolic efficiency.

These trends are consistent with previous work investigating the interaction between metabolic rate and growth. At a broader level, Steyermark (Steyermark, 2002) reported that juvenile snapping turtles (*Chelydra serpentina*) with high metabolic rates tend to grow more slowly than individuals with lower metabolic rates. In humans, FA has previously been negatively related to health measures in males but not females (Gangestad & Thornhill, 1997), and RMR has been differentially related to FA in males (a positive relationship) and females (no relationship) (Manning et al., 1997). The present study observed a similar pattern of sexual dimorphism, although we did not observe the sex differences in the relationship between FA and mass previously reported by Manning and colleagues (Manning, 1995).

	Unstandardized B	Coefficients SE	Standardized coefficients Beta	t	Sig	95% confidence interval for B	
						Lower bound	Upper bound
(Constant)	5924.8	405.3		14.6	0.000	5120.9	6728.7
Sex	1233.2	295.5	0.412	4.8	0.000	718.5	1748.0
CFA	525.5	196.4	0.232	2.7	0.009	135.9	915.1

4 | DISCUSSION

This study identified a significant positive correlation between male RMR and fluctuating asymmetry ($n = 57$, $r = 0.344$, $p = 0.009$, 1-tailed; standardized 95% CI, 0.090 to 0.598). No convincing evidence for a similar relationship was observed in the female cohort ($n = 48$, $r = 0.142$, $p = 0.169$, 1-tailed; standardized 95% CI, -0.152 to 0.435).

The increased intake hypothesis proposes that RMR reflects the size of the metabolic engine needed to capture, ingest, extract, and mobilize energy (Biro & Stamps, 2010; Careau et al., 2008). A higher RMR represents a larger engine that can process food more quickly

The association between RMR and FA was statistically significant in males, but not in females. We propose that this difference may arise from the additional metabolic burden imposed by greater male muscularity, organ size, and body size. As fat-free mass is a significant predictor of RMR (Cunningham, 1991; Owen, 1988; Ravussin & Bogardus, 1989), males experience a greater maintenance cost, and hence the costs of asymmetric growth may be amplified. This increases the overall metabolic cost of an individual, in turn enhancing the potential deleterious metabolic effects of poor prior developmental quality. Possible mechanisms include less efficient characteristics of organ structure.

The relationship between RMR and FA may also be influenced by early-life adversity. The experience of environmental stress during sensitive developmental windows can introduce asymmetry which persists into later life (Swaddle & Witter, 1994; Wells et al., 2006). Similarly, early-life developmental stress may also influence later-life RMR. Experimental work by Criscuolo and colleagues highlighted the influence of early life nutritional stress on subsequent adult metabolic rate. Dietary manipulation of zebra finches (*Taeniopygia guttata*) during the developmental phase induced compensatory catch-up growth, which led to a higher later-life RMR compared to control groups (Criscuolo et al., 2008). Thus, a positive association between FA and RMR may indicate that increases in both FA and RMR are later-life consequences of poor-quality growth arising from early-life exposure to stress. A potential mechanism would be that early developmental stress induces poor-quality catch-up growth, which leads to both measurable asymmetry in external traits and inefficient organs and metabolic systems (Manning & Ockenden, 1994). Since we did not collect any measures of growth patterns, further work including indices such as lower leg length is required to investigate this possible explanation.

A portion of an individual's fluctuating asymmetry is "short-term" rather than "fixed." It has been shown that some men exhibit short-term changes in asymmetry (Manning et al., 2002). While the mechanism driving these short-term increases in asymmetry is unknown, it is in part driven by increases in thyroxine levels. Thyroxine, which increases metabolic rate (Lebon et al., 2001), may therefore provide a link between metabolic rate this short-term component of overall FA.

Further work investigating the relationship between RMR and growth may consider the influence of nutrition. By experimentally manipulating caloric intake and stimulating the metabolism of cotton rats, Derting and colleagues (Derting, 1989) found that the compensation hypothesis and increased intake hypothesis may not be mutually exclusive. They observed that when rats were fed ad libitum and administered thyroxine (which increases RMR), the rats grew faster than controls. In contrast, when food-restricted rats were given thyroxine the result was severe growth restriction relative to controls. This study illustrates how changing energy acquisition rates can impact the relationship between metabolic rates and life-history variables. When food is unlimited, the increased intake hypothesis may appropriately describe the relationship between RMR and investment in other traits, while the compensation hypothesis may prevail when food is limited. Neglecting to consider energetic availability may lead to a false conflict between the two models.

A limitation of this study is the lack of body composition data. Both fat-free mass and fat mass are significant predictors of metabolic rate, so it is possible that individuals with high FA and high RMR also have a high fat-free mass. Further work is required to address this (Johnstone et al., 2005). It is also acknowledged that, although all participants were at rest under standardized conditions when RMR was measured, the physiological work being done was not directly assessed. However, the interpretation of the results in terms of metabolic efficiency is consistent with previous reports (Criscuolo et al., 2008).

To conclude, we observed a statistically significant positive relationship between RMR and FA in male (but not female) participants. This data suggests that poor-quality asymmetric growth early in life leads to adult metabolic inefficiencies. Sex differences in the levels of metabolically expensive muscle tissue may explain this sex difference.

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AUTHOR CONTRIBUTIONS

Daniel Longman: Conceptualization; data curation; formal analysis; methodology; project administration; writing-original draft; writing-review & editing. **Sakura Oyama:** Formal analysis; investigation; writing-original draft; writing-review & editing. **James Cracknell:** Formal analysis; investigation; writing-original draft; writing-review & editing. **Nathan Thompson:** Investigation; methodology; writing-original draft; writing-review & editing. **Dan Gordon:** Investigation; methodology; writing-original draft; writing-review & editing. **Jay Stock:** Conceptualization; funding acquisition; investigation; methodology; project administration; writing-original draft; writing-review & editing. **Jonathan Wells:** Conceptualization; formal analysis; methodology; writing-original draft; writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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