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Developmental stress reduces body condition across avian life-history stages: A comparison of quantitative magnetic resonance data and condition indices

Fanny-Linn O.H. Kraft*, Stephanie C. Driscoll, Katherine L. Buchanan, Ondi L. Crino

Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia

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ABSTRACT

Animals exposed to stressful developmental conditions can experience sustained physiological, behavioral, and fitness effects. While extensive research shows how developmental stress affects development, few studies have examined the effects on body composition. To test the effects of developmental stress on nestling and adult body composition, we dosed nestling zebra finches (*Taeniopygia guttata*) with either a corticosterone (CORT) or control treatment. We calculated condition indices (scaled mass, residual mass, and ratio indices) from morphometric measurements and used quantitative magnetic resonance (QMR) to assess body composition during early development and adulthood. We compared these three traditionally-used condition indices to QMR-derived body composition measurements, to test how well they predict relative fat mass. Our results show that developmental stress decreases body mass, and has a dose-dependent effect on tarsus length in nestling birds. Furthermore, stress treatment during the nestling period had long-lasting effects on adult body mass, lean mass and tarsus length. None of the three condition indices were good indicators of relative fat mass in nestlings, but all indices were closely associated with relative fat mass in adults. The scaled mass index was more closely associated with relative fat mass than the other condition indices, when calculated from wing chord length in nestlings. In adults however, the residual mass index and the ratio index were better indicators of relative body fat than the scaled mass index, when calculated from tarsus length. Our data demonstrate the short and long-term impact of developmental stress on birds, and highlight important age-related factors to consider when using condition indices.

1. Introduction

The environment animals experience during development can have sustained effects on their morphology, physiology, behavior, and fitness (Chaby, 2016; Lindstrom, 1999; Lupien et al., 2009; Schoech et al., 2011). For example, in birds, developmental stress decreases nestling growth and body size (Coslovsky and Richner, 2011; Crino et al., 2014; Merino and Potti, 1995; Schmidt et al., 2012). In birds, these effects can have consequences for behavior, longevity, and fitness later in life (Krause and Naguib, 2011; Metcalfe and Monaghan, 2001), which may be mediated in part by compensatory growth (Metcalfe and Monaghan, 2001).

Many studies have examined the impact of stress on nestling development, with mixed results as to the long- and short-term effects of stress on body mass (e.g. Crino et al., 2014; Naguib and Gil, 2005; Schmidt et al., 2012), but only a few have examined effects on nestling body composition (Farrell et al., 2015; Kriengwatana et al., 2013; Schmidt et al., 2012). Clutch size and food restriction have long-lasting effects (present in adults that were treated as nestlings) on body mass and body composition, which suggests that long-term changes in morphology can occur due to early life conditions (Kriengwatana et al., 2013; Naguib and Gil, 2005). However, the manipulations used in these studies directly or indirectly (through sibling competition) alter food access to the nestlings. While food restriction can elevate stress hormone levels (Lynn et al., 2003), food restriction may confound the effects of stress on morphology by directly limiting nestling growth. Stress treatment without food restriction has been shown to reduce nestling mass and affect body composition beyond the end of the treatment, but not into adulthood (Crino et al., 2014; Schmidt et al., 2012). Hence, there is no consensus as to whether developmental stress can have long-lasting effects on nestling body mass, body composition, and body condition.

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* Corresponding author.
E-mail address: f.hovringkraft@deakin.edu.au (F.-L. O.H. Kraft).

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Body condition is an ecologically important concept that is widely used in physiology, behavior, and ecology studies to evaluate the health and well-being of animals (e.g. Booth and Hixon, 1999; Jakob et al., 1996; Rowe and Houle, 1996; Wauters et al., 1995). Condition is a measure of the energetic or nutritional state of an animal, and is commonly defined as the relative size of energy reserves (i.e. relative fat mass) that an animal has available to allocate to life processes (e.g. daily maintenance, reproduction, immunocompetence; Hill, 2011; Jacobs et al., 2012; Schulte-Hostedde et al., 2001). This definition has received criticism for a number of reasons. Both fat and lean tissue (i.e. muscle) may be important for animal performance and fitness (Gerson and Guglielmo, 2011; Hedenström et al., 2009). Additionally, an animal's optimal body composition may vary across life-history stages. For example, in small passerines, larger fat stores may be beneficial for thermoregulation (Bednekoff et al., 1994), and are linked to nestling survival (Tinbergen and Boerlijst, 1990), but could be a hindrance during fledging when body mass can be a detriment to take-off flight (Kullberg et al., 1996; Sprague and Breuner, 2010).

Condition indices such as the scaled mass index, residual mass index, and ratio index are calculated from body measurements (i.e. mass, length etc; Maute et al., 2015; McWilliams and Whitman, 2013; Peig and Green, 2010) and are commonly used to estimate body condition in both adults and developing animals (Golet and Irons, 1999; Jakob et al., 1996; Schulte-Hostedde et al., 2001; Sockman and Schwabl, 2001). The scaled mass index accounts for errors associated with the dependency between length and body mass measurements and is considered by some to be a more accurate measure of condition than the residual body mass index and the ratio index (Bókony et al., 2012; but see Jacobs et al., 2012; Labocha et al., 2014). However, all three indices are widely used across taxonomic groups to quantify condition (Falk et al., 2017; Labocha et al., 2014; MacCracken and Stebbings, 2012). Condition indices rely on the assumption that increased relative body mass is equivalent to increased relative body fat (Hill, 2011; McWilliams and Whitman, 2013), but changes in body mass can occur due to changes in lean mass (Gerson and Guglielmo, 2011; Hedenström et al., 2009; McWilliams and Whitman, 2013). Here, we use quantitative magnetic resonance (QMR) to directly evaluate changes in body composition over life-history stages in zebra finches (*Taeniopygia guttata*) exposed to either a stress hormone, corticosterone (CORT), or control treatment (peanut oil) during development. We then compared QMR body composition data to three commonly used condition indices, to test whether these indices accurately represent relative fat mass in nestlings.

QMR is a relatively new technique for measuring body composition (EchoMRI™, 2016). It uses a magnetic field to align the spins of hydrogen nuclei, and estimates the amount of different tissue types (e.g. lean muscle, fatty tissue, etc.) based on the frequencies at which these hydrogen nuclei resonate in the sample (EchoMRI™, 2016; Guglielmo et al., 2011). Unlike some other magnetic resonance methods (such as MRI), QMR gives a value of the total mass of different tissues, but does not give a visual estimation of the distribution of tissues in the body (Guglielmo et al., 2011; Hedenström et al., 2009). QMR has been validated as a method of measuring body composition in birds by comparing QMR measurements to gravimetric analyses of carcasses (Guglielmo et al., 2011), and has been used in studies of both wild (Kennedy et al., 2016; Seewagen and Guglielmo, 2011) and captive birds (Farrell et al., 2015; Schmidt et al., 2012). Whereas traditional methods of evaluating whole animal body composition, such as bomb calorimetry, require destruction of the study animal, QMR provides an accurate assessment of soft tissue composition without harming the animal, allowing for longitudinal studies (Johnson et al., 2009; McWilliams and Whitman, 2013; Riley et al., 2016; Warner et al., 2016).

The goals of this study were threefold: 1) To quantify the effects of developmental stress on nestling body composition using QMR, 2) To determine if the effects of developmental stress on body composition persist to adulthood, and 3) To compare QMR measures of body composition to traditional condition indices (the scaled mass, residual body mass, and ratio indices). To accomplish this, we exposed nestling zebra finches to a physiologically relevant high or low dose of CORT or control treatment, and compared changes in body composition between experimental and control nestlings. We made the same comparison with a subset of adult birds that had received either a high-dose CORT treatment or control treatment. We predicted that CORT treatment would decrease nestling body mass and body fat, with more pronounced effects in the high-dose CORT treatment, but that there would be no/less effect on lean mass (in accordance with Farrell et al., 2015). We also predicted that there would be no differences in body mass or composition between the treatments by adulthood (Farrell et al., 2015; Schmidt et al., 2012). Finally, we predicted that condition indices would reflect the body fat of the nestlings more closely than lean mass, and that the scaled mass index (considered to be a more accurate estimate of condition, Peig and Green, 2009, 2010) would reflect fat mass more closely than the other two indices (but see Jacobs et al., 2012; Labocha et al., 2014).

2. Methods

2.1. Parental birds - housing and breeding

From December 2015 to November 2016, adult zebra finches were sourced from an existing breeding colony of wild-derived (12–14 generations from wild) zebra finches at Deakin University, Waurn Ponds, Australia. Eight pairs of zebra finches were each housed in four indoor flight cages measuring 3 × 1 × 2 meters, for a total of 32 breeding pairs used in the experiment. We housed birds on a 14:10 light/dark cycle at 20 °C (± 1 °C) with 50% humidity. We provided breeding birds with *ad libitum* commercial seed diet, water, cuttlefish, grit, and a daily provision of supplemental food consisting of hardboiled egg, spinach, and cucumber. Each flight contained 12 wooden nest boxes and six to eight wicker nesting baskets, and nesting material (shredded burlap and grass). Pairs were allowed to pair and breed freely over sequential breeding attempts, and nests were inspected daily to determine breeding activity.

2.2. Nestlings – experimental treatment

Starting on hatch day, we clipped nestling down feathers in unique patterns to identify individuals. We clipped the down once for each nestling and applied numbered leg bands at 10 days post-hatch. Within clutches, nestlings were randomly assigned to the CORT-treated and control treatment groups. Clutch size ranged from 1 and 6 nestlings, and was included as a fixed covariate in our statistical models (see Section 2.6). Nestlings were treated from 5 to 18 days post-hatching, and the treatment was ended before fledging (Zann, 1996). Nestlings exposed to the CORT treatment were fed oral boluses (25 µl) of CORT (Sigma Aldrich) dissolved in peanut oil and administered directly into the mouth of the nestling twice daily, approximately 5 h ± 1 h apart. From 5 to 15 days post-hatching, low-dose nestlings received 0.124 mg/ml of CORT in peanut oil for a total daily dose of 6.2 µg of CORT. Starting 16 days post-hatch, we increased the dose of CORT for birds in the low dose treatment group, to reflect increases in body mass, to 0.163 mg/ml for a total daily exposure of 8.15 µg of CORT (methods from Crino et al., 2014; Spencer et al., 2009). High-dose nestlings received 0.25 mg/ml of CORT solution twice daily for total dose of 12.5 µg of CORT during the same age period (methods from Spencer et al., 2003, 2005). For the high-dose nestlings, the dosage was consistent throughout the treatment period, to ensure that the dose was physiologically relevant, safe, and ethical for the birds. Control nestlings were fed 25 µl of peanut oil on an identical feeding schedule. These methods induce elevated CORT levels in nestlings (Spencer and Verhulst, 2007) that are comparable to CORT levels documented in wild zebra finches (Crino et al., 2018). We did not collect data on circulating CORT from the birds used in this study.

2.3. *Nestlings – morphometric data and body composition*

We sampled 136 nestlings (N = 69 controls, N = 38 low-dose CORT, and N = 29 high-dose CORT) from 48 nests. The sex of the nestlings was determined after 60 days of age (when sexually dimorphic traits become apparent, Zann, 1996), and due to mortality or birds losing their numbered leg bands, not all birds were sexed (N = 39, females; N = 44, males; N = 53, unknown sex). We collected morphometric (tarsus length, wing chord length, and body mass) and body composition data 10, 15, 20, and 25 days post-hatching (N = 127, 10 days; N = 126, 15 days; N = 121, 20 days; N = 52, 25 days). We measured tarsus length and wing chord length to the nearest 0.01 mm using digital calipers, and body mass to the nearest 0.01 g, using a digital balance. We used a QMR body composition analyzer (EchoMRI-B, Echo Medical Systems, Houston, USA) to quantify total fat, wet lean mass (non-structural tissues such as muscle), total water (free water and water contained in lean mass), and free water (water not bound to tissues, e.g. inside bladder). The body condition analyzer does not detect bone mineral content, nails, or feathers (EchoMRI™, 2016). We collected QMR measurements and morphometric measurements between 0700 and 0930 h, and used the time of day as a fixed covariate in statistical analyses (see statistical methods below). We calibrated the instrument daily using a 34.9 g canola oil standard. To measure body composition, we placed birds in a ventilated falcon tube within a plastic holding tube and inserted them into the instrument for three consecutive 60 s scans. We averaged body composition values from the three scans to the nearest 0.001 g and adjusted the values using calibration equations for zebra finches (fat g × 0.94 and lean mass g × 1.021: Guglielmo et al., 2011). To estimate the variance between scans, we calculated the repeatability of our QMR values using a mixed model approach. We used QMR values from all scans as the dependent variable and ID as a random effect (methods from Nakagawa and Schielzeth, 2010). We divided the squared between-group variance with the sum of the squared between-group and squared residual variances. The resulting repeatability for fat and lean mass were 97.1% and 99.7% respectively.

2.4. *Adults – housing and morphometric data and body composition*

We collected morphometric and body composition data from a subset of 75 birds (N = 38 controls, N = 37 high dose CORT, N = 37 females, N = 38 males) after they reached adulthood (388–718 days post-hatching) in late November 2017. Before data collection, the adults were housed in sex-specific groups in two outdoor aviaries measuring 3 × 1 × 2 meters. The outdoor temperature in Victoria (Australia) ranged between 21 °C (average day temperature) and 10 °C (average night temperature) during the period of data collection. We provided the adult birds with *ad libitum* commercial seed diet, water, cuttlefish and grit. Using the same methods as described above, we collected body mass, wing chord and tarsus length measurements, and measured body composition using QMR. Given the high repeatability of nestling body composition values determined using the QMR, we scanned adults once to minimize handling time.

Table 1
Model fixed effects for the condition variables in nestlings. *P*-values were generated using linear mixed models by restricted maximum likelihood and type three ANOVA. Significant *P*-values are highlighted in bold font ($P > 0.05$). Significance levels: $P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. N = 132 nestlings.

Fixed effects: Nestlings

Variable	Fixed effect	F-value	Degrees of freedom	P-value	
Mass (g)	Intercept	4.004	1	**0.046**	*
	Time of day	5.195	1	**0.023**	*
	Tarsus	230.580	1	< **0.001**	***
	Age	95.912	3	< **0.001**	***
	Treatment	3.679	2	**0.028**	*
	Clutch size	12.730	1	< **0.001**	***
Fat mass (g)	Intercept	17.436	1	< **0.001**	***
	Time of day	1.023	1	0.313	
	Tarsus	55.468	1	< **0.001**	***
	Age	99.008	3	< **0.001**	***
Lean mass (g)	Intercept	13.423	1	< **0.001**	***
	Time of day	3.118	1	0.078	
	Tarsus	230.581	1	< **0.001**	***
	Age	168.499	3	< **0.001**	***
	Clutch size	14.553	1	< **0.001**	***
Relative fat mass	Intercept	0.544	1	0.461	
	Time of day	0.051	1	0.821	
	Tarsus	14.390	1	< **0.001**	***
	Age × Clutch size	6.169	3	< **0.001**	***
	Age	4.630	3	**0.004**	**
	Clutch size	4.415	1	**0.0377**	*
Relative lean mass	Intercept	1656.894	1	< **0.001**	***
	Time of day	23.056	1	0.569	
	Tarsus	4.733	1	**0.030**	*
	Age	0.325	3	< **0.001**	***
Tarsus length (mm)	Intercept	2867.187	1	< **0.001**	***
	Time of day	0.008	1	0.930	
	Age	39.764	3	< **0.001**	***
	Treatment	15.632	2	< **0.001**	***
	Age × Clutch size	4.109	3	**0.007**	**
	Clutch size	0.030	1	0.862	
Scaled mass index	Intercept	1512.199	1	< **0.001**	***
	Time of day	5.660	1	**0.018**	*
	Age	440.752	3	< **0.001**	***
	Clutch size	12.450	1	< **0.001**	***
Residual mass index	Intercept	6.695	1	**0.014**	*
	Time of day	5.229	1	**0.023**	*
	Clutch size	15.038	1	< **0.001**	***
Ratio index	Intercept	1371.123	1	< **0.001**	***
	Time of day	5.457	1	**0.020**	*
	Age	146.159	3	< **0.001**	***
	Treatment	3.460	2	**0.034**	*
	Clutch size	11.071	1	**0.001**	**

2.5. *Calculating condition indices*

The scaled mass index is derived from a structural body measurement (e.g. tarsus length) with a high correlation to body mass (Peig and Green 2010). We examined correlations between body mass and tarsus length (log-log Pearson correlation, tarsus: $r = 0.833$, nestlings; $r = 0.201$, adults) and body mass and wing chord length (log-log Pearson correlation, wing chord: $r = 0.840$, nestlings; $r = 0.002$, adults). For nestlings, wing chord length had a stronger correlation compared to tarsus, but reflects both feather and skeletal growth. For these reasons, we calculated all condition indices from both tarsus and wing chord length.

The scaled mass index '$\widehat{M}_i$' was calculated using body mass together with the scaling relationship between body mass and body length (e.g. tarsus or wing chord length), in accordance with Eq. (1) (Peig and Green, 2009, 2010):

$$\widehat{M}_i = M_i\left[\frac{L_0}{L_i}\right]^{b_{SMA}} \tag{1}$$

where M_i and L_i are, respectively, the body mass (g) and body length (mm) of individual *i*, and b_{SMA} is the scaling exponent of the standardized major axis (SMA) regression of lnM and lnL. L_0 is an arbitrary value of *L*. In Eq. (1), *L* is the mean value derived from the study population and $\widehat{M}_i$ is the predicted body mass for individual *i* when the

Table 2
Tukey's post-hoc test for treatment main effects in nestlings. *P*-values showing dose-dependent effects (significant differences between low dose and high dose) are highlighted in bold font ($P < 0.05$). Note that both mass and tarsus length show significant differences between control and high dose, but it is not evidence of a dose dependent effect unless there is a difference between the high and low dose.

Post-Hoc test for dose-dependent effects in nestlings

Variable	Dose one	Dose two	Estimate	t-ratio	P-value
Mass (g)	Control	Low dose	0.175	1.384	0.352
	Control	High dose	0.373	2.616	0.026
	Low dose	High dose	0.197	1.206	0.451
Tarsus length (mm)	Control	Low dose	0.129	0.993	0.582
	Control	High dose	0.808	5.579	< 0.001
	Low dose	High dose	0.679	4.015	**< 0.001**

linear body measure is standardized to L_0. We considered each age class (10, 15, 20, 25 days and adult) as separate populations when calculating the scaled mass and the residual mass index, to account for differences in the body mass/body length relationship across development. Hence, there was a separate L and b_{SMA} for each age class (Supplementary material Table s1).

We calculated the residual body mass index values by taking the residuals from an ordinary least squares (OLS) regression between body mass and tarsus and for body mass and wing chord length. Both regressions were calculated separately for each age class. The relative mass index was calculated as body mass/tarsus and body mass/wing chord.

2.6. Statistics

We conducted statistical analyses using R version 3.4.4 and the lme4, lmerTest, cocor and emmeans packages. We determined the distribution of the data by examining Q-Q plots and histograms, and judged the normal distribution as the best fit for our data based on these plots. We examined residual plots to determine the fit of the statistical models.

We analyzed the nestling data using linear mixed effects models by restricted maximum likelihood. We used a type three ANOVA combined with the package lmerTest to generate *P*-values for the fixed effects. The models included age as random slope, and nestling ID, nested within nest ID, as random intercept, to account for repeated measurements of related individuals. We examined the effects of developmental treatment (high dose CORT, low dose CORT, or control) on condition and body composition using condition indices, body composition values (fat and lean mass; see above), body mass, relative body composition values (derived from dividing QMR fat mass and lean mass with total body mass), and tarsus length as dependent variables. Tarsus length and clutch size were entered as fixed covariates (numerical predictors). Time of day (minutes after 0700) was also entered as a fixed covariate, to control for measurement error due to food consumption. Treatment, age, sex, and the two-way interactions between age, treatment and clutch size were entered as fixed factors (categorical predictors). Observer was entered as a random intercept for the models with scaled mass index, residual mass index, ratio index and tarsus length, to control for error associated with collecting morphometric measurements. When treatment was significant as a main effect, we used Tukey's post-hoc test to test for a dose-dependent effect of the CORT

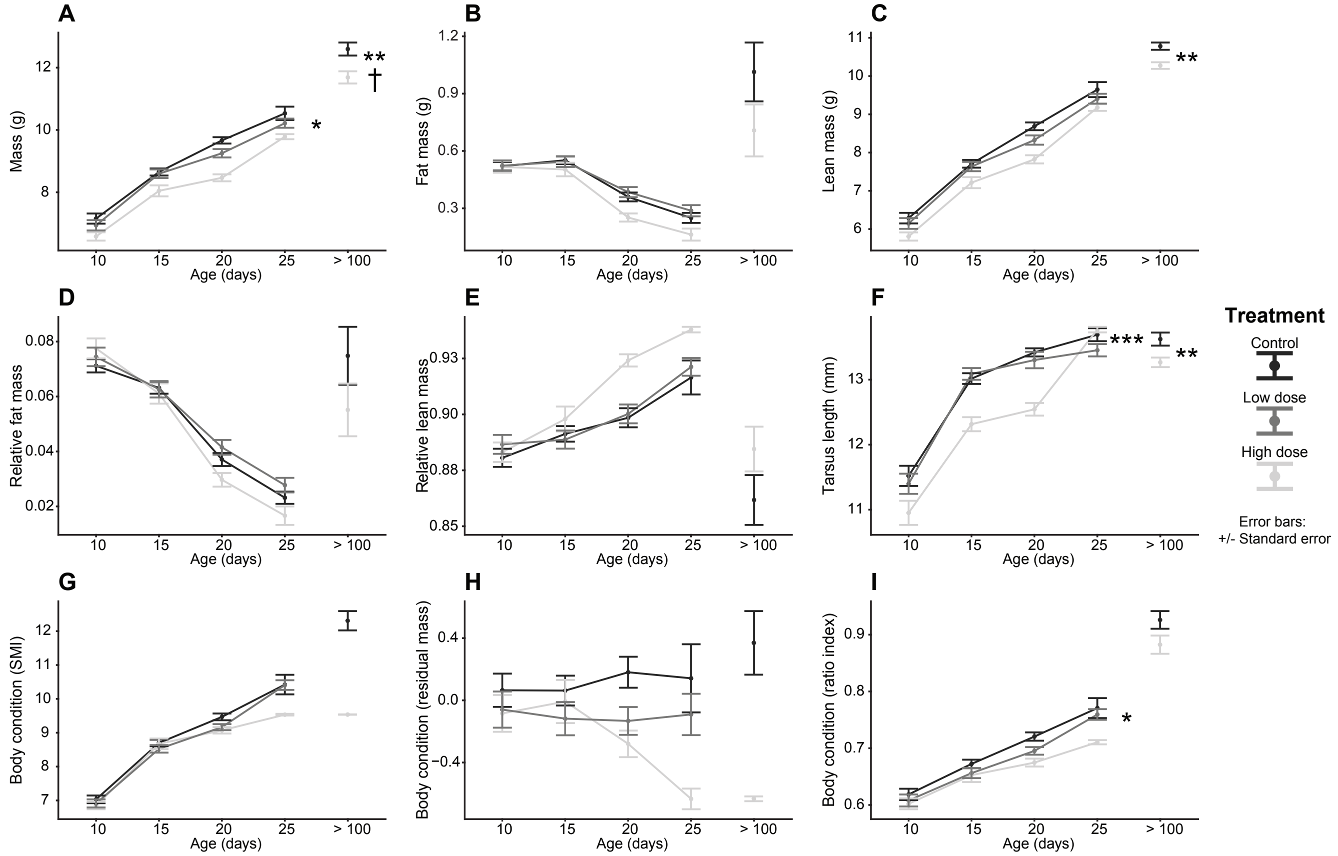

Fig. 1. (A) Mass (g), (B) Fat mass (g), (C) Lean mass (g), (D) Relative fat mass, (E) Relative lean mass, (F) Tarsus length (mm), (G) Scaled mass index values, (H) Residual mass values, and (I) Ratio index values with experimental CORT treatment across ages 10–25 days post hatch and age > 100 days (N = 132 nestlings, 75 adults). *P*-values for nestlings and adults were generated using linear mixed models by restricted maximum likelihood, and are reported in Tables 2 and 4 respectively. Significance levels: NS, $P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, †significant interaction effect. Means ± standard error.

Table 3

Model fixed effects for the condition variables in adult birds. *P*-values were generated using linear mixed models by restricted maximum likelihood and type three ANOVA. Significant *P*-values are highlighted in bold font ($P < 0.05$). Significance levels: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. N = 75 adults.

Fixed effects: Adults

Variable	Fixed effect	F-value	Degrees of freedom	P-value	
Mass (g)	Intercept	8.442	1	**0.006**	**
	Time of day	1.191	1	0.279	
	Tarsus	2.621	1	0.112	
	Sex × Treatment	4.262	1	**0.044**	*
	Treatment	9.067	1	**0.004**	**
	Sex	10.043	1	**0.002**	**
Fat mass (g)	Intercept	0.004	1	0.947	
	Time of day	0.219	1	0.641	
	Tarsus	0.306	1	0.583	
	Sex	5.108	1	**0.027**	*
Lean mass (g)	Intercept	15.459	1	**< 0.001**	***
	Time of day	1.165	1	0.284	
	Tarsus	7.117	1	**0.010**	**
	Treatment	8.314	1	**0.005**	**
Relative fat mass	Intercept	0.000	1	0.989	
	Time of day	0.505	1	0.480	
	Tarsus	0.267	1	0.608	
	Sex	5.700	1	**0.020**	*
Relative lean mass	Intercept	49.781	1	**< 0.001**	***
	Time of day	0.380	1	0.540	
	Tarsus	0.460	1	0.501	
	Sex	8.110	1	**0.006**	**
Tarsus length (mm)	Intercept	5985.625	1	**< 0.001**	***
	Time of day	0.322	1	0.572	
	Treatment	7.455	1	**0.008**	**
Scaled mass index	Intercept	652.470	1	**< 0.001**	***
	Time of day	1.481	1	0.227	
	Sex	6.833	1	**0.011**	*
Residual mass index	Intercept	0.831	1	0.365	
	Time of day	0.499	1	0.482	
	Treatment	4.680	1	**0.035**	*
	Sex	5.800	1	**0.019**	*
Ratio index	Intercept	1333.167	1	**< 0.001**	***
	Time of day	0.471	1	0.495	
	Sex	6.994	1	**0.010**	*

treatment. We used the emmeans package and the lsmeans function to derive pair-wise comparisons between the treatment doses.

For the adult data, we used linear mixed effects models by restricted maximum likelihood, and a type three ANOVA. We tested the following dependent variables: body mass, body composition values, relative body composition values, tarsus length and body condition index values. Nest ID was used as random intercept. Tarsus length and time of day were used as fixed covariates. Sex, treatment, and the two-way interactions between sex, age and treatment were used as fixed factors.

For all analyses, stepwise removal of non-significant variables was applied to obtain the best fitting model of the data. The most complex factors (i.e. interactions) and the factors with the largest *P* value were removed first. Tarsus length and time of day were constrained into the models, as these accounted for variance in the data due to body size and food intake. Tarsus length was not included in the any statistical model where tarsus length or the condition indices were the dependent variable. Parameter estimates for the final nestling and adult models were generated using the summary function, and are reported in the Supplementary material (Tables s2 and s3).

To test whether scaled mass index, residual mass index, and ratio index values more accurately reflected fat mass or lean mass, we ran Pearson correlations between the QMR data (lean mass and fat mass) and the condition indices. The correlations were run for these condition indices calculated based on both tarsus length and wing chord length, resulting in a total of 24 correlations. We limited the analysis to age groups 10 days, 20 days and adult to reduce the number of comparisons. These two age groups represent two different stages of pre-fledging development, and give a range of nestling morphology measurements (Zann, 1996). To test which condition index was most closely correlated with fat mass, we ran pairwise comparative tests of the correlation coefficient of each condition index and relative fat mass. We used the cocor package and Zou's confidence interval, with the confidence interval adjusted to 99.994% according to the Bonferroni correction for multiple comparisons. Zou's confidence interval is a preferred method of testing significance (Diedenhofen and Musch, 2015), and an interval not including zero is interpreted as a significant difference between the correlation coefficients.

3. Results

3.1. Nestling condition and developmental CORT

CORT treatment during development decreased nestling mass, tarsus length and ratio index value (Table 1, Supplementary material Table s2). CORT treatment did not affect any other body condition variable in nestlings. Post-hoc tests showed that there was a dose-dependent effect on tarsus length, such that birds from the high dose treatment had smaller tarsi compared to the low dose treatment group (Table 2).

Nestlings gained body mass, lean mass, relative lean mass, tarsus length, and increased all body condition index values as they aged (Table 1, Fig. 1). In contrast, nestlings lost fat mass and relative fat mass as they aged (Table 1, Fig. 1B and D). Nestlings from larger clutches had lower body mass, lean mass, and body condition index values, but higher relative fat mass and longer tarsi (Table 1, Supplementary material Table s2). Birds with longer tarsi had higher body mass, fat mass, lean mass, and relative fat mass, but lower relative lean mass (Table 1, Supplementary material Table s2). Nestlings gained body mass and condition index values throughout the day (Table 1, Supplementary material Table s2). We found no significant effect of sex in any of the models. All factors from the models on the nestling data are summarized in Table 1, and parameter estimates are summarized in Supplementary material Table s2.

3.2. Adult condition and developmental CORT

Adult birds that had received high-dose CORT treatment as nestlings had lower body mass, lean mass, tarsus length and residual mass (Table 3, Fig. 1A, C, F, and H) compared to controls. CORT treatment had no effect on adult fat mass, relative fat mass or relative lean mass. Female birds weighed more than males and had higher fat mass, relative fat mass, and body condition values, but lower relative lean mass (Table 3, Supplementary material Table s3). We found a treatment and sex interaction, such that the difference in body mass between males and females was larger in the control group (Table 3, Supplementary material Fig. s1). Age was not significant in any model. All factors from the models on the adult data are summarized in Table 3, and parameter estimates are reported in the Supplementary material Table s3.

3.3. Comparison of condition indices and QMR data

All condition indices, except for residual mass index and ratio index calculated from wing chord length at age 10, were correlated with relative fat mass (Supplementary material Table s4). For nestlings, all significant correlation coefficients between relative fat mass and condition index ranged between 0.2 and 0.45 (Supplementary material Table s4). For adults, all condition indices had strong positive correlations ($r = 0.65–0.90$) with relative fat mass, and strong negative

Table 4
Comparison of correlation coefficients for relative fat mass and condition indices. Differences in correlation coefficients were tested using Zou's confidence interval, and significance levels were adjusted to 99.994% in accordance with the Bonferroni correction for multiple comparisons. Significant differences are highlighted on bold font ($P < 0.006$). *Not a significant correlation, see Supplementary material Table s4.

Comparison of correlation coefficients						
Age (days)	Index one	Index two	Related correlation	Lower CI	Upper CI	Null hypothesis
Tarsus length						
10	Scaled mass	Residual mass	0.973	−0.0221	0.1723	Retained
	Scaled mass	Ratio	0.999	−0.0677	0.0611	Retained
	Residual mass	Ratio	0.971	−0.0219	0.1778	Retained
20	Scaled mass	Residual mass	0.996	−0.0589	0.0647	Retained
	Scaled mass	Ratio	0.972	−0.0774	0.1131	Retained
	Residual mass	Ratio	0.987	−0.0906	0.0597	Retained
Adult	Scaled mass	Residual mass	0.775	**−0.5202**	**−0.0455**	**Rejected**
	Scaled mass	Ratio	0.892	**−0.4698**	**−0.0711**	**Rejected**
	Residual mass	Ratio	0.977	−0.1463	0.0689	Retained
Wing chord length						
10	Scaled mass	Residual mass*	0.836	**0.0004**	**0.3982**	**Rejected**
	Scaled mass	Ratio*	0.350	**0.0609**	**0.8007**	**Rejected**
	Residual mass*	Ratio*	0.779	**−0.4754**	**−0.0240**	**Rejected**
20	Scaled mass	Residual mass	0.961	**−0.2261**	**−0.0007**	**Rejected**
	Scaled mass	Ratio	0.615	−0.4478	0.1445	Retained
	Residual mass	Ratio	0.789	−0.1750	0.2748	Retained
Adult	Scaled mass	Residual mass	0.975	−0.1288	0.1178	Retained
	Scaled mass	Ratio	0.999	−0.1155	0.1040	Retained
	Residual mass	Ratio	0.979	−0.1488	0.0825	Retained

correlations ($r = -0.65$ to -0.90) with relative lean mass (Supplementary material Table s4). For nestlings, there were no differences between the condition indices in terms of the relationship to relative fat mass when calculated from tarsus length (Table 4, Fig. 2). There was a difference between the indices calculated from wing chord length, such that the scaled mass index was the only index that had a significant correlation with relative fat mass in 10 day old nestlings, and a stronger correlation with relative fat mass compared to the residual mass index in 15 day old nestlings (Table 4, Supplementary material Table s4). Data from adults showed that the scaled mass index had a weaker correlation with relative fat mass compared to the other two condition indices when calculated using tarsus length (Table 4, Fig. 2), but there was no difference between the indices when they were calculated from wing chord length.

4. Discussion

4.1. Condition and CORT treatment

The effects of stress during early development on nestling body mass are well documented and robust (Naguib et al., 2004; Spencer et al., 2003). Here, we confirm that CORT treatment during development decreases nestling body size (mass and tarsus length), with a dose-dependent effect on nestling tarsus length. Interestingly, some of these effects persisted into adulthood, with high-dose CORT-treated nestlings having lower body mass, lower lean mass and shorter tarsus length as adults. Finally, when calculated from tarsus length, all three condition indices were similarly correlated to relative fat mass during the nestling phase, but in adults both the residual mass index and the ratio index were better predictors of relative body fat than the scaled mass index. When the indices were calculated from wing chord length, the scaled mass index was more closely related to relative fat mass than the other two indices in 10 day old nestlings, and the residual mass index was more closely related to relative fat mass than the ratio index. In 15 day old nestlings, the scaled mass index was more closely related to relative fat mass, compared to the residual mass index. This suggests that researchers interested in indicators of body fat should choose their condition index carefully, depending on the life stage and morphological data available.

As predicted, both high and low dose CORT treatment decreased nestling body mass. The negative effect of CORT treatment on body mass is consistent with previous studies showing that exposure to CORT during development can decrease nestling body mass (Buchanan et al., 2003; Crino et al., 2014; Spencer et al., 2009). While there are previous examples of dose-dependent effects of CORT (Johnson et al., 2006; Morici et al., 1997), this is the first study to show a dose-dependent effect of CORT on body size (tarsus length) in nestling birds. Previous studies on effects of developmental stress on body mass (Crino et al., 2014; Krause and Naguib, 2011; Spencer et al., 2003) show that treatment effects are not present in adulthood. Two studies that examined the effects of developmental stress on body composition in nestlings, Farrell et al. (2015) and Schmidt et al. (2012), found sustained effects that lasted days after the treatment stopped, but neither showed effects on body mass nor lean mass in adult birds. Naguib and Gil (2005) and Kriengwatana et al. (2013) showed that developmental conditions can have lasting, and even transgenerational, effects on body mass and fat mass, but using stressors that likely induce direct or indirect nutritional stress. Kriengwatana et al. (2013) also found that the post-natal timing (early development or juvenile) of the stressor can influence the effects of developmental stress on adult body composition, which might help explain inconsistencies between similar studies.

4.2. Mechanisms linking CORT to changes in body composition

Although developmental CORT exposure has been repeatedly linked to a reduction in nestling body mass, the causal mechanism(s) that modulate this effect have yet to be determined. Also, while previous studies have shown that CORT treatment increases circulating CORT levels (e.g. Spencer and Verhulst, 2007), we have no direct measures to confirm that circulating CORT was elevated in these birds. It is possible that nestlings treated with CORT beg less than their control siblings, which would result in CORT-dosed nestlings receiving less food from their parents. There is mixed evidence suggesting that CORT affects begging behavior in nestlings, with previous studies reporting either increased (Kitaysky et al., 2001) or reduced (Rubolini et al., 2005; Wada and Breuner, 2008) begging as a result of stress. However, differences in begging behavior would not explain the sustained effects of CORT treatment on adult birds. Compensatory growth following stressful developmental conditions is common, but can have detrimental long-term consequences on survival and fitness (Grace et al.,

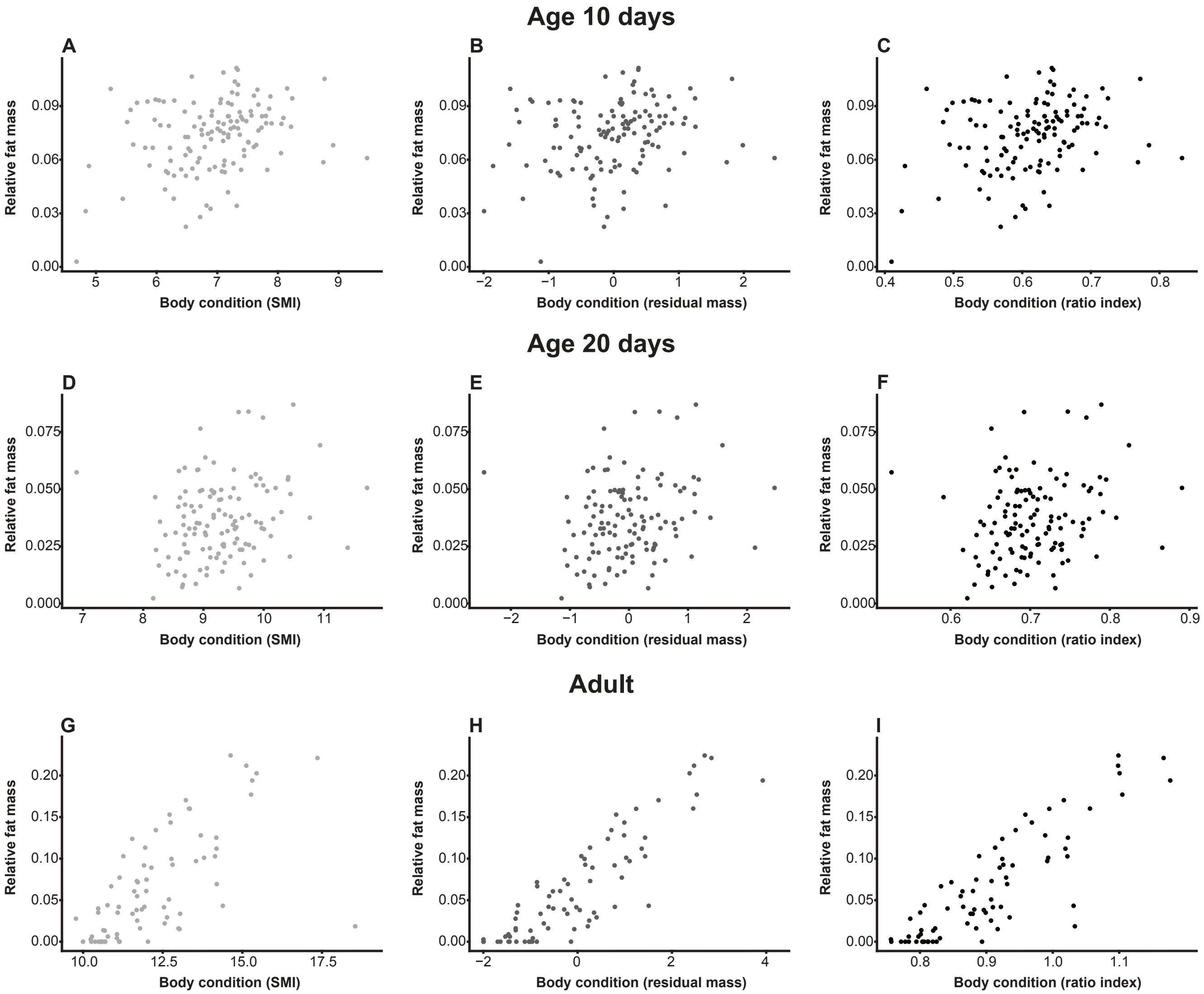

Fig. 2. Relative fat mass from 10 day old (A–C), 20 day old (D–F) and adult (G–I) birds and condition index values calculated with tarsus length: Scaled mass index (light gray, A, D, G), Residual mass index (dark gray, B, E, H), Ratio index (black, C, F, I). *P*-values were generated using Pearson correlations, and are reported in Table s4. $N = 132$ nestlings, $N = 75$ adults. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2017; Krause and Naguib, 2011; Metcalfe and Monaghan, 2001). Hence, even if it is possible for nestlings exposed to CORT to catch up to their conspecifics, this may not be the best strategy in the long-term.

Developmental CORT exposure may also affect nestling body mass by changes in metabolic function. There is some evidence that developmental stress reduces mitochondrial efficiency in rats (*Rattus rattus*), resulting in lower production of adenosine triphosphate (ATP; the dominant form of cellular energy: Pandya et al., 2004; Roussel et al., 2004). Lower mitochondrial efficiency may explain why CORT-treated animals have lower body mass compared to controls, without apparent food restriction (Pandya et al., 2004). Additionally, CORT can affect energy mobilization through changes in metabolism and gluconeogenesis (Astheimer et al., 1992; Remage-Healey and Romero, 2001). This might affect how stressed birds store fat or build muscle (Chin et al., 2009). Schmidt et al. (2012) found that CORT treatment decreased the standard metabolic rate of song sparrow females. Experimental manipulations of CORT during early development can permanently change the hypothalamic-pituitaryadrenal (HPA) axis, the neuroendocrine pathway by which corticosterone is released in the body, resulting in higher stress-induced CORT levels in adults (Spencer et al., 2009). In adult birds, stress-induced CORT levels are associated with lower adult body condition (e.g. Crino et al., 2017). If developmental CORT treatment permanently alters HPA activity, this could explain the sustained effects of developmental stress on adult body condition. It may also explain why there was an effect on lean mass in adults but not nestlings, as some effects of the treatment may have been present during early development but not apparent from morphological measurements. Future studies could parse between these non-exclusive hypotheses to examine the underlying mechanisms that modulate long-term effects of the developmental environment on body composition.

4.3. Condition indices

When considering the relationship with relative fat mass, all three condition indices had relatively weak correlations ($r > 0.4$) in nestlings, indicating that none were particularly good indicators of relative fat mass. In contrast, all three indices had relatively strong ($r > 0.65$) correlations with relative fat mass in adult birds, suggesting these indices are more reliable indicators of body fat in adult birds. The results from the condition index comparisons showed that the condition index that was most closely related to relative fat mass differed between nestlings and adults, and depending on whether the condition indices had been calculated using tarsus or wing chord length. This suggests that the best condition index to use, in terms of indicating relative body fat, depends on the data available to the research and the age of the birds.

According to the methods proposed by Peig and Green (2010), the measurement most closely correlated to body mass should be used to calculate the index values. Wing chord length and tarsus length should, therefore, be the measurement employed for nestlings and adults respectively, if seeking to estimate body fat. Accordingly, the scaled mass index is a better predictor of relative body fat in nestlings compared to the other two indices, and the residual mass index is a better predictor compared to the ratio index in young nestlings. In adults, the residual mass index and the ratio index perform better as indicators of body condition compared to the scaled mass index. We conclude that all three condition indices are poor indicators of relative body fat in nestlings, and that the condition indices are better suited for use on adult birds.

While some claim that the scaled mass index is a superior index for estimating relative body fat (Peig and Green, 2009, 2010), the performance of the scaled mass index varies depending on the species being examined (Falk et al., 2017; MacCracken and Stebbings, 2012), and is sometimes no better than other indices (Jacobs et al., 2012; Labocha et al., 2014). In this study, the scaled mass did perform better when used as a condition index for nestlings, but none of the condition indices showed a strong relationship with relative body fat. In contrast, the residual mass and ratio index were more accurate than the scaled mass index at predicting relative fat mass in adult birds. Finally, our results on nestlings support previous findings showing that condition indices may be ineffective indicators of relative body fat in growing birds (Jacobs et al., 2012; Labocha et al., 2014).

5. Summary and conclusions

In our experiment, developmental stress decreased body mass and body size in nestlings, and had lasting effects on body mass, lean mass and tarsus length across life history stages. More studies are needed to determine whether the effects seen in nestlings and adults have long-term consequences for reproductive success and survival, and whether the effects of stress are ultimately detrimental or adaptive. We found the scaled mass index was the best performing condition index for nestlings. However, all correlations were weak, showing that for nestlings, none of the condition indices were good indicators of relative body fat, as determined by QMR. In adults, all condition indices had a strong relationship with relative fat mass, and the residual mass index and the ratio index were better indicators of relative body fat than the scaled mass index. Future studies that evaluate condition should consider the limitations of condition indices, and take care when selecting morphological variables to calculate condition indices.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ygcen.2018.11.008.

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