1 **Relationship between early body condition, energetic reserves and fitness in an**

2 **iteroparous insect**

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Abstract

1. Body condition can be defined as the amount of energetic reserves present within an individual after structural size had been accounted for (i.e. relative amounts of energetic reserves), and estimated by Body Condition indices (BCIs)

2. Several methods have been proposed to calculate BCIs. However, they have traditionally been validated in vertebrate studies and evidence of their power to predict fitness in invertebrates is scarce. Ideally, the use of a particular BCI in an animal population should be validated based on its ability to accurately reflect the relative amount of reserves available to the animal as well as its relationship to fitness.

3. We aimed at increasing the variance in female body condition of *Tenebrio molitor* beetles by subjecting them to restricted or optimal food conditions at both the larval and/or adult stage. We then explored the predictive power of several BCIs on both the absolute and relative amount of lipids and sugars present in the insect's body, and their link with adult fitness. Using an iteroparous income breeder allowed us to assess the relative effects of larval vs. adult access to nutritional resources on fecundity along several reproductive events.

4. Simple measurements of phenotypically plastic traits (i.e. mass and volume) correlated well with absolute, but poorly with relative, measures of body reserves. Conversely, we found that BCIs that corrected for the interdependence between phenotypically plastic traits and structural size strongly correlated with relative amounts of body components.

5. We found that even though the adult feeding treatment had a stronger effect, body condition at emergence, but not larval feeding treatment, also affected fecundity. Moreover, while the effect of the adult feeding treatment varied along time (i.e. egg laying rank), the effect of body condition at emergence remained constant.

46   6. These results show that by carefully using simple morphometric measures and BCIs, it is

47   possible to distinguish between the effects of structural size and body condition on fitness

48   traits in invertebrates, and to show that an iteroparous income breeder can partially rely on

49   its early energetic state for its later fecundity.

50

Introduction

52   Body condition is classically defined as the amount reserves present in the body of an animal after

53   maintenance costs have been accounted for (Rowe & Houle, 1996 ; Barnett et al., 2015). Its

54   definition can also take various shapes ranging from the "general health state" to "physiological

55   state" of an animal, and is also sometimes referred to as its "quality" (Jakob, Marshall & Uetz, 1996

56   ; Wilson & Nussey, 2010). The relationship between the latter and the "quality" of an individual is

57   likely to be more complicated than stated in most studies (Hill, 2011 ; Wilder, Raubenheime &

58   Simpson, 2016 ; Barnett et al., 2015), since the resilience or resistance to different stressors is likely

59   to be dependent on a different set of biomarkers (Milot et al., 2014). In an attempt to capture the

60   concept of resilience underlying these definitions, Hill (2011) defined body condition as "the

61   relative capacity to maintain optimal functionality of essential cellular processes". In some cases,

62   this is assumed to rely strongly on the amount of energetic reserves an individual has at its disposal

63   (Schulte-Hostedde et al. 2005 ; Nandy et al., 2012), which has indeed been found to predict several

64   fitness traits in both vertebrates and invertebrates, such as dispersal (Bargielowski et al., 2012,

65   Evenden, Whitehouse & Sykes, 2014), resistance to diseases or chemicals (Townsend et al., 2010 ;

66   Reid & Purcell, 2011), overwintering success (Sinclair, 2015) and fecundity (Arrese & Soulages,

67   2010). This amount of reserves can be estimated by the direct dosage of several body components

68   from the organism, such as fat, glycogen and protein content, but invasive dosing is problematic

69   when an experiment requires the animals to remain alive along several sampling events. In such

70   cases, a non-invasive approximation of energetic reserves is needed.

71

72   Some studies use body mass or body size, because the larger the individual the more body reserves

73   it is able to store. However, a simple measurement of mass includes the mass of body structures that

74   are used as an energy source only in cases of extreme starvation (such as bones in vertebrates or

75   cuticular structures in invertebrates: van Niekerk, Mitchell & Engelbrecht, 2018 ; Locke, 1991).

76   This is the rationale behind the use of body condition indices (BCIs), which are indices based on

77   several morphological measurements, typically the measurement of a phenotypically plastic

78   morphological trait which varies according to the intake of resources from the environment (e.g.

79   mass or volume), corrected for a measurement of the fixed structural body size (e.g. body length).

80   The interdependence between these two parameters can be mathematically taken into account in

81   different ways which are still a matter of much debate in the literature (Peig & Green 2009, 2010,

82   Moya-Laraño et al., 2008, Labocha, Schutz & Hayes, 2014).

83

84   BCIs have been originally developed for use with vertebrates, in which ethical concerns require

85   non-destructive ways of assessing the quantity of reserves available to animals. Simple

86   measurements of size or mass are more frequently used by invertebrate ecologists since they have

87   been shown to be associated with fitness traits in some studies (Bista & Omkar, 2013 ; Reid &

88   Baruch, 2010 ; Zanchi et al., 2012). Insects have a discontinuous growth marked by the occurrence

89   of moults in between which the structural size is fixed by a rigid exoskeleton, whereas the quantity

90   of resources accumulated increases with the duration of the intermoult, and their adult body size is

91   also fixed. Thus, one could argue that a measurement of structural size would reflect the resources

92   accumulated during the larval development, and not present energy reserves of the insects, and that

93   the use of a BCI at a given growth stage is relevant (Anderson, 1974 ; Reim, Kaufmann &

94   Blamckenhorn, 2009 ; Knapp & Knappova, 2013).

95

96   Still, whether BCIs or simple measures of size/mass are more appropriate in predicting fitness in

97   invertebrates remains poorly understood, since to our knowledge no studies comprehensively

98   validate several BCIs based on both energetic reserves and fitness. Moreover, BCIs have been

99   criticized for their lack of predictive power on the absolute quantity of reserves present in

100   individuals (Wilder et al., 2016). However, BCIs have been introduced to take into account the

101   Absolute Energy Demand Hypothesis (Calder, 1984), which pertains that since large animals

102   require more energy to sustain their body function (Blanckenhorn, 2000 ; Reim, Teuschl &

103   Blanckenhorn, 2006), energy reserves relative to size is a better predictor of fitness than absolute

104   measures of reserves. BCIs should therefore not be expected to correlate with absolute values of

105   reserves, but rather with their quantity corrected for structural size (DeBano, 2008 ; Peig & Green,

106   2009 ; 2010).

107

108   The purpose of the present study is to compare the predictive power of several BCIs and

109   simple morphological measurements taken from females of the mealworm beetle, *Tenebrio molitor*

110   (Coleoptera: Tenebrionidae), on the actual quantities of energetic reserves stored in their bodies

111   both in absolute quantity and after correction for structural size. We then compared their predictive

112   power on the fitness of the beetles. *T. molitor* is a relatively long-lived insect and is iteroparous,

113   meaning that it feeds at the adult stage and lays eggs in several reproductive bouts along its lifespan

114   (Hughes, 2017). As such, it is an income breeder (Stearns, 1992, Jönsson, 1997). This feature is

115   predicted to complicate the identification of resource-based changes in life histories which could be

116   due to past as well as present food availability (Kasumovic, Brooks & Andrade, 2009). We use this

117   as an opportunity to explore the effects of early body condition on the long-term fitness of adult *T.*

118   *molitor* females, which we estimated by their fecundity along reproductive events.

119

120   Simple morphometric measurements were taken after metamorphosis, such as the structural size

121   and the mass of the beetles. From these measurements, we calculated several BCIs chosen from the

122   literature, and explore their adequacy in controlling for the interdependence between a

123   phenotypically plastic morphometric measurement and structural size.

124   -   The traditional and more frequently used BCI in vertebrates (Blem 1990, Brown

125   1996, Schulte-Hostedde et al. 2005) and invertebrates (Jakob et al., 1996 ; Reinhart,

126   2001 ; DeBano, 2008, Kasumovic et al., 2009) consists in the **residuals from**

127   **ordinary least squares (OLS) regressions with log-transformed mass as a**

128   **response variable and log-transformed structural size as an explanatory**

129   **variable** (hereafter referred to as **OLS_{resid}**) (Jakob et al., 1996; Hayes and

130   Shonkwiler, 2001). Their use has been criticized by some authors because despite

131   controlling for the lack of independence between mass and structural size, it fails to

132   control for the lack of independence between structural size and mass (see Green

133   2001, Peig and Green 2009, 2010).

134   -   To address the latter, it has been suggested that **residuals from standardised major**

135   **axis (SMA) regressions** are better suited to calculate BCIs (Green 2001, Peig and

136   Green 2009, 2010). Indeed, the authors found that in several small vertebrate

137   species, **Scaled Mass Index (SMI)** performed better than OLS_{resid} in predicting the

138   amount of reserves stored in the body relative to body size. However Peig and Green

139   (2009, 2010), did not assess which BCI predicted fitness best, which would be more

140   pertinent in most ecological studies.

141   -   Moreover, Moya Laraño et al. (2008) proposed that the **abdomen volume** might

142   reflect the amount of reserves stored in this compartment more faithfully than mass.

143   We therefore additionally calculated a **Scaled Volume Index**.

144

145   We did so on groups of female beetles having experienced food shortage or not at the larval

146 and/or the adult stage, in an attempt to increase the variance in their body condition. This

147 experimental approach sets a context of food imbalance and limitation, in which it makes sense to

148 restrain the definition of body condition to the amount of energetic reserves present in the bodies of

149 *T. molitor* females, and enabling them to maintain a reproductive output in harsh conditions.

150 Several physiological and morphometric measurements were taken after metamorphosis and before

151 measuring the fecundity of the beetle females. Thus, we were able to estimate whether different

152 BCIs were performing better at identifying potential differences between the treatment groups, as

153 well as how differences in early body condition shapes the life history traits of this iteroparous

154 beetle species.

155

156 **Materials and methods.**

157 **Insect rearing and maintenance**

158 Young larvae (~ 1cm) were collected from a mass rearing outbred stock kept in the laboratory in

159 wheat bran (as a substrate, is also used as a source of food) with *ad libitum* access to water, and

160 regularly supplemented with piglet flour (as a source of proteins) and a piece of apple (for

161 carbohydrates and vitamins). Our insects are kept at 25°C and in the dark. After collection, we

162 reared *T. molitor* larvae either in a rich or a poor larval feeding treatment, and subsequently

163 maintained adults in a matching or mismatching environment, i.e. similar or dissimilar to the larval

164 feeding treatment respectively.

165   We later measured the effects of these treatments on female body condition and fecundity.

166 To do so, a subset of the females generated in these treatments was killed in order to assess the

167 quantity of energetic reserves present in their abdomen, whereas we assessed the body condition of

168 the remaining females in a non-invasive way before allowing them to reproduce.

169

170 **Generation of larval feeding treatments (L.F.T.)**

171 After retrieving the larvae from the stock, we maintained them at a density of 250 larvae in a plastic

172 box (L xH x l = 30 x 22 x 25 cm) in 5 L of wheat bran with *ad libitum* access to water. We kept

173 them in 2 separate containers according to the larval feeding treatment we subjected them to while

174 controlling for density:

175   -   In "**poor larval feeding**" conditions (hereafter **P.L.**), larvae were simply kept in wheat bran

176   with unlimited access to water and no further addition of piglet flour or apple.

177   -   In "**rich larval feeding**" conditions (hereafter **R.L.**), larvae were kept similarly to our stock,

178   that is to say in wheat bran + piglet flour + apple.

179   We checked daily for the presence of pupae in these boxes.

180   The dynamics of pupation in our rearing conditions is such that a few larvae pupated early,

181   preceding a "pupation peak" over 3 days, after which some larvae kept pupating late. Moreover, the

182   growth of *T. molitor* is such that while getting closer to pupation, the food uptake of larvae stops as

183   the insects are undergoing the physiological changes preparing metamorphosis (Connat et al.,

184   1991). We retrieved pupae as soon as they were spotted, but we used in this experiment only the

185   pupae formed during this "pupation peak". This way, we assumed that we minimized as much as

186   possible the effect of the removal of conspecifics on the accumulation of energetic reserves by each

187   individual larva.

188   We counted the pupae produced until the boxes were empty, in order to check that there was

189   no difference in the number of pupae produced between the 2 boxes. There was less than 10 %

190   difference between both. The resulting pupae were kept separately in a plastic box and checked

191   daily for the presence of emerged adults in the teneral stage.

192   After emergence, adults were kept individually in Petri dishes supplied with wheat bran and

193   a piece of apple for 5 days, time during which they reach sexual maturity. Five days after

194   emergence the beetles were sclerotized enough to allow the determination of their sex by

195   observation of their genitalia. As our study focused on variation in females body condition only,

196   P.L. males were discarded, while R.L. males were transferred from their Petri dish into new plastic

197   boxes where they were kept together according to their emergence date in wheat bran + *ad libitum*

198   water + piglet flour + apple, waiting to be used in the later copulation experiments.

199

200

201 **Generation of adult female treatments (A.F.T.)**

202 Females on the other hand were still maintained individually in Petri dishes and kept differently

203 according to the adult feeding treatment we subjected them to:

204 - In "**poor adult feeding**" conditions (hereafter **P.A.**), females were kept in whole grain thin

205   wheat flour, with *ad libitum* access to water.

206 - In "**rich adult feeding**" conditions (hereafter **R.A.**), females were kept similarly but with

207   addition of piglet flour and apple every second day.

208 In this part of the experiment, wheat bran was replaced by thin flour in order to facilitate the

209 recovery of the eggs by sieving (600 µm).

210

211 Females of the four treatment combinations will be referred to as **P.L.P.A. for poor larval**

212 **rich adult, P.LR.A. for poor larval rich adult, R.L.P.A. for rich larval poor adult, and**

213 **R.L.R.A. for rich larval rich adult feeding treatments**.

214

215 **Body Condition Indexes**

216 **Measure of morphological parameters**

217 The mass of each female was measured on a Sartorius balance to a precision of 10^{-5} g before

218 the first reproduction. The females used for assessment of the energetic reserves were weighed and

219 measured before being frozen.

220 Three different measures were taken with a digital calliper (Mitutoyo, Absolute) to the

221 nearest 0.01 mm: the length of the elytron, the width of the abdomen at the level of the second

222 abdominal segment, and the thickness of the abdomen being the smallest thickness we can measure

223 after pressing the elytra against the abdomen (which has been shown to correlate with fecundity in

224 a mantid species in Maxwell, Galego & Barry, 2010). Repeatability of these measurements was

225 assessed by taking them twice in a non-consecutive way. From these measurements we calculated

226 the volume of the abdomen of the beetles (4/3*3.14*(length/2)*(width/2)*(thickness/2)), as advised

227 by Moya-Laraño et al. (2008). Being the site of storage of most energetic reserves in the fat body,

228 we can indeed expect the abdomen volume to be condition dependent.

229

230 **Dosage of the energetic reserves**

231 We used a dosage by colorimetry to assess the lipid content as well as the glycogen and the

232 circulating carbohydrates present in the abdomen of the beetles, by using a protocol detailed in

233 Rivero and Ferguson (2003). In brief, frozen beetles were dissected to remove their prothorax, head,

234 elytras and legs. The remaining abdomens were homogenized in microcentrifuge tubes containing a

235 2% sodium sulfate solution and incubated in a 2:1 mix of chloroform:methanol solution for 24

236 hours. They were then centrifuged, to separate the pellet (containing glycogen) from the supernatant

237 (containing fat and circulating sugars). The supernatant was divided into 2 equal parts. One part we

238 used to quantify lipids with vanillin-phosphoric acid reagent. After a brief incubation, the optical

239 density of the resulting solution was read in a spectrophotometer (SpectraMax®, Molecular

240 Devices) at 525 nm and compared to a standard curve made of a serial dilution of sunflower seed

241 oil. The other part was used to quantify mono and disaccharides from the supernatant and the pellet

242 (after breaking down of the glycogen of the pellet), by incubating each of these fractions with

243 anthrone reagent. The optical density of the resulting solutions was read at 625 nm and compared to

244 a standard curve made of a serial dilution of glucose. As there was a strong correlation between

245 circulating sugars and glycogen in the beetles (Pearson's correlation of log-transformed sugars and

246 glycogen [95% CI], r = 0.811 [0.725, 0.872], **supplementary material S1**), we considered both

247 compounds together in the results.

248 Mono- and disaccharides from the supernatant represent circulating sugars mostly in the

249 form of trehalose, as it is the main sugar present in the hemolymph of insects and serves as a

250 storage for the glucose used in locomotory activity (Candy, 1989, Thompson, 2003), whereas

251 glycogen stored in the fat body helps replenishing consumed trehalose (Candy, 1989).

252 Diacylglycerol is another fuel used in locomotory activity, which is stored in the fat body

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253   (Canavoso, 2001 ; Williams & Robertson, 2008).

254

255   **Copulations and fecundity assessment**

256   Dnervich et al. (2001) showed that the mating of T. molitor females every second day

257   prevented their sperm depletion. Our preliminary observations showed that females could lay eggs

258   for a week following a single copulation event, and that when mated every second day they barely

259   laid any eggs past 2 weeks after the first copulation. We thus designed our experiment in order to

260   prevent any sperm depletion and capture most of the fitness of the females.

261   Ten days after emergence females were exposed to one male for 4 hours. During copulation,

262   a male from the R.L feeding treatment and a focal female were placed in an empty Petri dish

263   containing only a piece of filter paper. We observed the pairs until we could record at least one

264   copulation for each one of them, and we noticed that several events of copulation can take place in

265   4 hours. At the end of these 4 hours, the males were removed, put back together in a box and fed *ad*

266   *libitum*, waiting to be reused 2 days later. Note that as males were not kept individually, they were

267   randomly chosen from their stock every second day, which controls for any effect of males on

268   female fitness. Females on the other hand were individually placed in a new Petri dish filled with

269   flour supplemented or not with apple and piglet flour, according to their adult feeding treatment,

270   and allowed to oviposit for 2 days until the next copulation event. The eggs of the previous Petri

271   dish resulting from the previous reproduction event were sieved off the flour and counted, as a

272   proxy for female fitness. There were in total 8 copulation sessions per female. Males that reached

273   17 days post emergence were removed from the experiment.

274

275   **BCIs calculations**

276   We decided to use three morphometric measures as indirect indices of energetic reserves:

277   elytron length, body mass and abdomen volume.

278   We then computed the **residuals from ordinary least squares (OLS) regressions with**

279   **log-transformed mass as a response variable and log-transformed structural size (elytron**

280   **length in our study) as an explanatory variable** (hereafter referred to as **OLSresid**) (Jakob et al.,

281   1996; Hayes and Shonkwiler, 2001). Both mass and structural size are log-transformed because the

282   relationships between morphological traits are known to follow a power function $Y = \alpha X^\beta$ (Y

283   being a morphological trait (e.g. mass) to be predicted, X being a second morphological trait (e.g.

284   structural size) and α and β being constants. The constant is known as the scaling exponent (Peig

285   and Green 2009). However OLS regressions assume that the dependent variable X is independent of

286   the response variable Y and that X is free of errors. Both assumptions are violated since structural

287   size will tend to be greater in individuals of higher condition and X will suffer from some error. It is

288   also important to note that measurement is not necessarily the main source of error in structural

289   size, a larger source of error may be variation between individuals in how well measures of

290   structural size actually reflect true body size due to variation in body shape (Warton *et al.,* 2006,

291   Green, 2001). The result of these violations in assumptions is that the slope of the OLS regression

292   will be underestimated, resulting in an over-estimation of condition for large individuals and vice-

293   versa for smaller individuals (see results).

294   Unlike OLS regressions, Major Axis (MA) regressions assume that X is not free of errors,

295   that the errors in *X* and *Y* are interdependent, and that the ratio in error variance in Y and X is equal

296   to 1 (Green, 2001; Warton *et al*., 2006). However, the error variance is expected to be greater in

297   measurements of plastic phenotypic traits (such as mass and volume) than in measurements of

298   structural size (Rising and Somers 1989; Green, 2001). In addition, measurements of plastic

299   phenotypic traits and structural size are generally not measured within comparable scales.

300   Therefore, in most cases, the error variance ratio Y/X assumption of MA regression will be violated

301   and will lead to inflated slopes that will approach an OLS regression slope of structural size (i.e. *X*)

302   on the plastic phenotypic trait (i.e. *Y*) (Green, 2001, see results).

303   To address the interdependence between mass and size, the use of **the residuals from standardised**

304   **major axis (SMA) regressions** (otherwise known as reduced major axis regression) have been

305   proposed to be a better suited BCI than OLS**resid** (Green 2001, Peig and Green 2009, 2010). SMA

306   regressions assume that the ratio of error variance Y/X is equal to the ratio of the true variance Y/X.

307   Since SMA regressions standardise data, it can deal with Y and X variables measured on different

308   scales. Its true and error variance assumptions are also more realistic than both OLS and MA

309   regressions in most cases (Warton *et al.*, 2006, Green, 2001, see results).

310   Peig and Green (2009) used the Thope-Lleonar (TL) model of scaling to estimate body

311   condition, **using the slope from an SMA regression of mass and structural size as the scaling**

312   **exponent**. The benefit of Peig and Green's (2009) formula is that it retains the original mass units.

313   We therefore corrected all of our non-fixed morphological measures (i.e. mass and volume), as well

314   body components (i.e. lipids and sugars) for structural size (i.e. elytron length) using Peig and

315   Green's (2009) formula. We refer to size-corrected morphological measures and body components

316   as "**scaled**", i.e. **scaled mass index (SMI), scaled volume index (SVI), scaled lipids and scaled**

317   **sugars**.

318

319   **Statistical analysis**

320   We tested the repeatability of our morphometric measures using the R package "rptR" (Stoffel and

321   Nakagawa, 2017). We investigated Pearson correlations between morphometric measures, BCIs and

322   measures of energetic reserves. Prior to correlations all morphometric measures and energetic

323   reserves were log transformed. We further investigated whether log-transformed measures of

324   energetic reserves, morphometric measures and BCIs differed between feeding treatments using

325   linear models.

326

327   We investigated the effect of each morphological measure and BCI on total fecundity,

328   controlling for each feeding treatment on total fecundity using a general linear model (GLM) with

329   negative binomial distribution and a log link function, with the total number of eggs as a response

330   variable and each morphological measure/BCI, larval feeding treatment, adult feeding treatment and

331   the three way interaction term as explanatory variables. Because of collinearity between the

332   morphological measures and BCI, each measure/BCI was entered in separate models and never

333   together in the same model. Therefore, in order to compare the relative support of each BCI, we

334   constructed candidate models with each BCI and controlling for the effect of the adult food

335   treatment, as well as models with each BCI but without the effect of adult food treatment, a model

336   with only the effect of adult food treatment and the null model. We then combined all of the

337   candidate models to assess the relative support of each morphological measure and BCI in

338   predicting total fecundity. We calculated the sum of AICc weight of all candidate models with each

339   morphological measure and BCI, the average R^2 across models with the measure/BCI, and the effect

340   size, partial r, of the BCI on fecundity when controlling for adult feeding treatment (since the effect

341   of adult feeding treatment was supported by model selection, see results).

342   *T. molitor* females mature eggs several times during their adult lifespan. Moreover, we

343   noticed that some females abstained from laying eggs during some sampling periods. Since the data

344   was zero-inflated, we considered the fecundity dynamics with a zero-inflated generalised mixed

345   model with a negative binomial distribution and log link function. The response variable was the

346   number of eggs laid at each egg laying event. The explanatory variables were larval feeding

347   treatment, adult feeding treatment, egg laying rank, OLS_{resid} and the four way interaction term. The

348   random intercept was female ID. We also present results when using mass and SMI instead of

349   OLS_{resid}.

350

351   For all analyses, we used the information-theoretic (I–T) approach to achieve model

352   selection (Burnham and Anderson, 2002). The relative strength of support of all possible candidate

353   models was assessed via Akaike's Information Criterion adjusted for small sample sizes (AICc) and

354   AICc weights (ω), the adjusted R^2 as defined by the MuMIn R package (Bartón, 2016). We also

355   report the Cohen's D and 95% confidence intervals (Nakagawa and Cuthill, 2007) using the

356   MBESS package (Kelley, 2018) for categorical variables. For continuous variables we report the

357   partial r effect size (Nakagawa and Cuthill, 2007) and estimated the 95% confidence intervals by

27

28

358   bootstrap (n = 10,000) using the "boot" package (Canty and Ripley, 2019).

359   Cohen (1988) has proposed 'conventional' values as benchmarks for what are considered to

360   be 'small', 'medium', and 'large' effects (r = 0.1, 0.3, 0.5 and d = 0.2, 0.5, 0.8, respectively). We

361   will refer to such terms along the manuscript.

362

363   **Results**

364   Elytron length is a good indicator of structural size in our insect since it correlates highly

365   with mass (Pearson's correlation [95% confidence intervals]; *r* = 0.776 [0.729-0.816]; **Figure 1a.**)

366   and its size is fixed after hatching from the pupal stage, since the cuticle gets tanned and sclerotized

367   after emergence.

368   The relationship between log-transformed mass and log-transformed size did not change

369   significantly according to our larval and adult feeding treatments (SMA regressions: larval feeding

370   treatment: LRT = 2.558, *p-value* = 0.110; adult feeding treatment: LRT = 2.080, *p-value* = 0.149).

371   Similarly the relationship between log-transformed volume and log-transformed elytron size, did

372   not change significantly according to our larval and adult feeding treatments (SMA regressions:

373   larval feeding treatment: LRT = 1.824, *p-value* = 0.177; adult feeding treatment: LRT = 2.535, *p-*

374   *value* = 0.111). Furthermore the relationship between all log-transformed energetic reserves (lipids

375   and sugars) and structural size also did not significantly differ between feeding treatments (SMA

376   regressions, all p-values > 0.05). Therefore we pooled all data together when calculating BCIs,

377   enabling the comparison of condition between treatment groups.

378   Although by construction OLSresid is not correlated with structural size (**Figures 1c.**), it is

379   positively correlated with mass (**Figures 1f**.). Therefore, as predicted, the slope of the OLS

380   regression between the log of mass and the log of elytron size is underestimated, resulting in an

381   over-estimation of condition for large individuals and vice-versa for smaller individuals (**Figure**

382   **1a.**; equivalent results were found when using volume instead of mass as a response variable: see

383   **supplementary material S2**).

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384   Once again as predicted, MA residuals did not correlate with mass (**Figure 1e.**) but strongly

385   negatively correlated with structural size (**Figure 1h.**). Therefore, when applying an MA regression

386   to log-transformed mass to log-transformed elytron size, we found as stated by Green (2001) that

387   the slope was much steeper than the slope of all other regression methods and is overestimated

388   (**Figure 1a.**; equivalent results were also found when using volume instead of mass as an

389   explanatory variable, see **supplementary material S2**).

390   When applying the SMA regression to our data, the slope of the SMA regression was within

391   the slopes of OLS and MA regression methods (**Figure 1a.**). However SMA regression does not

392   completely correct for the dependance between mass and size since when plotting SMA residuals

393   against mass and elytron length, they weakly correlated positively with the former (**Figure 1d.**) and

394   negatively with the latter (**Figure 1c.**).Because the slope of the SMA regression is used as the

395   scaling exponent, it is perfectly correlated with log-transformed SMA residuals (**Figure 1b.**).

396

397   **Correlation between estimates of body condition**

398   Morphometric measures of elytron length, abdomen width and abdomen thickness were

399   significantly repeatable ($p < 0.05$) with an R [95%CI] of 0.921 [0.902, 0.936], 0.572 [0.494, 0.641]

400   and 0.829 [0.790, 0.861] respectively. All morphometric measures (elytron length, mass and

401   volume) were highly correlated with absolute values of body components (lipids and sugars), with

402   correlations tending to be higher for mass and volume than elytron length. As expected, body

403   measures correlated poorly with body components that were scaled for structural size.

404   BCIs (OLS_{resid}, SMI and SVI) significantly correlated with most quantities of energetic

405   reserves which were scaled for body size. Correlation coefficients with scaled lipids or sugars

406   tended to be significantly higher for SVI than for SMI and $OLS_{resid,}$ suggesting that SVI is the best

407   estimator of body condition. Finally, OLS_{resid} and SVI also correlated significantly with absolute

408   values of energetic body reserves (with the exception of SVI with lipids) but not SMI. The latter

409   suggests that OLS_{resid} and SVI do not control adequately for the codependence between structural

410   size and the phenotypically plastic morphological trait, whereas SMI does. The results are shown in

Table 1.

Effect of feeding treatment on body condition

1. Body components

An additive effect of larval and adult feeding treatments on lipids content was strongly supported by model selection (ΔAICc = 6.19; **Supplementary Table S3a.**; **Figure 2a.**). The rich larval feeding treatment resulted in lower lipid content than the poor larval feeding treatment (d = 0.640 [0.197; 1.078]) and the rich adult feeding treatment resulted in lower lipid content than the poor adult feeding treatment (d = 0.961 [0.512; 1.405]).

An effect of the interaction of larval and adult feeding treatments on sugar content was strongly supported by model selection (ΔAICc = 10.87; **Table S1b.**; **Figure 2b.**). Sugar content was at its lowest in the rich larval and rich adult feeding treatment (R.L/R.A vs R.L/P.A: d = 1.843 [1.184; 2.489]; R.L/R.A vs P.L/R.A: d = 3.254 [2.386; 4.107]; R.L/R.A vs P.L/P.A: d = 3.450 [2.567; 4.319]), followed by the rich larval and poor adult feeding treatment (R.L/P.A vs P.L/R.A: d = 1.412 [0.656; 2.150]; R.L/P.A vs P.L/P.A: d = 1.607 [0.842; 2.356]).

2. Scaled body components

There was no evidence that larval and adult feeding treatments had an effect on adult scaled lipid composition since the best supported model was the null model (AICc ω = 0.322; **Supplementary Table S4a.**; **Figure 2c.**). There was, however, strong support that individuals reared in the "poor feeding" treatment at larval stages had higher levels of scaled sugar contents than individuals reared in the "rich food" larval treatment (ΔAICc = 9.58; d = 0.768 [0.321; 1.211]; **Supplementary Table S4b.**; **Figure 2d.**). Model selection did not support an effect of adult feeding treatment (**Supplementary Table S4b.**).

3. Measures of absolute body condition

Elytron length could not be affected by the adult feeding treatment in our experimental

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438 setting, since we had to keep all adults in the same conditions, regardless of their future adult

439 feeding treatment, until the sclerotization of their cuticle. We therefore only analysed the effects of

440 the larval feeding treatment on elytron length. Adults emerging from the rich larval feeding

441 treatment had a smaller elytron size compared to adults emerging from the poor larval feeding

442 treatment (ΔAICc = 7.94; **Supplementary Table S5a.**; **Figure 3a.**; RL vs. PL: d = 0.353 [0.133;

443 0.573]).

444   An effect of larval feeding treatment on mass was strongly supported by model selection

445 (ΔAICc = 5.34; **Supplementary Table S5b.**; **Figure 3b.**). Adults from the rich larval feeding

446 treatment had a lower mass than adults from the poor larval feeding treatment (d = 0.287 [0.067;

447 0.506]). An effect of adult feeding treatment on mass was also marginally supported by model

448 selection (ΔAICc = 2.11; **Supplementary Table S5b.**; **Figure 3b.**). However, we only found a

449 tendency (95% confidence intervals of the estimate overlap 0) for adults from the rich adult feeding

450 treatment to have a lower mass than adults from the poor larval feeding treatment (d = 0.193 [-

451 0.024; 0.411], **Figure 3b.**). An additive effect of larval food (ΔAICc = 85.40) and adult feeding

452 treatment (ΔAICc = 13.94) on the abdomen volume of adult females was strongly supported by

453 model selection (**Supplementary Table S5c.**; **Figure 3c.**). Adults originating from the rich larval

454 feeding treatment had a lower volume than adults from the poor larval feeding treatment (d = 1.108

455 [0.873; 1.341]). Similarly, adults originating from the rich adult feeding treatment had a lower

456 volume than adults from the poor adult feeding treatment (d = 0.443 [0.223; 0.662]).

457

458   **4. Scaled body condition**

459 We detected no effect of both larval and adult feeding treatment on OLS_{resid} and SMI, since

460 models with feeding treatments were not better supported than the null model (**Supplementary**

461 **Table S6a. and S6b.**; **Figure 3d. and e.**). However, we found strong support for an effect of the

462 larval feeding treatment on SVI (ΔAICc = 69.66), with higher estimates for individuals reared in

463 the "poor feeding" treatment at larval stages than in the "rich feeding" treatment (d = 1.239

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464 [0.931-1.545]; **Supplementary Table S6c.**; **Figure 3f.**). The latter result further supported that

465 SVI estimated better body component composition than OLS$_{resid}$ and SMI since it concurred with

466 results found with sugar components. Model selection did not support an effect of adult feeding

467 treatment on any of the 3 BCIs.

468

469 **Relationship between feeding treatments, body condition and fitness**

470   1. **Total fecundity**

471 Model selection revealed a strong support for an effect of adult feeding treatment (**Figure 4a.**) and

472 regardless of the BCI used when controlling for body condition at emergence on total fecundity

473 (range of ΔAICc = 17.01-23.55 depending on BCI used; see **Supplementary Table S7a.; b. and c.**

474 and **Figure 4c.; d. and e** for results using OLS$_{resid}$, mass and SMI at emergence respectively).

475 Estimates were higher for individuals kept in the "rich adult feeding" treatment than the "poor adult

476 feeding" treatment (Figure 4a.; when controlling for OLS$_{resid}$ at emergence: d = 0.671 [0.399-0.941],

477 when controlling for mass: d = 0.703 [0.430-0.974], when controlling for SMI: d = 0.659 [0.387-

478 0.929]). This represents a medium effect size according to Cohen (1988). There was however a low

479 support for an effect of larval feeding treatment and all interaction terms on total fecundity (see

480 **Supplementary Table S7a.**).

481   Partial r effect sizes and 95% confidence intervals suggest support for an association

482 between total fecundity and all BCIs (absolute and scaled) except elytron length and, surprisingly,

483 SVI (**Figure 4b.**). OLS$_{resid}$ and mass also had the largest effect size (partial r [95%CI] = 0.230

484 [0.110; 0.341] and 0.229 [0.105; 0.342] respectively), although 95%CI for all BCIs overlapped

485 (**Figure 4b.; Table S8**). This represents a small effect size (Cohen, 1988). OLS$_{resid}$ was by far the

486 predictor of total fecundity with the highest AICc sum of weights with a value of 0.669, compared

487 to 0.330 for the remaining models (**Table S8**). In addition, models with OLS$_{resid}$ predicted a larger

488 part of the variance (R^2 = 0.138) than models with any other BCI (next highest value was 0.125 for

489 SMI**; Table S8**).

490   We previously demonstrated that mass is the best predictor absolute body reserves, SMI is

491   the best mass based predictor of body condition, and we demonstrate here that OLS_{resid} and mass are

492   the best predictors of fertility. Therefore, for all subsequent analyses on fecundity, we will compare

493   the predictive power and variance explained of OLS_{resid}, mass and SMI only.

494

495   **2. Egg laying dynamics**

496   Model selection revealed a strong support for an interaction effect of adult feeding treatment and

497   the reproductive event on the number of eggs laid, with the number of eggs laid decreasing more

498   sharply at each successive reproductive event for individuals in the poor adult feeding treatment

499   compared to adults in the rich adult feeding treatment ($\Delta AICc = 42.47$ when using OLS_{resid} as a BCI;

500   **Figure 5a.**). There was also strong support for a positive effect of body condition at emergence

501   (estimated either as OLS_{resid}, mass or SMI; $\Delta AICc = 12.98$; $\Delta AICc = 5.57$ and $\Delta AICc = 9.94$,

502   respectively) on the number of eggs laid at each reproductive event (**Figure 5b., 5c. and 5d.** for

503   results with OLS_{resid}, mass and SMI respectively). There was low support of larval feeding treatment

504   and all interaction terms on the number of eggs laid at each reproductive event (**Supplementary**

505   **Tables S9, S10 and S11** for results with OLS_{resid}, mass and SMI respectively).

506

507   **Discussion**

508   In our study, we performed an extensive comparison of the ability of several morphometric

509   measurements and body condition indices to explain the variance in body components (lipids and

510   circulating sugars) and fecundity of *T. molitor* females, as well as their effect sizes. This approach

511   allowed us to decipher the effects of structural size, absolute and relative quantity of body reserves

512   on this fitness parameter. We found that volume, followed by mass, had the highest correlation

513   coefficients with lipid and sugar abdomen reserves of *T. molitor* females. Structural size, estimated

514   through elytron length, was the worst performing morphometric measure in predicting lipid and

515   sugar content in the abdomen. However, mass and volume did not correlate with scaled lipids and

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516   sugars (i.e. lipids and sugars adjusted for body size). Conversely, scaled volume index (SVI;

517   volume adjusted for body size), followed by scaled mass index (SMI; mass adjusted for body size),

518   had the highest correlation coefficients with scaled lipid and sugar abdomen reserves, but did not or

519   poorly correlated with their absolute measures. OLS_{resid} (i.e. residuals from an ordinary least square

520   (OLS) regression between log mass and log structural size) was the only body condition index

521   (BCI) that correlated equally well with both absolute and scaled measures of body reserves.

522

523   Moreover, we observed in our data that violations in assumptions that variables X (here

524   elytron length) and Y (here mass or abdomen volume) result in an overestimation of body condition

525   for big individuals, and an underestimation of body condition for small individuals when using the

526   residuals of an OLS regression between X and Y as a body condition index. On the contrary,

527   violations in the assumption that the ratio in error variance in X and Y is equal to 1 while

528   performing an MA regression between X and Y would lead to overestimation of body condition for

529   small individuals and an underestimation for big individuals. The use of the residuals or the slope of

530   the SMA regression between elytron size and mass or volume as a BCI offer a compromise between

531   OLS and MA regressions. Taken together, our results confirm results from studies in vertebrates

532   (Peig and Green, 2009, 2010), which state that OLS_{resid} does not control adequately for the

533   interdependence between body size and plastic morphological traits such as mass and volume.

534   However it is important to note that using SMA regressions to calculate a BCI remains imperfect,

535   since residuals correlate weakly with both structural size and the plastic morphological trait.

536

537   **Effect of feeding treatments on morphology, body composition and body condition**

538   We observed, though we did not quantify it, that there was approximately two months of delay

539   between the emergence of adults from the rich compared to the poor larval feeding treatments, the

540   larvae in the rich feeding treatment undergoing metamorphosis earlier, which desynchronized the

541   data collection between the two feeding treatments. *T. molitor* is indeed known to be very plastic in

542   its larval developmental time (Cotton & St. George, 1929). It has been shown in several insect

543   species that restricted access to food at the larval stage can sometimes lead to a delayed maturation

544   at a smaller adult body size (Day & Rowe, 2002, Dmitriew et al., 2009). We observed the contrary,

545   that adult females emerging from the poor larval feeding treatment were slightly bigger (2 %

546   difference in the elytron size) than females emerging from the rich larval feeding treatment.

547   While looking at the body composition of adult beetles originating from both well-fed or

548   poorly-fed larvae, the additive effects of larval and adult feeding treatment on lipid storage suggests

549   that *T. molitor* does not adjust its propensity to store fat according to the environment experienced

550   at the larval stage. The interaction between larval and adult feeding treatments on carbohydrates

551   content of adult beetles however suggests that insects which have experienced adverse feeding

552   conditions at the larval stage increase sugar storage later in life, and that even individuals which

553   were well-fed as larvae will increase carbohydrates storage if food is lacking at the adult stage. This

554   is the inverse pattern of what is found in a grasshopper species, where larval food restriction

555   influenced adult lipid but not carbohydrates storage (Hahn, 2005). In a ladybird species (Dmitriew

556   et al., 2009), food restriction at the larval stage produced adults that were lighter and storing more

557   fat relative to their wing area, which translated into a reduced wing loading. The authors have

558   proposed this to represent a plastic increase of the dispersal abilities of individuals having

559   experienced adverse juvenile conditions. In our study, beetles originating from poorly fed larvae

560   were heavier than their well-fed counterparts. Since *T. molitor* is a flightless burrowing insect, the

561   absence of preferential storage of fat over heavier reserves such as glycogen might reflect a

562   relaxation of the selection pressure imposed by dispersal via flight on lipid storage and mass

563   relative to size.

564   Since adult beetles originating from larvae reared in rich feeding conditions were smaller,

565   lighter and their abdomen less voluminous than beetles originating from larvae reared in poor

566   feeding conditions, mass relative to size was similar between feeding treatments. Therefore, body

567   condition indices OLS_{resid} and SMI were not significantly different between feeding treatments.

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568   However, the Scaled Volume Index (SVI), which is the only scaled index that is associated with our

569   larval feeding conditions, did differ between larval feeding treatments, suggesting that early body

570   condition was slightly higher in individuals reared in poor feeding conditions. Interestingly, SVI is

571   also the BCI which shows the highest correlation coefficients with our measurements of both

572   absolute and scaled energetic reserves, mirroring the fact that abdomen volume had the highest

573   correlation coefficients with the absolute amount of body reserves. SMI had the second highest

574   correlation coefficient with scaled body reserves, whereas OLS_{resid} was the BCI with the lowest

575   correlation coefficients.

576   **Predictive power of body condition indices on female fecundity**

577   The effect of both mass and the standardized mass index (SMI) on fecundity were supported by

578   model selection. Interestingly, the effect size of mass is roughly equal to the effect sizes of

579   structural size + standardized mass index on fecundity. This suggests that the effect of mass on

580   fecundity does indeed contain the effects of both structural size and body reserves corrected for it.

581   Following this reasoning, approximately 40 % of the effect size of mass on fecundity is represented

582   by structural size, whereas the other 60 % are represented by the body reserves corrected by

583   structural size. We cannot draw the same conclusions from the volume/standardized volume index

584   (SVI), because volume was a weaker predictor of fecundity than mass, and SVI is an even poorer

585   predictor. This might be due to the fact that the other phenotypically plastic morphological

586   measurements of our study correlate better with components that were not measured in this study

587   but contribute to energy storage (i.e. water, proteins, refs).

588   OLS_{resid} was the best supported BCI predictor of fecundity and explained the highest amount

589   of variance. However, mass, volume and SMI all had similar effect sizes with OLS_{resid} in predicting

590   fecundity. Similarly to mass, the effect size of OLS_{resid} on fecundity is roughly equal to the effect

591   sizes of SMI + size. We hypothesize that OLS_{resid} was the best supported predictor of fecundity not

592   because it is the best predictor of body condition, but rather because it incorporates both absolute

593   and relative quantities of body reserves slightly better than mass does, both of which are associated

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594 with fecundity. However, OLS_{resid} have a similar effect size to other BCI because it is body

595 condition, rather than structural size, which has the strongest predictive power on fecundity, as

596 suggested by the low predictive power of elytron length and the higher predictive power of SMI.

597

598 **Effect of feeding treatments and body condition on life history**

599 First, we can note that we found no evidence of adaptive phenotypic plasticity (Monaghan, 2008 ;

600 Dmitriew & Rowe, 2011), in the sense that insects having experienced poor larval feeding

601 conditions did not achieve a higher fecundity output than insects that experienced rich larval

602 feeding conditions when placed in poor adult feeding conditions. This is likely due to the fact that

603 *T. molitor* females, which experienced a food shortage at the larval stage, emerge as adults having a

604 similar quantity of body reserves (in terms of OLS_{resid} and SMI) or even a little higher (absolute

605 body reserves in terms of mass, volume and relative body reserves in terms of SVI) than beetles

606 having been well fed at the larval stage. As a result, we found no evidence for larval feeding

607 treatment to affect body condition at emergence. This shows that *T. molitor* females are able to

608 maintain homeostasis in their physiology to buffer differential availability of resources. This is

609 likely due to the high degree of developmental plasticity of this insect, allowing individuals to

610 compensate for adverse juvenile conditions to produce an optimal phenotype at the adult stage

611 (Beldade et al., 2011). This necessity to achieve an optimal adult phenotype might be a strong

612 selection pressure for developmental plasticity in this insect. There was however variation in body

613 condition at emergence.

614   As expected in an income breeder species, in which individuals rely on resources

615 accumulated during their adult life to produce offspring, the adult feeding treatment of the females

616 had an effect on fecundity. Even though the effect of the adult feeding treatment was stronger, we

617 also found support for a positive effect of body condition at emergence on the total fecundity of *T.*

618 *molitor*. Additionally, we could have expected to find support for an interaction between body

619 condition and egg laying rank while analysing the fecundity dynamics. This would have indicated

620 that early fitness depends more on resources accumulated before metamorphosis, whereas later in

621 life resources accumulated by the adult would play a more important role. Instead, while the

622 decrease in fecundity over time was sharper in females from the poor adult feeding treatment

623 compared to females from the rich adult feeding treatment, we found no evidence of such a

624 dynamic effect of body condition at emergence, i.e. the effect was constant across egg laying ranks.

625 Overall, our data show that it is possible to disentangle the effects of past and present food

626 availability on life-history changes in income breeders (Kasumovic et al., 2009). In our case, *T.*

627 *molitor* relies partly on resources accumulated in their early developmental stages for their lifetime

628 fecundity as income breeders.

629

630 **Conclusion**

631 We were able to determine that even though OLS_{resid} is not the best predictor of the quantity of fat

632 and sugars stored in the insect's body, it outperforms other BCIs in terms of variance explained of

633 the insect's fitness, but does not outperform a simple measurement of mass in terms of effect size.

634 SMI on the other hand is a good predictor of fecundity and adequately controls for the

635 interdependence between mass and size. Only structural size and SVI do not predict fecundity. In

636 our case, the use of OLS_{resid}, mass or SMI highlighted equally well that food restriction at the larval

637 stage in *T. molitor* females results in adults having a similar early body condition. It is this early

638 body condition as well as the adult feeding treatment, rather than the larval feeding treatment,

639 which influence the lifetime fecundity of this iteroparous insect. The choice of a given BCI or a

640 simple measurement of mass should therefore be dependant on the question asked:

641 - An investigator may not be interested in body condition or structural size when

642 predicting fecundity, but may want to control for it effects (e.g. when investigating

643 another unrelated variable). In such cases, OLS_{resid} should be preferred since it is the

644 parameter which explains the highest amount of variance and has the best predictive

645 power. Note here, however, that OLS_{resid} may not be the best predictor for other

646   fitness related traits (e.g. survival), thus should be compared with other BCIs when

647   investigating other fitness related variables.

648   -   If an investigator is interested in the effects of body condition but not structural size

649   (i.e. relative body reserves) on any given response variable (including fecundity)

650   then SMI or SVI should be preferred.

651   -   If an investigator is interested in the combined effects of body condition and

652   structural size (i.e. absolute body reserves) on any given response variable (including

653   fecundity) then mass or volume should be preferred.

654

658

659   **Authors contributions:** Conceived the study and designed the experiments: CZ, YM & MG.

660   Conducted the experiments: CZ & MG. Analyzed the data: MG. Wrote the manuscript: CZ & MG

661   with contributions from YM.

662

663   **Supporting information:** Supplementary Material 1, containing figures and tables S1 to S11.

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665

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Figure 1: a. Ordinary Least Squares (OLS, in black), Major Axis (MA in grey), and Standardized Major Axis (SMA, in red) regressions between the logarithm of elytron length and the logarithm of mass of individual *Tenebrio molitor* females. The correlation between the residuals of the OLS regression, mass and elytron length are represented respectively in **c.** and **f.**. The correlation between the residuals of the SMA regression, mass and elytron length are represented in **d.** and **g.**. The correlation between the residuals of the MA regression, mass and elytron length are represented in **e.** and **h.**.

b. Correlation between the residuals of the SMA regression and the logarithm of the Standardized Mass Index (SMI) calculated using the slope of the SMA regression according to the formula of Peig & Green (2009). Each dot represents an experimental individual.
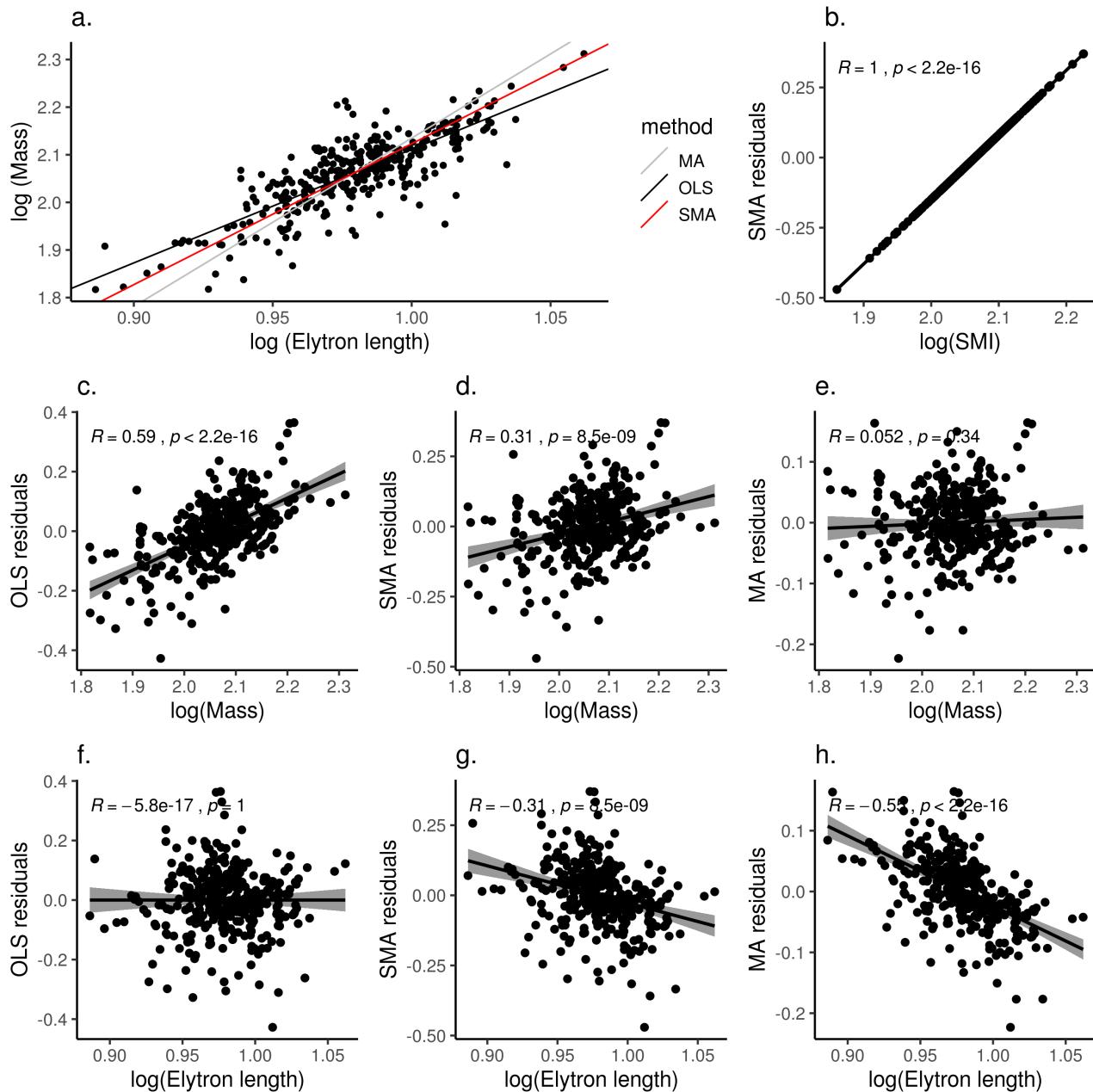
Figure 2: Relationship between the larval feeding treatment (LFT), adult feeding treatment (AFT) and **a.** the logarithm of the lipid quantities **b.** the logarithm of the quantities of sugars (glucose and glycogen) **c.** the logarithm of the lipids scaled for structural size (see methods) and **d.** the logarithm of the sugars scaled for structural size in *T. molitor* females. The boxes show the first to the third quartiles and the median. The bars indicate the 1.5 interquartile of the lower and upper quartiles. Each dot represents a data point. The open dots represent the individuals from the rich larval feeding treatment, whereas the plain dots represent individuals from the poor larval treatment. The black dots represent the rich adult feeding treatment, while the red dots represent the poor adult feeding treatment.
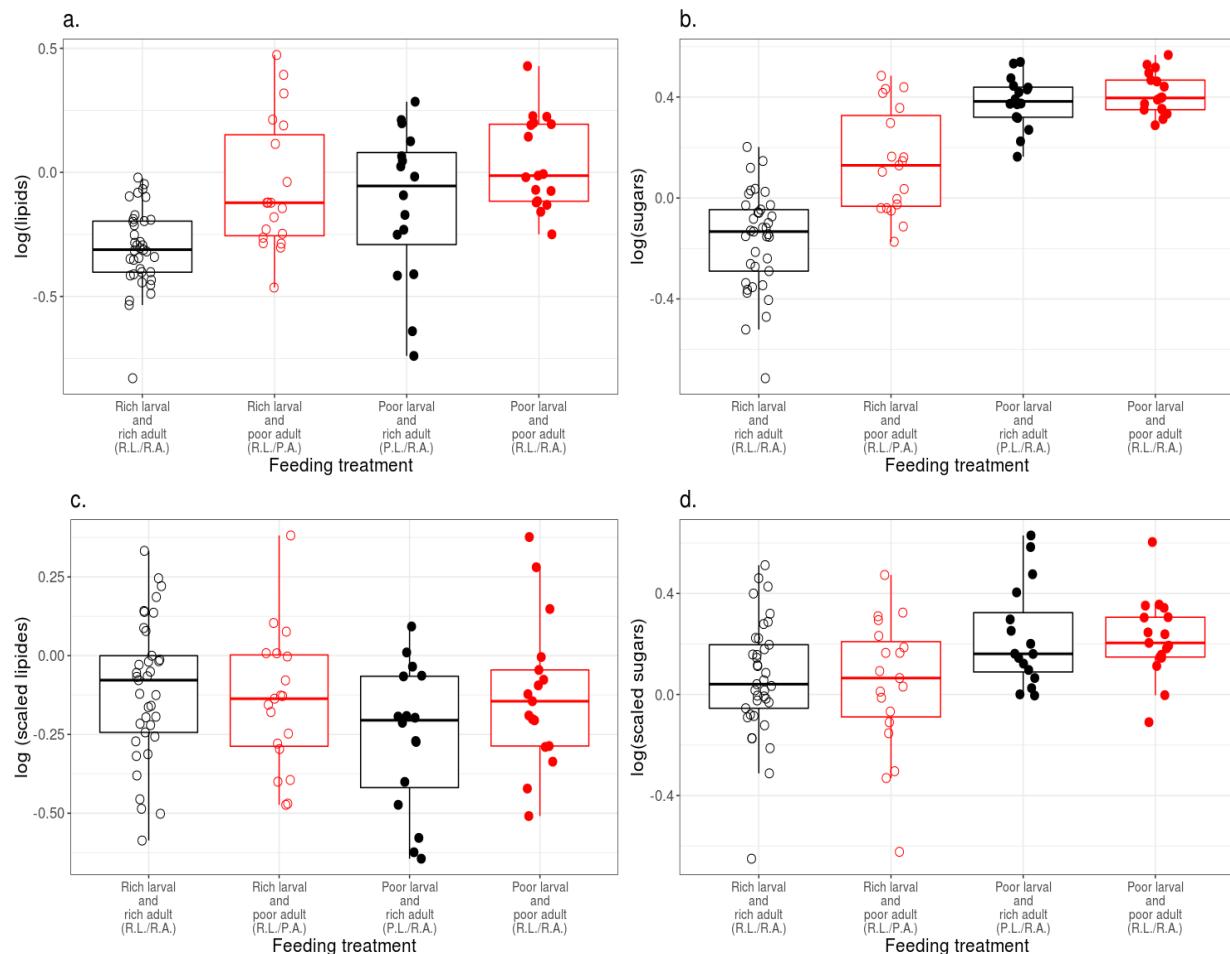
Figure 3: Effect of LFT and AFT on **a.** elytron length in centimeters (only according to LFT only), **b.** mass in milligrams, **c.** volume in cubic centimeters, **d.** OLS$_{resid}$, **e.** SMI in milligrams, **f.** SVI in cubic centimeters. The boxes show the first to the third quartiles and the median. The bars indicate the 1.5 interquartile of the lower and upper quartiles. Each dot represents an experimental individual. The open dots represent the individuals from the rich larval feeding treatment, whereas the plain dots represent individuals from the poor larval treatment. The black dots represent the rich AFT, while the red dots represent the poor AFT.
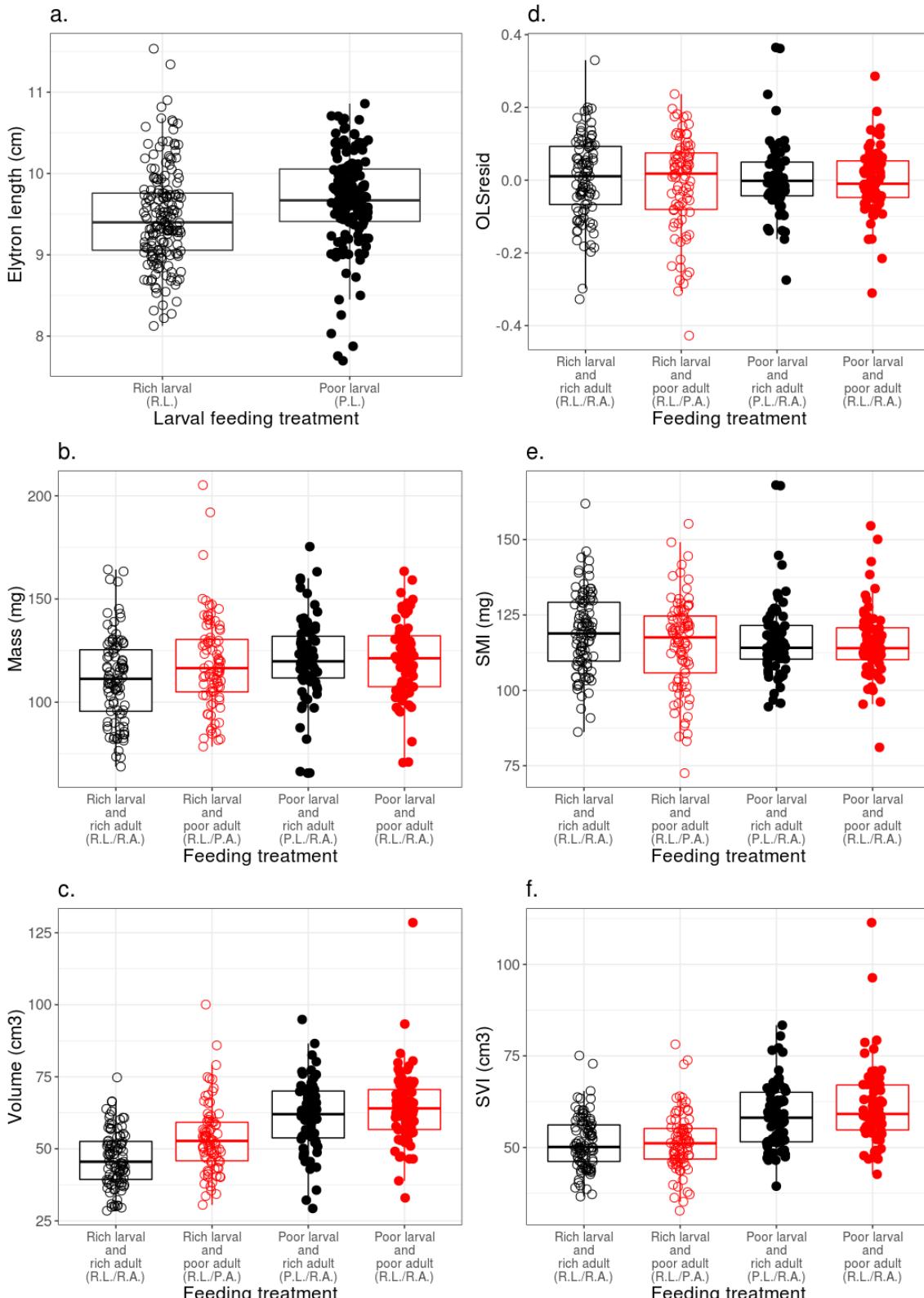
Figure 4: a. Total fecundity of *T. molitor* females according to LFT and AFT. **b.** The partial effect size of each morphological measurement and BCI on total fecundity controlling for AFT. The dots represent the estimate of each BCI, the horizontal bars represent the confidence intervals.
c., **d.** and **e.** represent the total fecundity according to respectively the residuals of OLS$_{resid}$, mass and SMI and the AFT. The black dots represent the rich AFT while the red dots represent the poor AFT, with the corresponding regression line and the 95% confidence intervals around it.
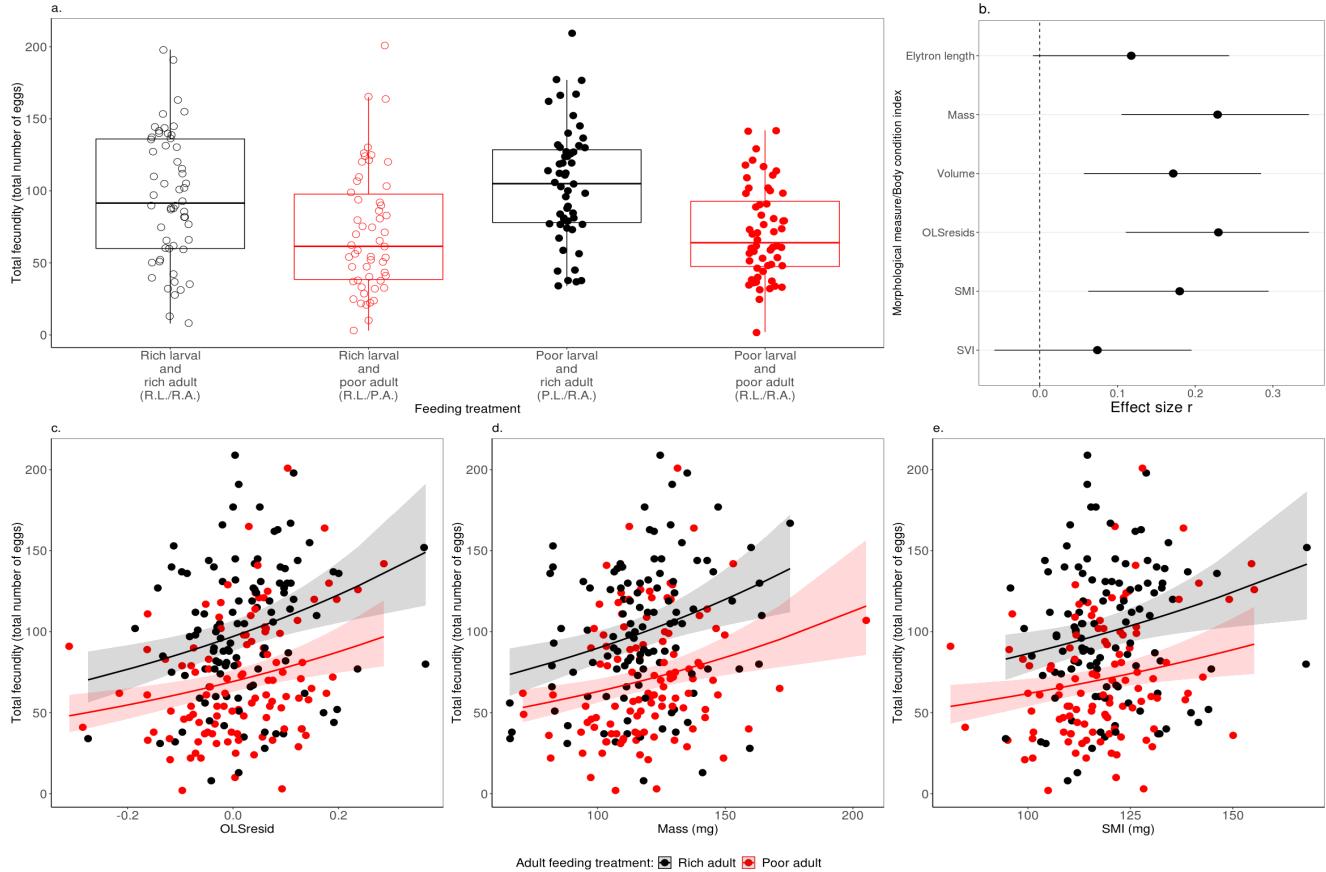
Figure 5: a. Effect of the interaction between rank (egg laying event) and AFT on the number of eggs laid, controlling for body condition at emergence as OLS$_{resid}$, using a zero-inflated mixed effect model with a negative binomial distribution. Effect of body condition at emergence as **b.** OLS$_{resid}$, **c.** mass, and **d.** SMI on fecundity controlled for the rank, using a zero-inflated mixed effect model with a negative binomial distribution. The black dots represent the rich AFT, while the red dots represent the poor AFT, with the corresponding regression lines and the 95% confidence intervals around it.