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2017-10-03
journal article
en
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Fitness implications of sex-specific catch-up growth in *Nephila senegalensis*, a spider with extreme reversed SSD

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Background. Animal growth is often constrained by unfavourable conditions and divergences from optimal body size can be detrimental to an individual's fitness, particularly in species with determinate growth and a narrow time-frame for life-time reproduction. Growth restriction in early juvenile stages can later be compensated by means of plastic developmental responses, such as adaptive catch-up growth (the compensation of growth deficits through delayed development). Although sex differences regarding the mode and degree of growth compensation have been coherently predicted from sex-specific fitness payoffs, inconsistent results imply a need for further research. We used the African *Nephila senegalensis*, representing an extreme case of female-biased SSD, to study fitness implications of sex-specific growth compensation. We predicted effective catch-up growth in early food-restricted females to result in full compensation of growth deficits and a life-time fecundity (LTF) equivalent to unrestricted females. Based on a stronger trade-off between size-related benefits and costs of a delayed maturation, we expected less effective catch-up growth in males.

Methods. We tracked the development of over one thousand spiders in different feeding treatments, e.g. comprising a fixed period of early low feeding conditions followed by unrestricted feeding conditions, permanent unrestricted feeding conditions, or permanent low feeding conditions as a control. In a second experimental section, we assessed female fitness by measuring LTF in a subset of females. In addition, we tested whether compensatory development affected the reproductive lifespan in both sexes and analysed genotype-by-treatment interactions as a potential cause of variation in life-history traits.

Results. Both sexes delayed maturation to counteract early growth restriction, but only females achieved full compensation of adult body size. Female catch-up growth resulted in equivalent LTF compared to unrestricted females. We found significant interactions between experimental treatments and sex as well as between treatments and family lineage, suggesting that family-specific responses contribute to the unusually large variation of life-history traits in *Nephila* spiders. Our feeding treatments had no effect on the reproductive lifespan in either sex.

Discussion. Our findings are in line with predictions of life-history theory and corroborate strong fecundity selection to result in full female growth compensation. Males showed incomplete growth compensation despite a delayed development, indicating relaxed selection on large size and a stronger trade-off between late maturation and size-related benefits. We suggest that moderate catch-up growth in males is still adaptive as a 'bet-hedging' strategy to disperse unavoidable costs between life-history traits affected by early growth restriction (the duration of development and adult size).

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JMS and RN dedicate this work to the memory of our late colleague
Nicole Ruppel (3.10.1978–24.2.2016)

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1 **Abstract**

3 **Background.** Animal growth is often constrained by unfavourable conditions and divergences

4 from optimal body size can be detrimental to an individual's fitness, particularly in species with

5 determinate growth and a narrow time-frame for life-time reproduction. Growth restriction in

6 early juvenile stages can later be compensated by means of plastic developmental responses,

7 such as adaptive catch-up growth (the compensation of growth deficits through delayed

8 development). Although sex differences regarding the mode and degree of growth

9 compensation have been coherently predicted from sex-specific fitness payoffs, inconsistent

10 results imply a need for further research. We used the African *Nephila senegalensis*,

11 representing an extreme case of female-biased SSD, to study fitness implications of sex-specific

12 growth compensation. We predicted effective catch-up growth in early food-restricted females

13 to result in full compensation of growth deficits and a life-time fecundity (LTF) equivalent to

14 unrestricted females. Based on a stronger trade-off between size-related benefits and costs of a

15 delayed maturation, we expected less effective catch-up growth in males.

16 **Methods.** We tracked the development of over one thousand spiders in different feeding

17 treatments, e.g. comprising a fixed period of early low feeding conditions followed by

18 unrestricted feeding conditions, permanent unrestricted feeding conditions, or permanent low

19 feeding conditions as a control. In a second experimental section, we assessed female fitness by

20 measuring LTF in a subset of females. In addition, we tested whether compensatory

21 development affected the reproductive lifespan in both sexes and analysed genotype-by-

22 treatment interactions as a potential cause of variation in life-history traits.

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25 LTF compared to unrestricted females. We found significant interactions between experimental

26 treatments and sex as well as between treatments and family lineage, suggesting that family-

27   specific responses contribute to the unusually large variation of life-history traits in *Nephila*

28   spiders. Our feeding treatments had no effect on the reproductive lifespan in either sex.

29   **Discussion.** Our findings are in line with predictions of life-history theory and corroborate

30   strong fecundity selection to result in full female growth compensation. Males showed

31   incomplete growth compensation despite a delayed development, indicating relaxed selection

32   on large size and a stronger trade-off between late maturation and size-related benefits. We

33   suggest that moderate catch-up growth in males is still adaptive as a 'bet-hedging' strategy to

34   disperse unavoidable costs between life-history traits affected by early growth restriction (the

35   duration of development and adult size).

37   **Introduction**

39   Body size and the duration of development are among the most fitness-relevant life-history

40   traits and have been extensively studied in various animal taxa (reviewed in Blanckenhorn

41   2005; Nylin & Gotthard 1998; Roff 2002). Generally constrained by a trade-off between a

42   favourable size at the onset of reproduction and the time necessary to reach it (Blanckenhorn

43   2000; Roff 1992), animal growth depends on both inherited growth trajectories and plastic

44   modifications of them (Chase 1999; Dmitriew 2011). Extrinsic factors that may influence the

45   mode of development include parasite infestations and other pathogens (Paez et al. 2015;

46   Vergauwen et al. 2011), cues of present or future environmental conditions (Kasumovic &

47   Brooks 2011), ambient temperature (Kingsolver et al. 2004), and food supply (Stearns 1992;

48   Wilson & Osbourn 1960).

49   Growth strategies and optimal body size may differ markedly between the sexes, which is

50   particularly evident in sexually size-dimorphic species (Blanckenhorn 2005). As large males tend

51   to succeed in male-male competition across animal taxa, body size in males is often subject to

52   sexual selection, resulting in male-biased sexual size dimorphism (SSD) (Kingsolver & Pfennig

53   2004). Still enigmatic conditions are found in species with female-biased SSD, which mainly

54   occurs in oviparous animals, like fishes (Barreto et al. 2003), amphibians (Hector et al. 2012;

55   Nali et al. 2014), and many invertebrates (Honek 1993; Smith & Brockmann 2014) including

56 spiders (Cheng & Kuntner 2015; Foellmer & Moya-Laraño 2007; Higgins et al. 2011; Schneider &

57 Andrade 2011). As females are strongly selected to produce large numbers of eggs, increased

58 female size through fecundity selection is generally well supported in these species

59 (Blanckenhorn 2005; Nylin & Gotthard 1998). Males, however, apparently are selected to stay

60 small, which has been related to improved mobility and agility during mate search (Moya-

61 Laraño et al. 2002; Moya-Laraño et al. 2009), a decreased risk of predation and female sexual

62 cannibalism (Foellmer & Fairbairn 2004), benefits of protandry through rapid maturation

63 (Blanckenhorn et al. 2007), and reduced energy expenditures (Blanckenhorn 2000;

64 Blanckenhorn 2005).

65   Optimization of development and growth may be difficult in non-constant environments.

66 Basic strategies that permit fitness maximization under invariant conditions may need to be

67 refined in response to environmental changes (Foster & Kreitzman 2009). While alterations of

68 environmental conditions often appear as recurring sequences, irregular fluctuations of

69 environmental parameters are also common in a range of habitats. Such unpredictable

70 conditions pose a threat to an individual's fitness, particularly in species in which reproductive

71 success depends on a single reproductive period (Abrams et al. 1996). For example,

72 unfavourable temperatures or food restriction may result in a delay of development, which can

73 increase juvenile predation risk, but also lower reproductive prospects in individuals that reach

74 maturity too late (end-of-season penalty; e.g. De Block et al. 2008; Higgins 2000).

75   Phenotypic plasticity (the capacity of a genotype to express different phenotypes in different

76 environments; West-Eberhard 2003) provides the potential to counteract a period of

77 unfavourable growth conditions in juvenile stages by means of adaptive developmental

78 responses, e.g. compensatory growth and catch-up growth (Dmitriew 2011; Krause & Caspers

79 2016; Metcalfe & Monaghan 2001; Walzer et al. 2015). Compensatory growth refers to

80 elevated growth under improved conditions, whereby a delay of sexual maturation is

81 minimized. In contrast, adaptive catch-up growth is defined as a strategy to reach a favourable

82 adult size at the expense of delaying maturation (Hector & Nakagawa 2012; Livingston et al.

83 2014). Compensatory developmental mechanisms enable animals to either limit or entirely

84 prevent fitness costs that would follow from a period of adverse growth conditions without the

85   capacity for such flexible responses. However, early food restriction and subsequent growth
86   compensation may entail intrinsic costs that can even lead to a reduction in lifespan (English &
87   Uller 2016; Hornick et al. 2000; Reichert et al. 2015).

88   As benefits and costs of developmental compensation may differ considerably between
89   males and females, integrating pre-estimated divergent selection on body size may substantiate
90   experimental work on such strategies. Plastic modifications of life-history traits have been
91   related to experimental feeding regimes in a range of studies (Bauerfeind & Fischer 2005;
92   Bonneaud et al. 2016; Dahl et al. 2012; Davidowitz et al. 2003; Fernandez-Montraveta & Moya-
93   Larano 2007; Kleinteich & Schneider 2011; Krause & Caspers 2016), but relatively few of these
94   have addressed sex-specific differences regarding compensatory development (Arnold et al.
95   2007; Chin et al. 2013; Tawes & Kelly 2017).

96   In general, predictions concerning such differences are based on (1) proposed sex-specific net
97   benefits of growth compensation (i.e. the sex whose fitness depends stronger on large body
98   size is expected to show a higher degree of growth compensation), (2) on the possibility to
99   increase size after sexual maturation (i.e. determinate versus indeterminate growth; with
100   determinate growth generating stronger selection pressure to compensate growth deficits),
101   and (3) on potential long-term costs of compensatory development (Livingston et al. 2014).
102   Previous studies, however, are inconsistent as to whether predictions were met or not (Barreto
103   et al. 2003; Livingston et al. 2014; Stillwell & Davidowitz 2010; Tawes & Kelly 2017), thus
104   indicating that possible trade-offs between growth compensation, taxon-dependent life-
105   history, and environmental conditions that determine the adaptive value of compensation
106   require further research.

107   Species showing strong SSD are particularly suitable model systems to investigate sex-specific
108   compensatory mechanisms, because especially pronounced sex-differences concerning size
109   selection can be comparatively studied in a single species. Golden-silk spiders (genus *Nephila*,
110   family Araneidae) show some of the most extreme cases of female-biased SSD (Kuntner et al.
111   2013). Male and female size in these spiders has been suggested to have evolved
112   independently, with steady fecundity-driven selection on increased female size, whereas
113   phylogenetic analyses did not reveal a consistent evolutionary trend towards male size-

114   reduction (Higgins et al. 2011; Kuntner & Elgar 2014). In addition, several studies have reported

115   large male advantages in the context of mating (Christenson & Goist 1979; Elgar et al. 2003;

116   Elgar & Fahey 1996; Rittschof 2010). Causes of small male size remain thus ambiguous, which

117   also applies to the remarkable within-sex size variation in many species (Elgar & Fahey 1996;

118   Higgins et al. 2011; Schneider & Elgar 2005). *Nephila* spiders are short-lived animals with

119   determinate growth (Fromhage et al. 2007; Miyashita 2005; Rittschof 2011) and individuals of

120   both sexes mature and reproduce within a limited time frame and within their own cohort

121   (Higgins 2000; Higgins et al. 2011).

122   Natural populations exposed to different environmental conditions have been studied in the

123   American *N. clavipes* (Higgins 1993; Higgins 1992). This species is bivoltine in some populations,

124   where first-generation females mature at larger average size than second-generation females.

125   However, first-generation females pass through early development in the dry season,

126   experiencing low feeding success and hence unfavourable juvenile growth conditions. These

127   females may have adaptively delayed maturation, later taking advantage of improving feeding

128   conditions to eventually mature at large size (Higgins 1992). While these observations hint

129   towards catch-up growth in females, experimental work is needed to test predictions following

130   from this mechanism; specifically in comparison with permanently food-restricted and

131   permanently well-fed individuals. Furthermore, the inclusion of males is essential to access sex-

132   specific differences in an integral procedure to understand selection in this system.

133   Here, we consider the above-mentioned observations in the light of current research

134   focussing on plastic compensatory mechanisms in sexually size-dimorphic species (Chin et al.

135   2013; Kahn et al. 2012; Livingston et al. 2014). Using the African *N. senegalensis*, we

136   implemented a comprehensive approach consisting of two successive experimental sections. In

137   the first section, we manipulated the study animals´ feeding conditions, rearing split broods

138   under constant low or high food supply, or in treatments in which the food supply was

139   reciprocally reversed at a fixed point in time. Based on strong fecundity-selection for large

140   female size (Higgins & Goodnight 2011; Kuntner et al. 2012), we predicted effective catch-up

141   growth after treatment reversal in initially food-restricted females to compensate the

142   preceding deficits. As *Nephila* males generally benefit from protandry (Danielson-Francois et al.

143   2012; Kasumovic et al. 2009), selection should act against an exceedingly delayed development

144   in males. Furthermore, flexible mating strategies have been found to balance reproductive

145   success between differently-sized competitors (Neumann & Schneider 2015). Therefore, we

146   assumed weaker selection on large male size and predicted less effective catch-up growth in

147   males.

148   Following the rearing treatments, we used a subset of adult females to measure life-time

149   fecundity (LTF), thereby providing a direct test concerning the adaptive significance of growth

150   compensation, which is often omitted in empirical studies (Dmitriew 2011; Hector & Nakagawa

151   2012). We predicted growth compensation to result in equivalent numbers of offspring in

152   initially food-restricted females compared to constantly well-fed females.

153   As another measure of fitness, we tested whether growth compensation affected the post-

154   maturation lifespan and hence the potential time-frame of reproduction in both sexes. Finally,

155   we report treatment-related mortality and analyse genotype-by-treatment interactions as a

156   potential cause of the remarkable variation of life-history traits in our model system.

157

158   **Material & Methods**

159

160   *Developmental duration, body size and weight, pre-maturation mortality*

161

162   We collected eight gravid females near Cradock, Eastern Cape, South Africa in March, 2008.

163   Field-collected females were transferred to the laboratory and housed individually in 60 x 60

164   cm-sized Perspex frames. We maintained females under standardized conditions and all of

165   them built viable egg sacs that were incubated in air-vented plastic containers until the

166   offspring hatched (see Schneider et al. 2011 for our standard methods concerning housing,

167   feeding, and watering of spiders as well as temperature conditions). The hatchlings were

168   separated at very small body size (2-4 mm) before they had reached the third instar (the first

169   two moults in *Nephila* spiders occur inside the egg sac). Separated spiders were housed in small

170   plastic cups but were transferred to larger cups as they increased in body size. We haphazardly

171   allocated the study animals to the following feeding treatments: (1) High-High, (2) High-Low, (3)

172 Low-High, and (4), Low-Low. Equal numbers of spiders from individual maternal lineages were

173 used in each treatment. Spiders in the High-High treatment were provided with *ad libitum* food

174 over the entire duration of development to maturity, whereas spiders in treatment Low-Low

175 were kept at low-food conditions throughout the experiment. Study animals in treatment High-

176 Low received *ad libitum* food during a fixed period of four weeks (defined as early experimental

177 conditions) but were kept under low-food conditions in the period following the first four

178 weeks (defined as late experimental conditions). The inversed pattern was adopted in

179 treatment Low-High. The spiders were fed *Drosophila* and *Calliphora* flies. Low-food conditions

180 conform to 4 *Drosophila* flies per week during early experimental conditions and 6-10

181 *Drosophila* flies (depending on the spider's size) per week during late experimental conditions,

182 respectively. Low-food spiders large enough to eat *Calliphora* received 2 flies per week.

183 *Drosophila* flies were raised on Carolina Biological Supply instant *Drosophila* medium Formula

184 4-24, which was enriched with additional nutrients, especially protein and vitamins. For this

185 purpose, we mixed the medium with commercial high quality dog food according to a study by

186 Mayntz & Toft (2001), which demonstrated positive effects on growth and survival in a wolf

187 spider fed with flies cultivated on this specific mixture. *Calliphora* flies were obtained by

188 incubating fully grown larvae purchased from a commercial supplier. All study animals were

189 reared in a daylight lab and hence were exposed to slight photoperiod changes. We checked

190 the spiders on five days per week and tracked the development of each individual by recording

191 the following data: sex, duration of development from the start of the experiment to

192 maturation, weight at completion of the early experimental period, adult weight and adult body

193 size (given as patella-tibia length).

194 As morphology-based sex-determination is impossible in small juvenile spiders, individuals

195 could be sexed only at larger developmental stages in the late experimental period, but 85

196 spiders died unsexed. Immature males were identified by their swollen pedipalps indicating the

197 ongoing transformation into copulatory organs; the lack of this trait in juveniles with a body

198 length ≥ approximately 12 mm indicated female sex.

199

200 *Post-maturation longevity*

201

202   In addition to developmental modifications, we analysed treatment-related effects on adult
203   longevity. For this purpose, we chose 137 males and 251 females across treatments upon
204   reaching maturity. The spiders were maintained on our regular laboratory feeding schedule
205   irrespective of the developmental feeding treatment experienced before. Spiders were chosen
206   randomly; paying attention, however, to exclude animals to be used in the mating experiments
207   (see 'Life-time fecundity and hatching success') or in our general breeding schedule. The
208   remaining study animals were killed by hypothermia after reaching maturity and preserved at -
209   80°C. In total, 1280 spiders were used in this study, of which 30 disappeared and another three
210   were accidently killed during daily routine at early juvenile stages.

211

212   *Life-time fecundity and hatching success*

213

214   We randomly chose 38 adult females originating from the treatments High-High (*N* = 14), Low-
215   High (*N* = 11), and Low-Low (*N* = 13) to investigate whether compensatory growth enables
216   females to overcome a period of poor feeding conditions during juvenile development and
217   achieve a reproductive outcome equivalent to constantly well-fed females. We did not include
218   High-Low females in this experiment (females in treatments High-Low and Low-Low did not
219   differ significantly in developmental duration and size; see results). Females were maintained
220   on our regular feeding schedule. We randomly chose adult males from the High-High feeding
221   treatment to arrange mating trials. Prior to mating, each female was transferred to a Perspex
222   frame (measuring 60 × 60 × 12 cm) and given at least one day to build an orb-web, which is
223   necessary for courtship and mating to take place. We positioned an unrelated male on the
224   upper frame threads of the web. Each virgin couple was allowed to copulate once in a
225   predefined period of 3 hours. If copulation did not occur within the given time, we excluded the
226   male from the study and arranged a second mating trial with a different male at a later date
227   (each male was used only once). Six females remained unmated after the second trial and were
228   excluded from the study.

229   At the beginning of each trial, the female received one *Calliphora* fly (males prefer mating

230   with feeding females; Schneider et al. 2011). We measured the duration of copulation and

231   removed the spiders from the web afterwards. Females were maintained in Perspex frames to

232   build egg sacs until they died of age. Four females did not build egg sacs at all, despite

233   apparently normal copulations. The egg sacs produced were incubated in air-vented plastic

234   containers and preserved in alcohol after approximately five weeks. We carefully opened each

235   egg sac and assessed the number of normally developed spiderlings, undeveloped eggs, and

236   total clutch size. All experiments were carried out at the Zoological Institute, University of

237   Hamburg.

238

239   *Statistical analyses*

240

241   The study animals originated from eight maternal lineages from which we allocated equal

242   numbers of individuals to each rearing-treatment. As a premise for further analysis, we tested if

243   family lineages were evenly distributed among individuals that had passed through the feeding

244   treatments and finally matured. The test confirmed no significant differences in the numbers of

245   individuals originating from different family lineages between our feeding treatments (G-tests:

246   males: χ^2 = 15.16, *P* = 0.82; *N* = 362; females: χ^2 = 19.24, *P* = 0.57; *N* = 559). We tested

247   predictions with respect to adult body size, body mass, developmental durations, life-time

248   fecundity (LTF), and post-maturation longevity using t-tests for normal data with equal

249   variances and non-parametric Wilcoxon or Kruskal-Wallis tests if data diverged from these

250   assumptions (indicated by Shapiro- and Bartlett's tests). Results are given as means ± SE,

251   providing medians and interquartile ranges (IQRs) for non-parametric tests. Complementary

252   post-hoc analyses were performed using pairwise Steel-Dwass tests that correct for Type I error

253   inflation in multiple comparisons. We performed three linear mixed models to analyse sex-

254   specific and family-related effects of our feeding treatments on development and growth. We

255   tested effects of the variables 'Early treatment' (High or Low), 'Family lineage', and 'Sex' on

256   body mass after completion of the early experimental period with a model containing all three

257   variables and the interactions between Early Treatment and Family linage as well as between

258   Early treatment and Sex. Models on total developmental duration (beginning with the day on

259   which hatchlings were separated and allocated to individual treatments) and adult body size

260   were equally specified with 'Treatment' (early and late conditions), Family, and Sex as well as

261   the respective interaction terms. The variable 'Start date' (the day of allocation to experimental

262   treatments) was entered into the models as a random effect to account for a potential

263   influence of photoperiod on development (Start date had nine levels ranging from June 11 to

264   July 25, 2008). Body mass and developmental duration were log-transformed to improve the fit

265   of the models. We analysed variation in LTF with a standard least-square model containing the

266   interaction between Treatment and the number of clutches produced. All analyses in this study

267   were conducted in JMP Pro 13 (SAS Institute Inc., Carey, NC, USA). Effect tests for individual

268   variables in JMP are based on ANOVA-model comparisons between the full model and a

269   reduced model lacking the respective variable. Additional statistical tests are denoted in the

270   results section. Sample sizes within experiments may differ due to missing data.

271

272   **Results**

273

274   IMPLICATIONS OF EARLY EXPERIMENTAL CONDITIONS

275

276   Mortality rates during the first four weeks of the experiment did not differ significantly

277   between early treatments; 59 of 626 spiders died under high feeding conditions (9.4 %) and 74

278   of 630 spiders died under low feeding conditions (11.8 %) (G-test: χ^2 = 1.79, P = 0.18; N = 1256).

279   (Sex-determination is impossible in small juvenile spiders; hence mortality rates were analysed

280   independent of sex.)

281   In both sexes, body mass after the first four weeks differed considerably between early low

282   and high feeding conditions. Males weighed 2.6±0.11 mg at the end of the early low food

283   period (median = 2.35 mg, IQR = 1.65); significantly less than those reared under early high

284   feeding conditions, weighing 9.56±0.43 mg (median = 8.26 mg, IQR = 6.46) (Wilcoxon test: Z =

285   13.96, P < 0.0001; N = 363). In females, early low feeding conditions resulted in a body mass of

286   4.08±0.12 mg (median = 3.84 mg, IQR = 2.15), whereas early high-feeding females weighed

287   23.95±0.68 mg (median = 22.25 mg, IQR = 17) (Wilcoxon test: Z = 21.26, *P* < 0.0001; *N* = 665).

288   We conducted a linear mixed model to test for sex-specificity of juvenile growth as well as a

289   potential family-relatedness of growth responses. The model revealed highly significant effects

290   of the interactions between Early feeding treatment and Family lineage as well as between

291   Early treatment and Sex on the spiders´ body mass at completion of the early experiment

292   (Table 1).

293

294   IMPLICATIONS OF FULL EXPERIMENTAL CONDITIONS

295

296   *Pre-maturation mortality*

297

298   We analysed pre-maturation mortality in spiders that survived to experience both early and late

299   experimental conditions and found distinctly different mortality rates (G-test: χ^2 = 29.1, *P* <

300   0.0001; *N* = 1114; Table 2).

301   As mortality rates during the first four weeks did not differ between early high and low

302   feeding conditions (see above), mortality differences concerning full experimental conditions

303   may have solely been caused by late conditions. Pairwise between-treatment comparisons

304   corroborated this assumption; irrespective of early feeding conditions, pre-maturation

305   mortality rates differed significantly in treatment pairs exhibiting different late feeding

306   conditions, but not in treatment pairs in which late feeding conditions were identical (Table 2).

307

308   *Adaptive catch-up growth*

309

310   In accordance with our predictions, late developmental durations in Low-High females

311   significantly exceeded those of females in the High-High treatment (Late female developmental

312   duration L-H: mean = 57.39±1.04 days, median = 54 days, IQR = 8); H-H: mean = 46.72±0.59

313   days, median = 46 days, IQR = 8.75; Wilcoxon test: Z = 9.81, *P* < 0.0001; *N* = 292). This delay of

314   development resulted in full compensation of adverse early feeding conditions (Fig. 1). Females

315   matured at similar size and weight in both treatments (Female adult size L-H: mean =

316   12.24±0.13 mm, median = 12.22 mm, IQR = 1.9; H-H: mean = 12.45±0.59 mm, median = 12.32

317   mm, IQR = 1.39; Wilcoxon test: Z = 0.81, *P* = 0.416; *N* = 283; Female adult weight L-H: mean =

318   433.84±14.07 mg, median = 416.7 mg, IQR = 174.73; H-H: mean = 441.7±12.6 mg, median =

319   410.83 mg, IQR = 159.67; Wilcoxon test: Z = 0.22, *P* = 0.826; *N* = 282).

320   Males in the Low-High treatment also delayed development compared to High-High males

321   (Late male developmental duration L-H: mean = 45.46±1.16 days, median = 45 days, IQR = 15;

322   H-H: mean = 33.11±1.05 days, median = 31 days, IQR = 11; Wilcoxon test: Z = 7.56, *P* < 0.0001;

323   *N* = 190). In contrast to females, however, prolonged development did not fully compensate

324   differences in male adult size and body mass (Male adult size L-H: mean = 4.95±0.11 mm; H-H:

325   mean = 5.62±0.09 mm; t-test: *t* = 4.86, *P* < 0.0001; *N* = 184; Male adult weight L-H: mean =

326   26.59±1.09 mg, median = 25.25 mg, IQR = 13.81; H-H: mean = 34.23±1.03 mg, median = 32.57

327   mg, IQR = 14.05; Wilcoxon test: Z = 5.06, *P* < 0.0001; *N* = 191) (Fig. 1).

328

329   *Developmental durations and adult size in the remaining treatments*

330

331   Complementary post-hoc analyses of the remaining treatment-pairs confirmed the overall

332   limiting effects of low experimental nutrition on development and growth (Table 3). Females in

333   the Low-Low and High-Low treatments took much longer to mature and were still very much

334   smaller than females in the two other treatments (Fig. 2, Table 3).

335   Males responded differently from females, as they took longer to reach adulthood and

336   matured at smaller size in the Low-Low treatment compared to High-Low males (Fig. 2, Table

337   3). Further different from females, males showed intermediate developmental durations and

338   adult size in the High-Low and Low-High treatments relative to Low-Low and High-High males

339   (Fig. 2), indicating less adverse effects of late low feeding conditions in males. In both sexes,

340   High-High conditions resulted in shortest developmental durations as well as largest adult size

341   (Fig. 2).

342

343   *Effects of Treatment, Sex, and Family lineage on developmental duration and adult size*

344

345 We used linear mixed models to test whether phenotypic variation regarding developmental

346 duration and adult body size can be attributed, in part, to family-specific plastic responses and

347 to ascertain overall sex differences with respect to development and growth. The models were

348 specified with Treatment, Sex, and Family lineage as well as the Treatment-by-Sex and

349 Treatment-by-Family lineage interactions as explanatory variables ('Start date' was included as

350 a random effect to account for slight photoperiod changes; see methods). Highly significant

351 effects of both interactions confirmed sex-specific development and family-specific plasticity

352 (Table 4).

353

354 POST-MATURATION IMPLICATIONS

355

356 *Life-time fecundity and hatching success*

357

358 Females originating from the Low-High treatment delayed maturation, but achieved similar

359 adult body size and weight as High-High females through catch-up growth (see above). We

360 predicted equivalent fecundity in Low-High females compared to High-High females and tested

361 differences between feeding treatments High-High, Low-High, and Low-Low (we did not include

362 High-Low females; High-Low and Low-Low females did not differ significantly in developmental

363 duration and size; see Table 2). Fecundity was measured as the total number of eggs

364 (comprising hatched and undeveloped eggs) produced by each female during her entire

365 reproductive lifespan (Life-time fecundity, LTF). The mean number of clutches was 2.82±0.25

366 (range 1-6) and did not differ significantly between treatments (pairwise Tukey-Kramer HSD

367 tests: $P > 0.1$; $N = 28$). Females originating from the Low-High treatment achieved the highest

368 LTF of all treatments (LTF L-H = 2832.8±448.02; $N = 10$), producing more eggs than the High-

369 High females (LTF H-H = 2071.64.±320.12, $N = 11$) and about twice as many as females

370 originating from the Low-Low treatment (LTF L-L = 1343.86±262.65; $N = 7$). A linear model

371 showed that the interaction between treatment and the number of clutches explained a large

372 proportion of variation in LTF ($F = 4.154$, $P = 0.03$, adjusted $R^2 = 0.83$). The model suggested that

373 LTF increased over a series of clutches similarly in Low-High and High-High females, whereas

374   Low-Low females were unable to achieve an equivalent increase of fecundity (Fig. 3). A Tukey-

375   Kramer HSD test performed on model least square means showed significant differences in LTF

376   between the Low-Low treatment and both other treatments (pairwise comparisons: L-H − H-H:

377   P = 0.264, N = 21; L-H − L-L: P = 0.0002, N = 17; H-H − L-L: P = 0.005, N = 18).

378   Treatment effects on LTF did not correspond to absolute hatching success in our study.

379   Although the total number of hatchlings produced differed considerably between treatments,

380   variation was high and the differences were not significant (Number of hatchlings H-H: mean =

381   962.45±290.47, median = 701, IQR = 2287; L-L: mean = 421.57±133.05, median = 528, IQR =

382   738; L-H: mean = 1726.2±364.68, median = 2138, IQR = 2070.75; Kruskal-Wallis test: χ^2 = 4.95, P

383   = 0.084; N = 28). We also asked if feeding regimes affected relative hatching success (i.e. the

384   proportions of normally developed hatchlings and undeveloped eggs), but again there were no

385   significant differences between treatments (Proportions hatched H-H: mean = 46.9±9.86,

386   median = 57.58, IQR = 71.81; L-L: mean = 38.01±12.76, median = 35.31, IQR = 53.1; L-H: mean =

387   55.41±10.41, median = 56.56, IQR = 49.19; Kruskal-Wallis test: χ^2 = 1.5, P = 0.47; N = 28).

388   A post-hoc test revealed a positive correlation between copulation duration and the total

389   number of hatchlings (F = 18.97, P < 0.001, N = 28, R^2 = 0.42). In nature, female *N. senegalensis*

390   are polyandrous and females have been shown to mate repeatedly in other studies (Neumann

391   & Schneider 2015; Schneider & Michalik 2011). In this study, single copulations were probably

392   insufficient to fertilize all eggs produced by a female.

393

394   *Post-maturation longevity*

395

396   We tested whether a period of juvenile food restriction and subsequent catch-up growth

397   reduced the study animals´ post-maturation lifespan, but found no significant effects in both

398   sexes (Male adult lifespan H-H: mean = 148.08±7.85 days, median = 144 days, IQR = 46; L-L:

399   mean = 169.91±9.98 days, median = 178 days, IQR = 75; L-H: mean = 150.98±5.77 days, median

400   = 147 days, IQR = 34; H-L: mean = 147.31±8.53 days, median = 150.5 days, IQR = 38; Kruskal-

401   Wallis test: χ^2 = 4.83, P = 0.185; N = 137; Female adult lifespan H-H: mean = 61.55±4.09 days,

402   median = 60 days, IQR = 55; L-L: mean = 72.1±4.61 days, median = 69.5 days, IQR = 40; L-H:

403   mean = 57.75±3.9 days, median = 54 days, IQR = 34.5; H-L: mean = 63.08±5.46 days, median =

404   61 days, IQR = 38; Kruskal-Wallis test: χ^2 = 4.67, *P* = 0.198; *N* = 251).

405

406   **Discussion**

407

408   Female *Nephila senegalensis* reared under food restriction in early development (Low-High

409   females) used catch-up growth to counteract the restriction period and attain an adult body

410   size and mass similar to those reared under constant food abundance (High-High females). As

411   expected, Low-High females delayed maturation to fully compensate previous growth deficits.

412   Size compensation had to be charged against an average developmental delay of 9-12 days;

413   extending development by approximately 23 % compared to High-High females. This additional

414   investment in time and growth enabled Low-High females to achieve a life-time fecundity (LTF)

415   equivalent to High-High females; substantially exceeding LTF in constantly food-restricted

416   females (Low-Low females). These findings further corroborate strong fecundity selection on

417   large female size in *Nephila*. Consistent with our predictions, males did not implement catch-up

418   growth as efficiently, showing incomplete compensation of body size. Although Low-High males

419   delayed their development by 10-14 days, extending development by approximately 37 %

420   compared to High-High males, they matured significantly smaller than the latter. The

421   divergence between the sexes likely reflects generally weaker selection on large male size and

422   hence compensatory ability, but may also indicate a stronger trade-off between timely

423   maturation and growth in males. Juvenile food restriction and compensatory development did

424   not affect the post-maturation lifespan in either sex.

425   The benefits of catch-up growth have to be offset against costs of a delayed development,

426   which certainly affect fitness under natural conditions. Environmental parameters, such as

427   temperature, food abundance and weather conditions, may generally fall off in quality with the

428   season approaching its end (Hut et al. 2013). This constitutes an 'end-of-season penalty' for late

429   maturing individuals in semelparous species (De Block et al. 2008; Higgins 2000). Determinate

430   growth and annual life cycles eliminate the opportunity to optimize body size after sexual

431   maturation and to increase fitness in future reproduction, forcing animals into a narrow time
432   frame in which to grow and to reproduce.

433   In *N. senegalensis*, females produce long-lasting egg sacs which overwinter and hatch in the
434   following spring. The spiders generally mature in late summer and early autumn to experience
435   a relatively short reproductive period that declines with increasingly adverse weather
436   conditions in late autumn (Neumann & Schneider, pers. observations). Such strong seasonality
437   generates several trade-offs to cope with. For instance, a prolonged pre-maturation
438   development entails a higher predation-risk (Blanckenhorn 2000), but at the same time, large
439   *Nephila* females outgrow the risk of being preyed upon by various invertebrate predators and
440   parasitoids (Chase 1999; Higgins 2002). However, they may become more attractive to larger
441   vertebrate predators. To make use of large body size in terms of fecundity also requires an
442   increased amount of food and more time to produce the large numbers of eggs that can
443   potentially be laid in multiple clutches (Higgins 2000; Neumann & Schneider 2015). Therefore,
444   the adaptive significance of catch-up growth may vary between environments, for example,
445   depending on predation pressure and the level of physical disturbance caused by extreme
446   weather events (Higgins 2000). Females are hence expected to integrate environmentally-cued
447   information into implementing catch-up growth.

448   The prospects of fitness optimization through catch-up growth seem to be more limited in
449   males, which showed less growth compensation despite a significant developmental delay.   In
450   *Nephila*, body size has often been shown to play a role in male-male competition (Kuntner &
451   Elgar 2014), but the relationship between physical dominance and increased reproductive
452   success has been oversimplified in the past. Indeed, large males may successfully execute their
453   physical strength in specific competitive settings, e.g. in mating contests involving multiple
454   males (Rittschof 2010). On the other hand, there is evidence from both experimental work
455   (Neumann & Schneider 2015; Schneider & Elgar 2005) and theoretical modelling (Rittschof et
456   al. 2012) that small and medium-sized males adopt alternative mating strategies that balance
457   overall paternity in competition with large rivals. Furthermore, the modelling approach
458   suggested a decrease of average male reproductive success over the course of the season
459   (Rittschof et al. 2012). This might be due to the fact that unmated females become increasingly

460   rare and mated males may guard their females against successive competitors (Cohn et al.

461   1988; Schneider et al. 2008). In addition, late maturing females are generally smaller and hence

462   less fecund than early females (Higgins 2000; Miyashita 1986). These factors may favour

463   protandry and amplify the trade-off between developmental time and adult size in males. The

464   importance of a timely maturation was further supported in an experimental study, showing

465   that male *N. senegalensis* are able to adjust the duration of their subadult instar (i.e. the last

466   developmental stage preceding maturity) to the presence of receptive females by shifting

467   maturation in the order of several days (Neumann & Schneider 2016). Immature males use

468   female silk (or probably silk-borne pheromones) as a cue to perceive females. Such plastic fine-

469   tuning of life-history may increase males´ chances to locate receptive females in time and avoid

470   male-male competition, thus further relaxing selection on large male size. However, since males

471   at least showed incomplete catch-up growth, such compensation to the minor extant should

472   nevertheless be adaptive. Males may use moderate catch-up growth to disperse unavoidable

473   fitness costs between both traits affected by early food restriction (the duration of

474   development and adult body size), rather than to mend only one of them.

475   Sex-specific differences with respect to adaptive developmental modifications addressed in

476   this study probably result from an evolutionary history of divergent size selection, giving way to

477   sexual size dimorphism (SSD). Extreme reversed SSD in *Nephila* is likely facilitated by the genetic

478   uncoupling of body size between the sexes (Kuntner & Elgar 2014). The task of explaining the

479   evolution and maintenance of extreme SSD requires identification of sex-related selection

480   pressures. In our experiment, individuals of both sexes developed more slowly and matured

481   smaller in the Low-Low treatment than those in the High-High treatment, but apart from that,

482   we observed considerable differences between the sexes. Males in the High-Low treatment

483   showed similar life-history responses as Low-High males; both treatments resulting in

484   intermediate average developmental duration and adult size relative to High-High and Low-Low

485   males.

486   In females, however, the respective treatments had markedly different effects. In High-Low

487   females, the late decrease of food supply resulted in severe limitations, as these females

488   neither matured significantly faster nor achieved a larger size than Low-Low females. Thus, in

489   contrast to males, females in the High-Low treatment significantly fell behind Low-High females

490   in terms of developmental compensation, probably bearing high fitness costs. The fact that

491   development and adult size did not differ between High-Low and Low-High males indicates less

492   adverse effects of late-development food stress in males. A previous study addressing sex

493   differences in *Nephila* with respect to food quantity showed that females demand an increased

494   food supply and especially require more food than males to reach sexual maturation (Higgins &

495   Goodnight 2010). The reduction of energetic requirements associated with small male size may

496   therefore help to avoid fitness costs under food stress (Blanckenhorn et al. 1995); potentially

497   representing an important evolutionary driver to promote the uncoupling of body size between

498   the sexes in spiders.

499   Although females in the Low-Low and High-Low treatments faced significant limitations

500   regarding pace of development and adult body size, it is important to note that a large

501   proportion of those females were still able to reach sexual maturity. Moreover, Low-Low

502   females included in our mating trials and analyses of fecundity proved to be able to reproduce;

503   albeit at a lowered level. Such small females that are also observed in natural populations may

504   be able to escape reproductive failure by making "the best of a bad job" (Higgins et al. 2011).

505   These findings indicate that the general trade-off between the time invested in growth and the

506   resulting adult size can be enforced substantially by periods of food limitation. Favourable

507   conditions, on the other hand, may alleviate this trade-off, as males and females in the High-

508   High treatment took the shortest average developmental duration to reach the largest average

509   body size.

510   Irrespective of sex and treatment, variation of developmental duration and adult size was

511   high. Our analyses revealed that these life-history traits were modulated by an interaction

512   between experimental treatments (i.e. the spiders´ environment) and family lineage,

513   representing inherited genetic variation and/or maternal effects. Hence, part of the variation in

514   these traits was caused by family-specific responses to feeding conditions, which has also been

515   observed in other web-building spiders (e.g. Kleinteich & Schneider 2010).

516   The ability to survive under different feeding conditions is a basic requirement to implement

517   adaptive developmental plasticity against impending costs of food restriction. Our results

518 suggest that juvenile *N. senegalensis* are well able to survive a period of poor feeding

519 conditions in early developmental stages. Although early high- or low-food conditions

520 significantly influenced the study animals´ growth, these differences did not affect the chance

521 of survival. Very low metabolic rates in general enable spiders to subsist on low quantities of

522 food (Foelix 2011; Mayntz et al. 2003). It is possible that phenotypic plasticity is also used to

523 adjust metabolic rates to present conditions in order to survive food stress (Collatz &

524 Mommsen 1975). Larger juvenile stages, however, develop higher nutritional requirements to

525 maintain all vital physiological functions, making fluctuations in food supply more dangerous

526 (Higgins & Goodnight 2010). Accordingly, we recorded a significant increase of mortality rates

527 in spiders experiencing low-food conditions during late development.

528 Adaptive catch-up growth clearly bears costs of a delayed sexual maturity, but may also

529 involve intrinsic long-term costs arising from developmental compensation, e.g. through partial

530 elevated growth (Hector & Nakagawa 2012; Metcalfe & Monaghan 2001). Physiological stress

531 can even reduce an organism's longevity (English & Uller 2016; Hornick et al. 2000), but our

532 feeding treatments had no effect on the spiders´ adult lifespan. In contrast, permanent juvenile

533 food restriction reduced adult longevity in another araneid, the Bridge spider, *Larinioides*

534 *sclopetarius* (Kleinteich et al. 2015). As in *Nephila*, female Bridge spiders delayed development

535 and grew as large as control females; hence there was no apparent elevated growth and it

536 remains unclear whether adverse effects on longevity resulted from dietary restrictions or the

537 compensatory mechanism itself. Although female Bridge spiders reared under food restriction

538 fully compensated adult size, their fecundity lagged behind control females, because they

539 produced smaller clutches (Kleinteich et al. 2015). Such findings point to limitations of fitness

540 approximations based on size measurements. It is thus important that our study could not only

541 confirm the proposed size-increase through delayed maturation (Higgins 1992), but also

542 evaluated LTF as a direct consequence of experimentally induced developmental responses.

543 While our results are in accordance with our predictions, findings in other studies addressing

544 compensatory development in size-dimorphic species diverged from predictions in whole or in

545 part. For example, similar to our model system, fecundity-selected females in the mosquitofish,

546 *Gambusia holbrooki*, were expected to show pronounced catch-up growth after juvenile food

547 restriction, whereas minor catch-up growth was expected in the much smaller males whose

548 fitness was proposed to depend less on large size. Different from predictions, however, both

549 sexes delayed maturation and grew as large as control fish (Livingston et al. 2014). Male

550 mosquitofish exhibit large size variation in nature and the authors suggest that size-related

551 fitness consequences might depend on variable external conditions, including the social

552 environment. Male developmental strategies may thus be influenced by population density and

553 the intensity of male-male competition (or cues of such conditions) (Livingston et al. 2014). It is

554 important, in general, to note that other environmental variables may often interact with food

555 supply to induce specific responses, which is challenging to incorporate into experimental work

556 (Davidowitz et al. 2004; Stillwell & Davidowitz 2010).

557   In the pholcid spider *Pholcus phalangioides*, presenting a rare case of male-biased sexual size-

558 dimorphism in spiders (Uhl, 1994a), males benefit from both timely maturation and large body

559 size by avoiding male-male competition, or by succeeding in it (Schaefer & Uhl 2003). Food-

560 restricted males were predicted to use developmental plasticity to increase body size either by

561 delaying development or through accelerated growth. However, although males took longer to

562 mature than control siblings, they could not catch up in terms of adult size (Uhl et al. 2004).

563 Males were apparently unable to resolve the trade-off between the benefits of protandry and

564 advantages of large size under dietary restrictions (Uhl et al. 2004). Similarly to our findings, the

565 observed developmental response may reflect a way of dispersing disadvantages with respect

566 to developmental duration and adult size across both traits. It would be worthwhile, in general,

567 to evaluate whether this kind of 'bet-hedging' through intermediate life-history traits in

568 moderate catch-up growth is truly adaptive and how external conditions may influence

569 developmental responses. Future studies addressing these aspects should integrate field-based

570 knowledge regarding existing phenotypes, the social environment, and time regime, and

571 preferably include potential interactions between multiple environmental factors that might be

572 involved in the expression of plastic traits.

573

574 **Conclusions**

575

576 Male and female *Nephila senegalensis* performed significantly different with respect to catch-

577 up growth. Our study indicates strong fecundity selection on females, resulting in efficient

578 growth compensation and hence prevention of fecundity-related fitness costs. Matching our

579 predictions, catch-up growth in males did not evolve to the same capacity as in females.

580 Relaxed selection on large male size and a stronger trade-off between costs of a delayed

581 maturation and size-related benefits were reflected in incomplete growth compensation.

582 Nonetheless, the moderate degree of catch-up growth in males is likely adaptive in dispersing

583 unavoidable costs of food restriction across affected traits. The adaptive value of moderate

584 compensatory development and the potential adjustment of such mechanisms to

585 environmentally or socially cued conditions should be addressed in future studies.

586

587 **Acknowledgements**

588

589 We are grateful to Tomma Dirks, Angelika Taebel-Hellwig, Stefanie Zimmer, Janine Helms, and

590 Jessica Suhr for invaluable help in the rearing of study animals and data recording, Claudia

591 Drees and Luca Neumann for graphing advice, and Matthias Foellmer and an anonymous

592 reviewer for valuable comments on the manuscript.

593

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Effects of interactions between the variables early treatment, family lineage, and sex on body mass at completion of the early experiment.

Results derive from a linear mixed model including the variable Start date (the time of allocating hatchlings to individual treatments) as a random effect to account for a potential influence of photoperiod on development. Body mass was log-transformed. Significant *P*-values are shown in bold.

1 Explanatory variable	Body mass at completion of the early experiment	
	F	P
Early treatment	1822.1	**<0.0001**
Family lineage	6.5	**<0.0001**
Sex	427.6	**<0.0001**
Early treatment * Family lineage	8.6	**<0.0001**
Early treatment * Sex	45.5	**<0.0001**

Pre-maturation mortality compared between feeding treatments.

Treatment pairs were compared using G-tests. Significant *P*-values are shown in bold.

Treatment pair (% mortality)	χ^2	P	N
High-Low (21 %) – Low-Low (24.7 %)	1.044	0.307	569
High-Low (21 %) – High-High (9.3 %)	15.393	**<0.0001**	564
High-High (9.3 %) – Low-High (13.9 %)	2.816	0.093	545
High-High (9.3 %) – Low-Low (24.7 %)	24.156	**<0.0001**	563
Low-High (13.9 %) – Low-Low (24.7 %)	10.264	**0.001**	550
High-Low (21 %) – Low-High (13.9 %)	4.886	**0.027**	551

Total developmental durations and adult size compared between feeding treatments.

Treatments were compared with Steel-Dwass pairwise tests (excluding treatment pair High-High - Low-High subject to predefined analysis of catch-up growth; see results). Significant *P*-values are shown in bold.

Treatment pair	Males				Females			
	Total duration of development		Adult body size		Total duration of development		Adult body size	
	Z	*P* (*N*)	Z	*P* (*N*)	χ²	*P* (*N*)	Z	*P* (*N*)
High-High – Low-Low	10.42	**<0.0001** (184)	9.06	**<0.0001** (181)	284.84	**<0.0001** (283)	13.55	**<0.0001** (275)
High-High – High-Low	7.17	**<0.0001** (182)	6.86	**<0.0001** (179)	226.58	**<0.0001** (296)	13.74	**<0.0001** (285)
Low-Low – High-Low	7.24	**<0.0001** (172)	5.32	**0.0008** (168)	4.67	0.2 (267)	2.11	0.151 (262)
Low-Low – Low-High	6.47	**<0.0001** (180)	4.92	**<0.0001** (173)	108.55	**<0.0001** (263)	12.26	**<0.0001** (260)
High-Low – Low-High	0.15	0.999 (178)	0.95	0.776 (171)	71.9	**<0.0001** (276)	12.14	**<0.0001** (270)

Effects of interactions between treatment, family lineage, and sex on total duration of development and adult size.

Results derive from linear mixed models including the variable Start date (the time of allocation of hatchlings to individual treatments) as a random effect to account for a potential influence of photoperiod on development. Developmental durations were log-transformed. Significant *P*-values are shown in bold.

Explanatory variable	Total duration of development		Adult body size	
	F	P	F	P
Treatment	339.96	**<0.0001**	343.43	**0.007**
Family lineage	10.3	**<0.0001**	2.31	**0.033**
Sex	821.48	**<0.0001**	7219.27	**<0.0001**
Treatment * Family lineage	3.14	**<0.0001**	1.94	**0.007**
Treatment * Sex	27.54	**<0.0001**	115.98	**<0.0001**

Figure 1

Adaptive catch-up growth in (A) male and (B) female *Nephila senegalensis*.

Symbols indicate median values for body mass at the beginning of the Late-experiment development and body mass at sexual maturation in treatments High-High (blue squares) and Low-High (red triangles). Late-experiment development in the High-High treatment followed four weeks of early high feeding conditions. Late-experiment development in the Low-High treatment followed four weeks of early low feeding conditions. Body mass is given as a proxy of body size (*, indicates significant differences).
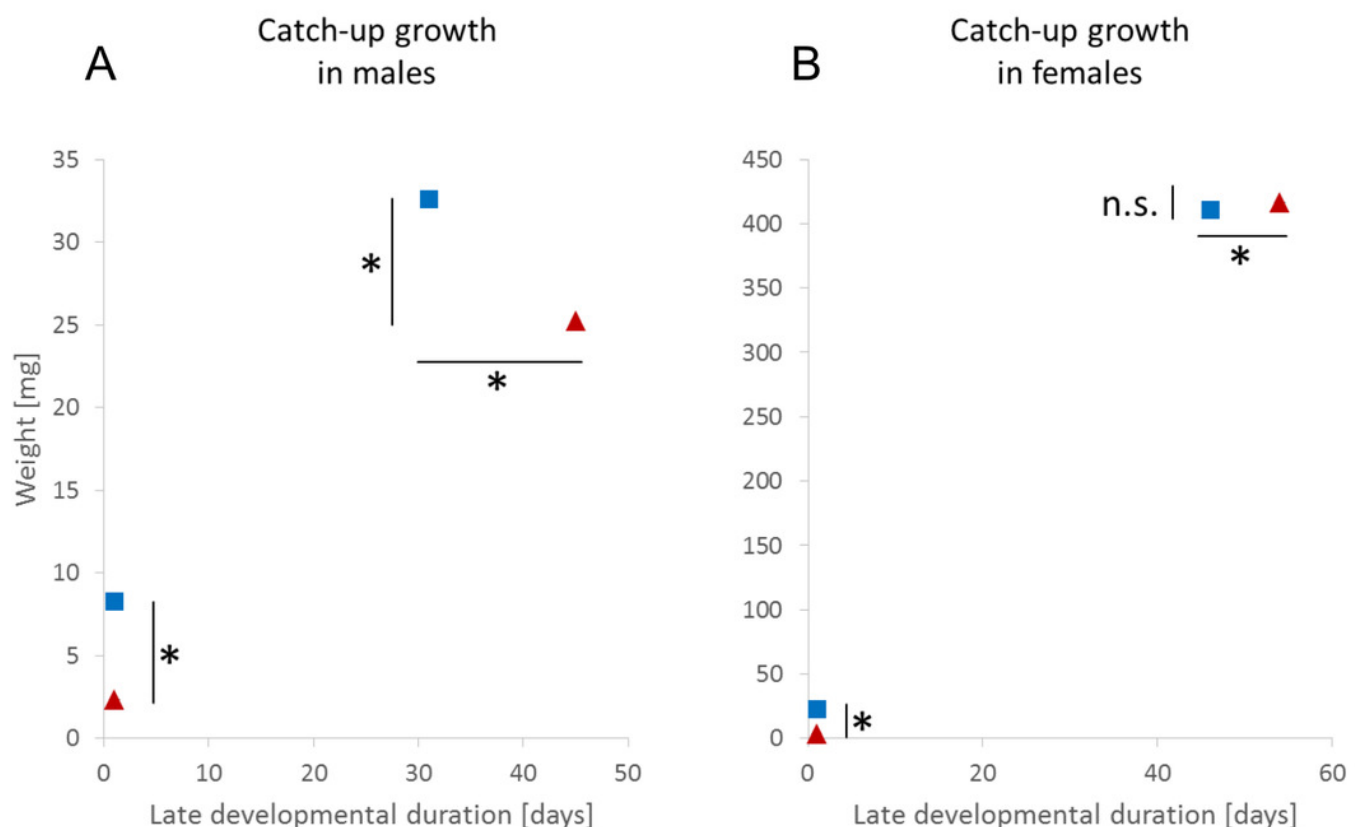
Figure 2

Effects of feeding treatments on the duration of development and adult size in *Nephila senegalensis*.

Top row (A, B): Males. Bottom row (C, D): Females. Treatments were High-High (H-H), Low-Low (L-L), High-Low (H-L), and Low-High (L-H).
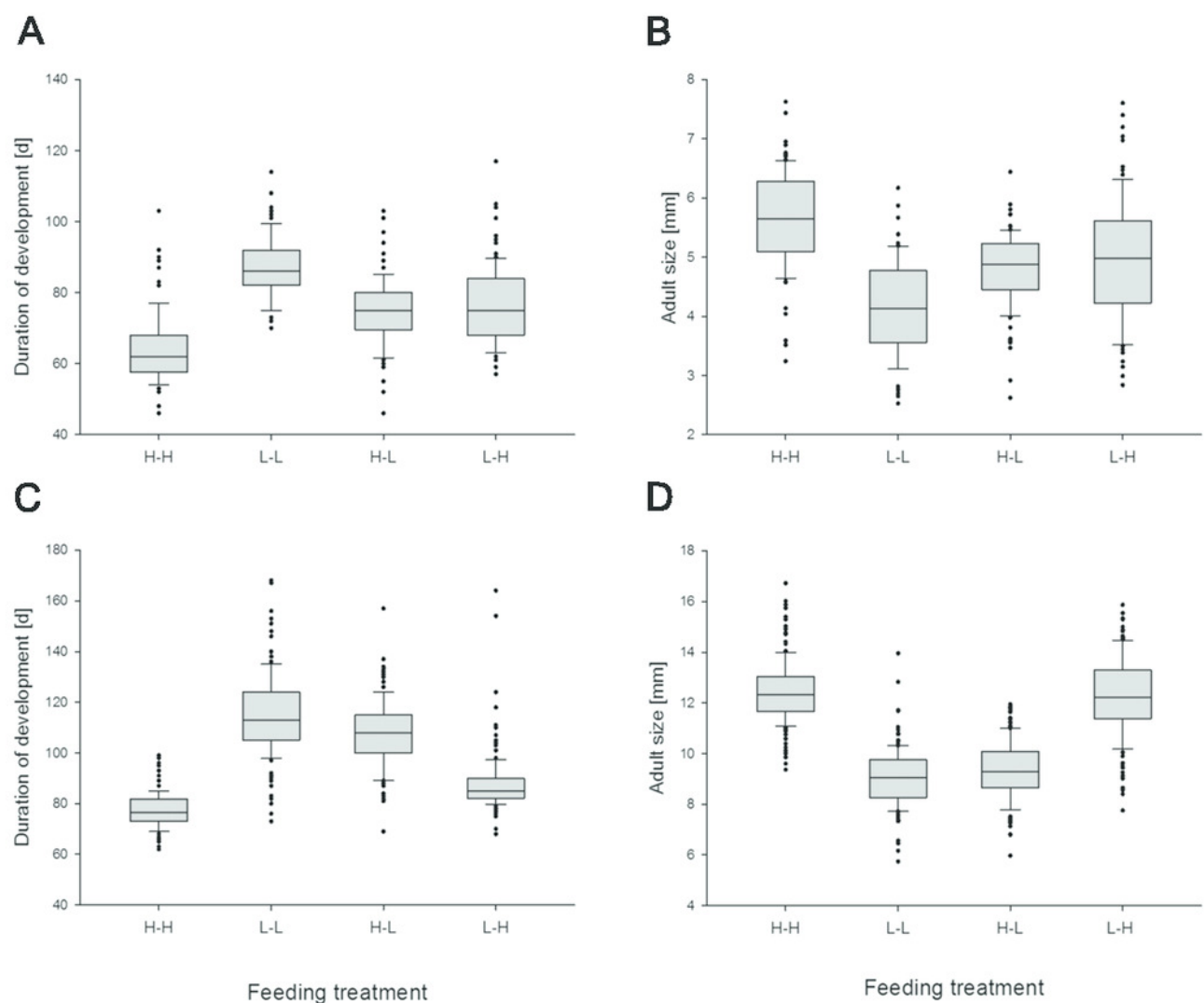
Figure 3

Effects of feeding treatments on life-time fecundity (LTF) in *Nephila senegalensis*.

The interaction between feeding treatment and the number of clutches produced explained life-time fecundity in a linear model (adjusted R^2 = 0.83). Treatments were High-High (blue), Low-High (red), and Low-Low (green). Shaded areas indicate 95 % confidence intervals.