Inter-class competition in stage-structured populations: Effects of adult density on life-history traits of adult and juvenile common lizards

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18 **Abstract**

19 Ecological and evolutionary processes in natural populations are largely influenced by the

20 population's stage-structure. Commonly, different classes have different competitive abilities, e.g.,

21 due to differences in body size, suggesting that inter-class competition may be important and

22 largely asymmetric. However, experimental evidence that inter-class competition is important is

23 rare and restricted to marine fish. Here, we manipulated the adult density in six semi-natural

24 populations of the European common lizard, *Zootoca vivipara*, while holding juvenile density

25 constant. Adult density affected juveniles, but not adults, in line with inter-class competition. High

26 adult density led to lower juvenile survival and growth before hibernation. In contrast, juvenile

27 survival after hibernation was higher in populations with high adult density, pointing to relaxed

28 inter-class competition. As a result, annual survival was not affected by adult density, showing that

29 differences in pre- and post-hibernation survival balanced each other out. The intensity of inter-

30 class competition affected reproduction, performance, and body size in juveniles. Path analyses

31 unravelled direct treatment effects on early growth (pre-hibernation) and no direct treatment effects

32 on the parameters measured after hibernation. This points to allometry of treatment-induced

33 differences in early growth, and it suggests that inter-class competition mainly affects the early

34 growth of the competitively inferior class and thereby their future performance and reproduction.

35 These results are in contrast with previous findings and, together with results in marine fish, suggest

36 that the strength and direction of density-dependence may depend on the degree of inter-class

37 competition, and thus on the availability of resources used by the competing classes.

38 **Keywords:** density-dependence, experimental populations, inter-class competition, intra-class

39 competition, population dynamics

Introduction

The structure of a population (*e.g.*, age or stage structure) is a major source of heterogeneity in natural populations (Miller and Rudolf 2011; Kendall et al. 2011; Rudolf and Rasmussen 2013). Individuals belonging to distinct age classes commonly differ in their morphology (Werner and Gilliam 1984), physiology (Stoinski et al. 2002), and behaviour (Werner 1992), and in some cases they can be as different as individuals from two different species (Polis 1981). Individuals belonging to different age or size classes are predicted to differ in their competitive ability, since competitive ability often scales with traits such as body size (Aljetlawi and Leonardsson 2002; de Roos and Persson 2003; van der Meer 2006). Consequently, the ecological and evolutionary consequences of intraspecific competition in age- (stage-) structured populations are expected to differ from unstructured populations, where intraspecific competition is less asymmetric (De Roos, Persson, & McCauley, 2003).

In age-structured populations, competition among age classes (hereafter referred to as inter-class competition) is suggested to induce plastic responses (Maret and Collins 1994; Blanckenhorn 1998), alter population dynamics (De Roos et al. 2003), and even promote evolutionary change (Werner and Gilliam 1984; Bolnick and Doebeli 2003). For instance, when adults limit the juveniles' access to food or space, juveniles may plastically reduce growth and delay maturation and thus the timing of first reproduction (Hill 1992). These effects are predicted to affect population dynamics given that impaired growth and delayed reproduction of juveniles extend the generation time (De Roos et al. 2003, although see: Pechenik and Cerulli 1991). Consequently, population density cycles can occur (Claessen *et al*. 2000). More specifically, reduced juvenile survival due to adults is predicted to lead to a lower future adult density, and thereby, to a decrease in future inter-class competition. Under lower inter-class competition, juveniles will show a higher survival

63 rate, more juveniles will become adults, and adult density will increase again. Fluctuations in the

64 magnitude of inter- and intra-class competition may thus translate into fluctuations in population

65 and class density (Claessen et al. 2000; De Roos et al. 2003). Inter-class competition can also

66 induce selection on the phenotype and trigger the evolution of different life-history strategies and

67 physiological adaptations that may lead to niche divergence between stages and to relaxation of

68 inter-class competition (Werner and Gilliam 1984). Recent theoretical and empirical studies further

69 suggest that the success of r- and K- life-history strategies may depend on population density and

70 their success may determine the levels of inter-class competition (Lande et al. 2009; Sæther et al.

71 2016). Theoretical models also suggest that inter-class competition may be essential to understand

72 density- and frequency-dependent mechanisms of selection, maintenance of genetic diversity

73 (Asmussen 1983), the evolution of context-dependent mate choice (Sinervo et al. 2007), assortative

74 mating, and sympatric speciation (Bürger et al. 2006; Pennings et al. 2008).

75   Despite the implications of inter-class competition for key ecological and evolutionary

76 processes, its importance has been mainly studied using theoretical approaches, and empirical tests

77 only stem mainly from marine fish species (Jones 1987; Forrester 1990; Post et al. 1999; Szabo

78 2002; Webster 2004; Samhouri et al. 2009; Ayllón et al. 2013). In terrestrial organisms, research

79 has focused on interactions among age-classes during parental care (Ekman and Griesser 2002;

80 Buchan et al. 2003), during antagonistic behaviours like cannibalism (Jenssen et al. 1989), and on

81 the differences among age-classes in their ecological niches (Marchetti and Price 1989;

82 Magnussoni et al. 2001; Natusch and Lyons 2012). However, its importance for population

83 dynamics and life-history strategies is poorly understood. Studies manipulating population density

84 of age/size-structured terrestrial vertebrate populations showed that age classes asymmetrically

85 respond to population density. Smaller and younger, but not necessarily larger and older

86   individuals, exhibit density-dependent growth and survival (Gaillard *et al*. 1998; Mugabo *et al*.

87   2013). However, these studies do not allow disentangling whether inter-class competition between

88   adults and juveniles or intra-class competition among juveniles, account for the observed negative

89   effects on the juvenile cohort. Only density manipulations of adults, but not of juveniles, allow

90   testing for the effect of inter-class competition. Manipulation of the adult density leads to

91   differences in the overall population density and, if present, pure density-dependent effects would

92   predict treatment effects on both, adults and juveniles. If intra-class competition is important,

93   adults, but not juveniles, are predicted to be affected by adult density, given the equal density of

94   juveniles. In contrast, under inter-class competition , the competitively superior adults are predicted

95   to be less or not affected by the adult-density treatment, while negative effects on the competitively

96   inferior juveniles may exist. For instance, if adults outcompete juveniles for resources, higher adult

97   density will lead to fewer resources for juveniles and thus to negative effects on juvenile growth

98   and survival. Manipulation of adult, but not of juvenile density has been conducted in reef fishes

99   (e.g., Webster 2004), but, to the best of our knowledge, never in a terrestrial vertebrate species.

100 The dynamics of terrestrial populations are predicted to be mostly influenced by local demographic

101 processes, like competition or predation, while the population dynamics of marine species are more

102 strongly influenced by dispersal (Kinlan and Gaines 2003). Consequently, case studies on the

103 importance of inter-class competition outside of marine systems are needed in order to understand

104 the generality of the studies conducted on these systems.

105   Here, we experimentally test the importance of inter-class competition in stage-structured

106 populations of a terrestrial species. We manipulated the density of adults, but not of juveniles, and

107 tested for its effect on life-history traits of adults and juveniles, including growth, performance,

108 survival and reproduction. The common lizard, *Zootoca vivipara* (Lichtenstein, 1823) was used as

109   a model species. Juvenile *Z. vivipara* are on average 2.42 times smaller [snout-to-vent length, SVL]

110   and 15.80 times lighter than adults (L.M. San-Jose, *unpublished data*, see also Pilorge 1987).

111   Individuals do not defend territories. Home ranges, prey size, and prey type of adults and juveniles

112   overlap to a large degree (Le Galliard *et al*. 2003; prey size: Pianka's index = 0.62 to 0. 74, a full

113   overlap corresponds to 1; prey type: 0.88-0.89; Heulin 1986), and in our semi-natural populations

114   adults and juveniles can feed on the same small prey (e.g., Collembola, LMSJ *personal*

115   *observation*). Juveniles are completely independent after hatching (i.e., no parental care exists) and

116   they may be exposed to competition with older cohorts immediately after birth. Important life-

117   history traits (snout-to-vent length [SVL], growth rate, and reproductive success) show negative

118   density dependence in juveniles and adults, and density-dependent effects are more pronounced in

119   juveniles (Massot et al. 1992; Mugabo et al. 2013). The adult and juvenile densities vary between

120   populations and years (ratio of adults = 0.48 ± 0.13 SD, range: 0.26 - 0.68; Khodadoost *et al*. 1987;

121   Pilorge 1987; Cavin 1993; Heulin *et al*. 1997), suggesting that the intensity of inter-class

122   competition might vary over time and space. Moreover, juvenile survival depends on population

123   density and on the frequency of adult male colour morphs (Sinervo et al. 2007; San-Jose et al.

124   2014). These findings point to the existence of inter-class competition, but no robust experimental

125   evidence exists in *Z. vivipara* for adult density-dependent effects on life-history traits of juveniles.

126   By manipulating adult density, we predicted that, if inter-class competition is responsible

127   for the observed effects, juvenile, but not (or to a lower extent) adult life-history traits (growth,

128   performance, survival and reproduction), will be negatively affected by increasing adult density,

129   given the competitive superiority of adults over juveniles. If intra-class competition is important,

130   we predicted that adult, but not juvenile life-history traits will be affected by density manipulations,

131   because juvenile density was equal in all populations. Alternatively, if class-independent density

132   dependence exists, we predicted that juvenile and adult life-history traits will be similarly affected,

133   i.e., competition will be symmetric between and within classes.

134   **Material and Methods**

135   **Species description**

136   Common lizard females generally produce one clutch per year and in exceptional years they

137   can produce up to three clutches (Horváthová et al. 2013). Juveniles hatch between mid-summer

138   and the beginning of autumn and can be distinguished from adults by their smaller body size and

139   black pigmentation. Under optimal conditions, juveniles can attain adult size and colour within one

140   year and they can no longer be distinguished from adults. Consequently, in populations exhibiting

141   optimal conditions, only adults and juveniles are found during late summer and autumn (Pilorge

142   1987). Under sub-optimal environmental conditions, especially at high altitudes, up to two

143   additional body size classes can be distinguished (yearlings and 2-yr-old lizards: Heulin et al. 1997,

144   Sinervo et al. 2007). Once survived the first year, average life-expectancy of males and females is

145   4-5 and 5-6 years, respectively, and most studies on Z. *vivipara*, summarize population structure

146   into 2 to 3 size-classes, namely, juveniles, adults, and yearlings.

147   **Experimental design**

148   In July 2009, 6 independent semi-natural common lizard populations were established at

149   the Research Station of 'El Boalar' (Instituto Pirenaico de Ecología, Jaca, Spain, 40º 33' N, 0º 37'

150   W, 700 m a.s.l.). Lizards were released in enclosures of 100 m^2 delimited by galvanized metal walls

151   and covered with a fine-meshed net, which prevented lizards from escaping and avoided predation.

152   Enclosures contained planted natural grassland and stone and log piles, providing lizards with

153   naturally occurring prey and hiding and basking sites.

154   In all the enclosures, an average of 10.7 ± 1.75 (± standard deviation) recently hatched

155   female and 15.2 ± 0.98 recently hatched male juveniles were released (juvenile density did not

156   differ among treatments; $\chi^2 = 1.3$, d.f. $= 2$, $P = 0.5$). In two enclosures, 12 adult females and 9 adult

157   males were released, corresponding to high adult density (HAD treatment) and, in two other

158   enclosures, 4 adult females and 3 adult males were released, corresponding to low adult density

159   (LAD treatment). In the remaining two enclosures, no adult individuals were released (NA

160   treatment), corresponding to habitat newly colonized by juveniles. Previous to release, SVL

161   (precision: 1 mm) and body mass (precision: 1 mg) were measured and lizards were marked by toe

162   clipping for individual recognition. Adult and juvenile lizards were randomly assigned to adult

163   density treatments and enclosures. No significant differences existed between treatment levels in

164   SVL, body mass, or body condition of adults and juveniles, or in the proportion of adult male colour

165   morphs (all $P \geq 0.2$). To avoid confusion, we refer to the juveniles released in 2009 as 'juveniles'

166   all throughout the manuscript even though some of the juveniles already reproduced in 2010.

167   **Life-history traits, performance, and spatial distribution**

168   In mid-September 2009 (before entering into hibernation) and at the beginning of May

169   2010, lizards were recaptured over a three-day period, which guaranteed that all surviving lizards

170   were caught (no uncaught lizards were captured in subsequent capture sessions). For each

171   individual, prehibernation survival (from release to September 2009), hibernation-to-spring

172   survival (from September to 2009 to May 2010), and annual survival (from release to May 2010)

173   was noted. Hibernation takes place between the end of November and the end of March and,

174   therefore, hibernation-to-spring survival does not only consider the time the lizards were

175   hibernating. At each recapture, the capture location within the enclosures was registered using an

176   8 x 8 grid to determine whether the spatial distribution of juveniles depends on the presence of

177 adult males and females. SVL and body mass of each individual were also measured and growth

178 rate calculated as SVL increment between captures divided by the number of days between

179 captures. To calculate spring growth rate, the days spent inactive were subtracted (*i.e.*, the

180 approximate days spent hibernating: between 1st of November and 1st of March).

181   In May, the reproductive status of juvenile and adult females, *i.e.*, whether females carried

182 eggs, was determined by carefully palpating their bellies. The number of scars on the entire body

183 of all individuals was counted. In females, scars result from mating interactions (males bite females

184 during copulation), and the number of scars is a good proxy of mating activity and the number of

185 copulations (Bauwens and Verheyen 1987; Fitze et al. 2005). In males, scars result from intra- and

186 inter-sex aggressive behaviour (females can bite males during copulation; Bauwens and Verheyen

187 1985; Fitze et al. 2005). Moreover, performance (bite force and sprint speed) was measured using

188 the protocol described in Huyghe *et al.* (2013). In brief, bite force was measured by making lizards

189 bite five times onto two metal plates (at a fixed distance) of a bite force transducer and sprint speed

190 was determined by chasing lizards three times down a 2-m long racetrack and simultaneous digital

191 video taping. The strongest bite and the fastest sprint measured over any 25-cm distance were used

192 for subsequent analyses.

193 **Statistics**

194   The statistical analyses were conducted in R 3.0.1 (R Core Team, 2015). For both adults

195 and juveniles, treatment effects on survival were analysed using generalized linear mixed models

196 with a binomial error distribution (*glmer* function in *lme4* package; Bates *et al*. 2015). These

197 analyses were conducted at the individual level (dead = 0; survivor = 1). Adult density treatment,

198 sex, and their interaction were included as fixed factors and enclosure as a random effect. Hatching

199 date (only for juveniles), body mass, and SVL were included as covariates. SVL and body mass

200   measured upon hatching or before hibernation were included in the analyses of prehibernation and

201   annual survival or hibernation-to-spring survival, respectively. Their interactions with treatment

202   and sex were included as well. Co-variables were not highly correlated (all $r < 0.27$).

203   For both adults and juveniles, treatment effects on SVL and growth rate were analysed using

204   linear mixed models (*lme* function of the package *nlme*: Pinheiro *et al*. 2016) including treatment,

205   sex, date of recapture, and their interactions as fixed factors, and enclosure and lizard identity

206   (nested within enclosure) as random effects. Treatment effects on the reproductive status of female

207   juveniles were analysed using generalized linear mixed models with a binomial error distribution

208   and enclosure as a random effect. As for survival, this analysis was conducted at the individual

209   level by denoting gravid and non-gravid females as zero and one, respectively. Effects on the

210   number of scars and performance traits were analysed using generalized linear models (Poisson

211   error distribution) and linear mixed models, respectively. These models included treatment, sex,

212   and their interaction as fixed factors, and enclosure as a random effect. To test if adult density

213   directly affected performance and reproductive traits of juveniles or if, contrarily, it indirectly

214   affected these traits, for example, by affecting early growth and subsequent scaling, path analyses

215   based on directional separation tests were conducted (Online Resource 1; Shipley 2000, 2009).

216   Spatial distribution of juveniles was analysed using generalized linear mixed models with

217   a Poisson error distribution. Juvenile abundance (number of juveniles captured in a given grid

218   square) was determined for each grid square of each population and it was modelled as a dependent

219   variable. Treatment, presence of adult males, presence of adult females, and their interactions were

220   modelled as fixed effects, and enclosure as random effect. All models were simplified using

221   backward elimination of non-significant terms and, in all cases, model assumptions were tested.

222   For linear models, the best within-group variance and correlation structure was selected using the

223 Akaike information criterion (Pinheiro and Bates 2000) and, in Poisson models, individual ID was

224 included as a random effect to account for overdispersion (Maindonald and Braun 2003). For all

225 tests, the significance level (α) was 0.05 (two-tailed). We used posterior contrasts to test for the

226 differences among treatment levels and adjusted the *P* values from the contrasts following the

227 procedure described by Benjamini and Hochbert (1995) to control for multiple testing.

228 **Results**

229 **Adult density effects on survival**

230 Adult density significantly affected prehibernation and hibernation-to-spring survival in

231 juveniles, whereas annual survival was not affected (Table 1). Post-hoc contrasts show that juvenile

232 survival before hibernation was significantly lower in HAD populations than in LAD and NA

233 populations, and significantly higher from hibernation to spring in HAD populations than in LAD

234 and NA populations (Fig. 1). LAD and NA populations did not statistically differ in survival during

235 any of the studied time periods (Fig. 1). Body condition and SVL were positively related with

236 juvenile survival from hibernation to spring (Table 1), indicating that larger juveniles and juveniles

237 in better body condition survived better, and there were no significant effects in the other time

238 periods nor in annual survival (Table 1). The later in the season juveniles hatched, the lower was

239 their prehibernation survival (negative effect of hatching date, Table 1). None of the interactions

240 was significant (Table 1; all $P \geq 0.1$).

241 There was no significant difference in adult survival among adult density treatments (2-

242 tailed Fisher exact test $P = 0.179$) and adult density was higher in HAD compared to LAD

243 populations throughout the entire experiment. The evolution of total and juvenile densities per

244 treatment is depicted in the figure 2a and 2b.

245

Adult density effects on SVL and growth

246

247 There was a significant interaction between adult density and time on juvenile SVL (Table

248 2; Fig. 3a). HAD juveniles were significantly smaller than NA juveniles before hibernation and in

249 spring (all $t_{200} > 3.15$, $P_{adj} < 0.003$). HAD juveniles were also smaller than LAD juveniles in spring

250 ($t_{200} = 2.18$, $P_{adj} = 0.046$), but not before hibernation ($t_{200} = 1.40$, $P_{adj} = 0.194$). No significant

251 differences existed in SVL between LAD and NA juveniles before hibernation or in spring (all t_{200}

252 < 1.85, $P_{adj} > 0.090$). Females were significantly larger than males (estimate $\pm$ SE: 11.07 mm $\pm$ 0.8)

253 and all other interactions were not significant (Table 2). There was a significant interaction between

254 treatment and time on juvenile growth (Table 2; Fig. 3b). Before hibernation, HAD and LAD

255 juveniles grew slower than NA juveniles (HAD vs NA: $t_{83} = 3.59$, $P_{adj} < 0.001$, LAD vs NA: $t_{83} =$

256 2.28, $P_{adj} = 0.045$, HAD vs LAD: $t_{83} = 1.56$, $P_{adj} = 0.156$), whereas in spring, no significant

257 differences existed in growth rate among treatments (all $t_{83} < 1.60$, $P_{adj} > 0.16$). Males grew

258 significantly faster than females (estimate $\pm$ SE: 0.017 mm day^{-1} $\pm$ 0.006) and no significant

259 interactions between sex and treatment, between sex and time, or between sex, treatment, and time

260 were found (Table 2).

261 Adult SVL was not significantly affected by adult density (adult density: $F_{1,2} = 0.76$, $P =$

262 0.475; adult density $\times$ time: $F_{2,93} = 0.63$, $P = 0.534$). There was a significant interaction between

263 time and sex on adult SVL (time: $F_{2,95} = 10.33$, $P < 0.001$, sex: $F_{1,53} = 72.65$, $P < 0.001$; time $\times$ sex:

264 $F_{2,95} = 3.78$, $P = 0.026$). In males, SVL was significantly bigger before hibernation and in spring

265 (all $t_{95} > 2.51$, $P_{adj} < 0.016$) than at release, whereas in females, SVL in spring ($t_{95} = 3.89$, $P < 0.001$)

266 but not before hibernation ($t_{95} = 0.99$, $P = 0.322$) was significantly bigger than at release. Adult

267 growth rate was affected by a significant interaction between sex and initial SVL, but not by adult

268 density ($F_{1,2} = 4.39$, $P = 0.17$), time ($F_{1,42} = 1.38$, $P = 0.25$), or their interaction ($F_{1,40} = 0.46$, $P =$

269   0.50). Male growth rate decreased faster with increasing SVL compared to female growth rate (sex

270   [males]: ß = 0.39 mm day^{-1} ± 0.09, $F_{1,45}$ = 19.42, P < 0.001, SVL: ß = – 0.003 mm day^{-1} ± 0.001,

271     $F_{1,42}$ = 13.31, P < 0.001, sex × SVL [males]: ß = – 0.008 mm day^{-1} ± 0.002, $F_{1,42}$ = 22.84, P < 0.001).

272   **Adult Density Effects on Performance, Space use, and Reproductive Status**

273   Adult density significantly affected bite force in juveniles ($F_{2,3}$ = 11.09, P = 0.041).

274   Juveniles in HAD populations tended to have a lower bite force than juveniles in NA populations

275   (estimate ± SE: – 0.72 N ± 0.16, t_3 = 4.70, P_{adj} = 0.055, respectively). There were no significant

276   differences between juveniles from LAD populations and juveniles from the other populations (all

277   t_3 < 2.63, P_{adj} > 0.12). Male juveniles had a significantly higher bite force than females (estimate ±

278   SE: 1.38 ± 0.24 N; $F_{1,62}$ = 19.81, P < 0.0001) and no significant interaction between treatment and

279   sex existed ($F_{2,60}$ = 1.67, P = 0.20). Adult density did not significantly affect juvenile sprint speed

280   ($F_{2,3}$ = 3.27, P = 0.18), which tended to be higher in male juveniles (estimate ± SE: 12.58 ± 4.26

281   cm s^{-1}; $F_{1,62}$ = 3.49, P = 0.06). No significant sex per treatment interaction existed for juvenile sprint

282   speed ($F_{2,60}$ = 1.45, P = 0.24).

283   Juvenile abundance was significantly higher in grid squares where adult males were present

284   (before hibernation: estimate ± SE [adult male present]: 0.39 juveniles ± 0.14; χ^2 = 6.11, d.f. = 1,

285   P = 0.013; spring: estimate ± SE [adult male present]: 0.32 juveniles ± 0.13; χ^2 = 5.20, d.f. = 1, P =

286   0.022) and it was not significantly related to the presence of adult females (before hibernation: χ^2 =

287   0.32, d.f. = 1, P = 0.57; spring: χ^2 = 0.97, d.f. = 1, P = 0.32). No significant interactions existed

288   between treatment and the presence of adult males or adult females (all χ^2 < 2.18, P > 0.14),

289   indicating that the positive association between juveniles and adult males and the absence of a

290   significant association with adult females existed in all treatment groups.

291   In spring, the number of scars exhibited by juveniles significantly differed among treatment

292   levels (χ^2 = 10.70, d.f. = 2, = 0.005) and sexes (female estimate ± SE = 8.33 scars ± 1.42, χ^2 =

293   32.16, d.f. = 1, P < 0.0001), and the interaction between treatment and sex was not significant (χ^2

294   = 1.07, d.f. = 2, P = 0.58). HAD juveniles had significantly less scars than juveniles from NA and

295   LAD populations, which exhibited no significant differences (Fig. 4a). The probability of female

296   juveniles being gravid was significantly affected by adult density (χ^2 = 8.41, d.f. = 2, P = 0.015).

297   The proportion of gravid juvenile females was higher in NA than in HAD populations (χ^2 = 5.97,

298   P = 0.014) and it tended to be higher in NA compared to LAD populations (χ^2 = 3.74, d.f. = 1, P

299   = 0.053; Fig. 4b).

300   In adults, adult density did not affect bite force ($F_{1,2}$ = 1.84, P = 0.31) or sprint speed ($F_{1,2}$

301   = 0.42, P = 0.58), and both were higher in males than in females (all $F_{1,43}$ > 8.17, P < 0.006). All

302   adults females were gravid and adults had significantly more scars in HAD than in LAD

303   populations (estimate ± SD: 0.35 ± 0.16, χ^2 = 5.01, d.f. = 1, P = 0.025).

304

305   **Path Analyses**

306   The path analyses show that treatment had a direct effect on juvenile SVL before

307   hibernation, but not on any of the measures taken in spring. This indicates that the above reported

308   effects of adult density on juvenile performance traits, scars, and reproductive status were more

309   likely mediated by the indirect effect of adult density on body size before hibernation (Fig. 5,

310   Online Resource 1) and thus on pre-hibernation growth. The final model (Fig. 5) fitted the data

311   better than models including direct effects of adult density on performance traits and number of

312   scars (ΔAIC = 3.56, evidence ratio = 5.94; Table A1) or reproduction (direct effects on the

313   probability of being gravid: ΔAIC = 3.28, evidence ratio = 5.16; Table A2).

314

Discussion

Many studies demonstrated important effects of population density on population stability and life-history strategies (e.g., Olafsson 1986; Both 1998; Gaillard et al. 1998; Mugabo et al. 2013) and, in stage-structured populations, inter-stage competition may importantly contribute to density dependence (Blanckenhorn 1998; Gaillard et al. 1998; Mugabo et al. 2013). However, experimental evidence for the importance of inter-stage competition almost exclusively stems from marine fish. Adult density negatively affected survival and feeding position of competitively inferior juvenile fairy basslets (*Gramma loreto*; Webster 2004), and survival and growth rate of goldspot goby juveniles (*Gnatholepis thompsoni*; Samhouri et al. 2009). In the latter, increasing adult density led to stronger selection on size at settlement and thus to positive density effects. More specifically, bigger juveniles were more likely to survive in high adult density and smaller juveniles were more likely to survive in low adult density (Samhouri et al. 2009). However, given the absence of evidence in terrestrial organisms, it is not clear yet whether the observed patterns are general or restricted to marine systems.

Here, we observed in the common lizard that adult density did not affect survival, performance, and reproduction of adults. However, higher adult density resulted in lower pre-hibernation survival, reduced growth and body size, and lower performance in juveniles, and in a lower proportion of reproducing juvenile females. Adult density thus negatively affected the development, pre-hibernation survival, and reproduction of the younger/smaller individuals, showing that responses of adults and juveniles were asymmetric. The negative effects on the competitively inferior individuals (and the absence of an effect on the competitively superior individuals), are in line with inter-class competition and with the findings in marine fish (Webster

337 2004; Samhouri et al. 2009). These results cannot be explained by differences in the total

338 population density, since survival and/or life-history traits of adults and juveniles should have

339 differed among treatment groups in a density-dependent manner (*i.e.*, HAD < LAD < NA, Fig. 2a).

340 Similarly, intra-class competition cannot explain differences in pre-hibernation survival of

341 juveniles, given that juvenile density, and thus competition in the juvenile class, was the same in

342 all populations. Given that adult density differed among treatments, intra-class competition among

343 adults would lead to differences in adult survival and reproduction, but no statistically significant

344 differences existed in these parameters.

345 The here detected asymmetric response of juveniles and adults more likely resulted from

346 differences in inter-class competition, with highest competition in the presence of high adult

347 densities and no inter-class competition in the absence of adults. The observed effects on juveniles

348 may have resulted from antagonistic interactions between adults and juveniles, or from adults

349 restricting juvenile access to good microhabitats or food (*e.g.*, through indirect or direct

350 competition; Imre *et al.* 2005), the former potentially leading to spatial exclusion (Nakayama and

351 Fuiman 2010). The space use models revealed no spatial exclusion of the juveniles in this study.

352 On the contrary, juveniles positively associated with adult males and the strength of the association

353 was unaffected by adult density (*i.e.*, no significant interaction between treatment and male

354 presence). Moreover, juveniles did not exhibit any scars or injuries before hibernation, suggesting

355 that inter-class competition did not result from direct agonistic interactions between adults and

356 juveniles, and behaviours such as cannibalism are thus very unlikely to explain the differences in

357 pre-hibernation survival. However, exploitative competition might explain treatment differences

358 in pre-hibernation survival of juveniles (Schoener 1983), because prey size of adults and juveniles

359 largely overlap (Pianka's index: 0.62-0.74, Heulin 1986; the entire prey size range of juvenile *Z.*

360   *vivipara* is also consumed by adults, but juveniles cannot consume the bigger prey eaten by the

361   adults), and reduced food availability is consistent with the observed lower body growth at high

362   adult densities (for effects of food consumption of juvenile growth see Le Galliard et al. 2005).

363   The adult density treatment affected the number of scars exhibited by juveniles in spring, a

364   proxy of mating activity (Bauwens and Verheyen 1987; Fitze et al. 2005). In populations with high

365   adult density, juveniles exhibited the lowest number of scars and none of the females were gravid

366   (Fig. 4b). In low adult density populations and in the absence of adults, juveniles exhibited a

367   significantly higher number of scars (Fig. 4a), and the proportion of gravid females was highest in

368   the absence of adults (Fig. 4b). This indicates that reproductive activity was negatively affected by

369   adult density. At low adult density, juveniles were less reproductively active compared to juveniles

370   at high adult density. However, only a very low proportion of LAD females was gravid, suggesting

371   that many LAD females were not yet mature. In contrast, in the absence of adults more mating

372   scars were present and the proportion of gravid females was significantly higher (Fig. 4b). This

373   pattern is consistent with the effects of adult density on juvenile growth before hibernation (growth

374   rate: HAD<LAD<NA; Fig. 3a) and it indicates that high levels of inter-class competition

375   substantially affect maturation of the juvenile class.

376   The path analyses suggest that the detected adult density effects on spring body size,

377   performance, maturation, and reproductive traits of juveniles, were mediated by direct adult-

378   density effects on early growth (before hibernation) and indirect effects by means of allometry

379   (Fig. 5). More specifically, a model including direct adult density effects on juvenile spring body

380   size, performance, number of scars, and reproductive status, fitted substantially worse than the final

381   model ($\Delta AIC = 3.56$; Table A1). This indicates that early growth conditions crucially affected life-

382   history traits later on and that entering hibernation with a smaller body size may have delayed

383   sexual maturation. The importance of early growth conditions is in line with previous studies

384   (Lindström 1999; Fitze et al. 2004; Le Galliard et al. 2005; Mugabo et al. 2010; Massot and Aragón

385   2013), and suggests that inter-class competition can have long-term consequences. The adult

386   density effects on juvenile reproduction may also affect population dynamics, since delayed

387   maturation is expected to result in longer generation times (De Roos et al. 2003), pointing to

388   potential effects of early developmental conditions on population dynamics (Beckerman et al.

389   2002).

390   Juvenile survival before hibernation was negatively affected by adult density. However,

391   from hibernation to spring, juveniles survived better at high adult densities, even though the adult

392   and overall population densities remained higher than in the LAD and NA populations (Fig. 2).

393   Increased survival in high adult density populations could be the result of differential survival

394   induced by inter-class competition previous to hibernation, as observed in the goldspot goby, where

395   increasing adult density led to stronger selection on body size and thereby to positive density-

396   effects (Samhouri et al. 2009). It could also be the result of differential competitive abilities of

397   juveniles during inter-class competition. The former hypothesis predicts that body size or body

398   condition will be more strongly selected in the high adult density treatment compared to the other

399   two treatments, and thus that there would have existed a significant interaction between the adult

400   density treatment and juvenile body size or body condition on survival previous to hibernation. The

401   latter hypothesis predicts that juveniles of high adult density populations will be more competitive,

402   *i.e.*, of bigger body size or better body condition. In our study, the interactions of the density

403   treatment with juvenile body size or body condition on survival were not significant and juveniles

404   in high adult density populations grew less and attained smaller pre-hibernation body size.

405   Consequently, there is no evidence that higher survival of high adult density juveniles could have

406   resulted from differential selection or increased competitive ability. Interestingly, not only low

407   adult density juveniles exhibited reduced survival, but also juveniles in populations where adults

408   were absent (Fig. 1). Pre-hibernation juvenile density and body size were lowest and smallest in

409   the high adult-density treatment, and pre-hibernation juvenile density was almost identical in LAD

410   and NA populations (Fig. 2b). This suggests that intra-class competition among juveniles might

411   have differed between HAD and the other populations. Higher intra-class competition among

412   juveniles in LAD and NA populations may indeed explain why juveniles of HAD populations

413   survived better from autumn to spring (Fig. 1), which would be in line with findings in the brown

414   trout, *Salmo trutta* (Kaspersson et al. 2012, see also Calsbeek and Smith 2007), where bigger

415   juveniles outcompeted smaller juveniles. The here detected higher juvenile survival between

416   autumn and spring in HAD populations is consistent with positive density dependence and it is in

417   line with delayed effects of high adult density (i.e. high inter-class competition), positive density-

418   dependent effects detected in the goldspot goby (Samhouri et al. 2009), and predictions from

419   theoretical models (Claessen et al. 2000; Beckerman et al. 2002; van de Wolfshaar et al. 2008).

420   Previous experimental studies conducted in semi-natural enclosures showed that the

421   survival of juvenile common lizards showed positive density dependence (Mugabo et al. 2013),

422   and studies in wild populations rendered opposing results; one study unravelled positive (Meylan

423   et al. 2007) and the other study negative density dependence of juvenile survival (Massot et al.

424   1992). All three studies manipulated the overall population density and thus differences in inter-

425   class competition, intra-class competition, or overall density may have led to the observed results.

426   In our study, we found negative density-dependent effects on pre-hibernation juvenile survival and

427   positive density-dependent effects on autumn to spring survival of juveniles, and the two effects

428   seem to have balanced each other out. As a result, the annual juvenile survival did not differ

429   between treatments. The fact that the here detected negative density-dependent effects were caused

430   by inter-class competition, allows us to hypothesize that differences in the strength of inter-class

431   competition might be at the origin of the opposing results found in the experiments manipulating

432   overall density (Massot et al. 1992; Meylan et al. 2007; Mugabo et al. 2013). Furthermore, in our

433   study exploitative competition among adults and juveniles may explain the observed patterns. This

434   suggests that the opposing results may have originated from differences in food availability among

435   studies, and differences in food availability among seasons might have been responsible for

436   negative and positive density dependence of juvenile survival detected in our study. However,

437   alternative mechanisms that explain the observed opposite density-dependent effects (Massot et al.

438   1992; Meylan et al. 2007; Mugabo et al. 2013) cannot be ruled out and future experiments need to

439   corroborate the importance of food availability for density-dependent juvenile survival.

440   In conclusion, we showed that inter-class competition has important direct effects on

441   survival and early growth of juveniles. Inter-class competition induced delayed effects on body

442   size, performance, and reproduction of juveniles. This highlights the importance of inter-class

443   competition in stage-structured populations of terrestrial vertebrates, which is in line with findings

444   in fish. In goldspot sand gobies, juvenile survival was negatively related with adult goby density

445   and the intensity of this density dependence was reduced in habitats with a high compared to

446   habitats with a low number of refuges (Samhouri et al. 2009). These results, together with our

447   results and results from other experimental studies on the common lizard, suggest that the

448   availability of resources shared by individuals of different classes (*e.g.*, food, refuges, mate partner,

449   etc.; Amarasekare 2003, Cresswell 1998), may lead to differences in density-dependence. More

450   specifically, a lack of resources may intensify the inter-class competition and thereby lead to

451 negative density-dependent effects in juveniles, while abundant resources may relax inter-class

452 competition and thereby lead to positive density dependence in juvenile traits.

453

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Tables

Table 1. Effects of adult density on prehibernation, hibernation-to-spring, and annual survival of juveniles. Depicted in bold are parameters included in the final generalized linear mixed models for each time period. Statistics of non-significant terms correspond to values before backward elimination.

	Prehibernation survival				Hibernation-to-Spring survival				Annual survival		
	Estimate (S.E.)	χ^2	d.f.	P	Estimate (S.E.)	χ^2	d.f.	P	χ^2	d.f.	P
Treatment	**1.76 (0.80)***	**6.57**	**2**	**0.037**	**-2.10 (0.83) ***	**10.61**	**2**	**0.005**	1.38	2	0.501
	2.39 (1.02)**				**-2.68 (0.88)****						
Sex		1.24	1	0.266		0.12	1	0.727	0.29	1	0.588
Treatment × Sex		0.57	2	0.754		1.66	2	0.436	1.97	2	0.373
Body condition		0.20	1	0.656	**4.49 (1.61)**	**7.75**	**1**	**0.005**	0.37	1	0.549
SVL		0.14	1	0.705	**0.13 (0.06)**	**4.50**	**1**	**0.003**	0.52	1	0.471
Hatching date	**-0.07 (0.03)**	**9.94**	**1**	**0.002**		3.02	1	0.082	2.27	1	0.131

* estimate of the LAD with respect to the HAD group.
** estimate of the NAD with respect to the HAD group.

Table 2. Effects of adult density on juvenile growth. Depicted in bold are parameters included in the final linear mixed models for each variable. Statistics of non-significant terms correspond to values before backward elimination.

	SVL			Growth rate		
	F	d.f.	*P*	*F*	d.f.	*P*
Treatment	1.03	2,3	0.458	6.46	2,3	0.082
Sex	**17.04**	**1,148**	**<0.001**	4.90	1,110	0.029
Treatment × Sex	1.38	2,146	0.255	1.21	2,108	0.302
Time	**118.15**	**2,200**	**<0.001**	**142.12**	**1,83**	**<0.001**
Treatment × Time	**3.47**	**4,200**	**0.009**	**7.15**	**2,83**	**0.014**
Sex × Time	1.40	2,198	0.245	0.02	1,82	0.878
Treatment × Sex × Time	1.61	4,194	0.329	0.79	2,80	0.456

651 **Figure legends**

652 **Figure 1.** Effects of adult density (HAD: high adult density, LAD: low adult density, NA: no

653 adults) on juvenile survival. Shown are the juvenile's survival probability during each time period.

654 Statistics correspond to significant *post-hoc* contrasts between treatment groups (* $P < 0.05$, ** P

655 < 0.01). N for spring and annual survival was 155 and 120 for hibernation-to-spring survival.

656 **Figure 2.** Evolution of total density and juvenile density over the course of the experiment. Mean

657 ($\pm$ S.E.) number of individuals (adults plus juveniles, a) and mean number of juveniles (b) per

658 population and treatment.

659 **Figure 3.** Effects of adult density on juvenile (a) snout-to-vent length (SVL, mm) and (b) growth

660 rate. Shown are the means $\pm$ standard errors for each of the three adult density levels. Note: the

661 standard errors associated with juvenile SVL at hatching are very small and thus not visible. N

662 upon hatch $= 155$, N before hibernation $= 120$, N spring $= 91$.

663 **Figure 4.** Effects of adult density on (a) the number of scars exhibited by juvenile males and

664 females and (b) on the reproductive status of juvenile females ($1 =$ gravid; $0 =$ non-gravid). Shown

665 statistics correspond to *post-hoc* contrasts between treatment groups (* $P < 0.05$, *** $P < 0.001$).

666 N number of scars $= 91$, N reproductive status $= 38$.

667 **Figure 5.** Path analyses of the direct *vs*. indirect effects of adult density on juvenile performance

668 and reproductive status. The causal paths linking adult density, performance traits, and the number

669 of scars of male and female juveniles were analysed separately from the causal paths linking adult

670 density and the probability that a juvenile female was gravid (Online Resource 1). For simplicity,

671 both path diagrams were merged and presented here. Solid and dashed arrows respectively indicate

672 significant and non-significant direct relationships and black and grey arrows indicate positive and

673 negative relationships, respectively. The sign of treatment and sex effects are given for NA

674   populations and males, respectively. Arrow thickness is proportional to the standardized path

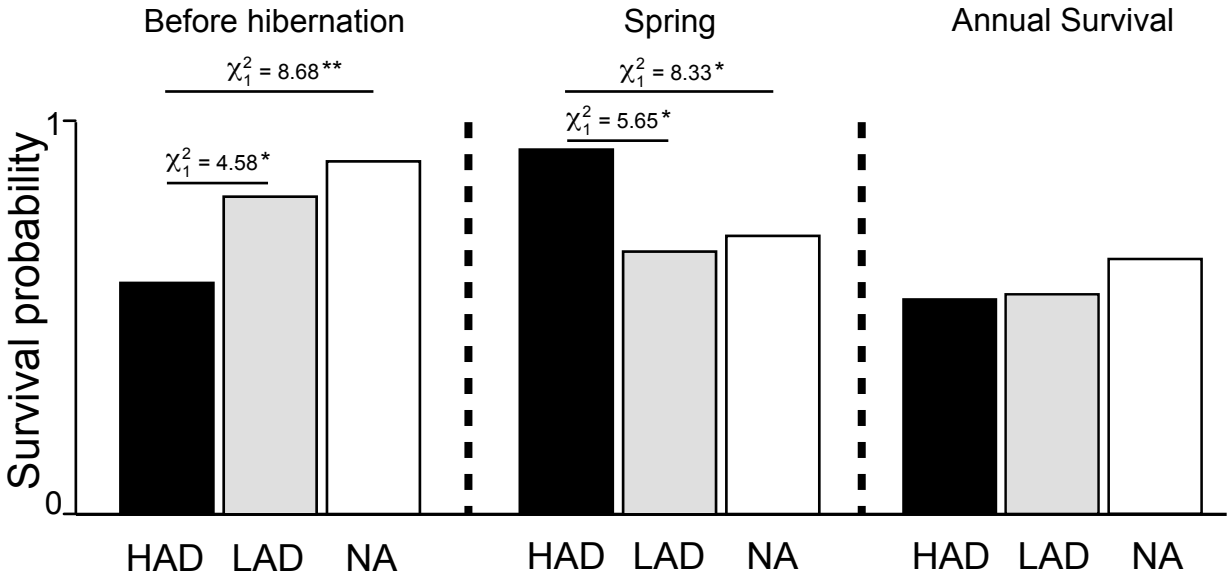675   coefficients, which represent the effect size of the associations.
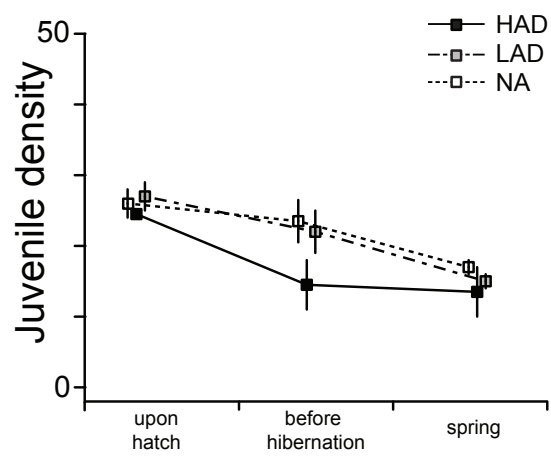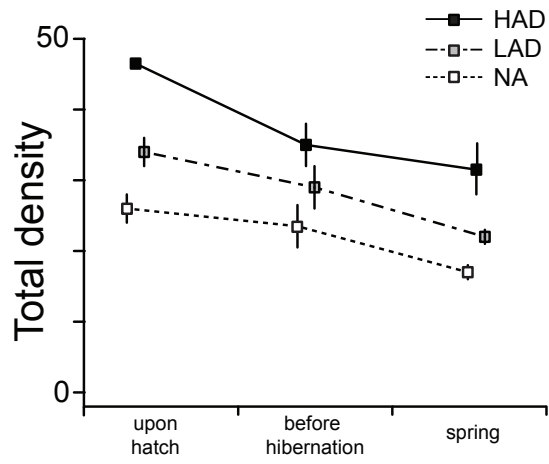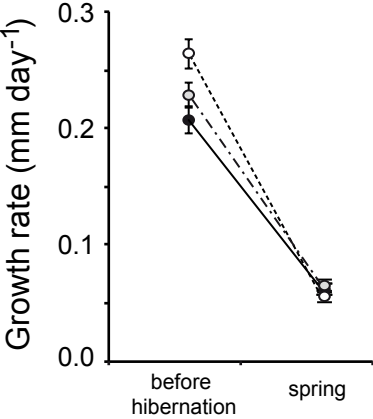
Figures

Figure 1.

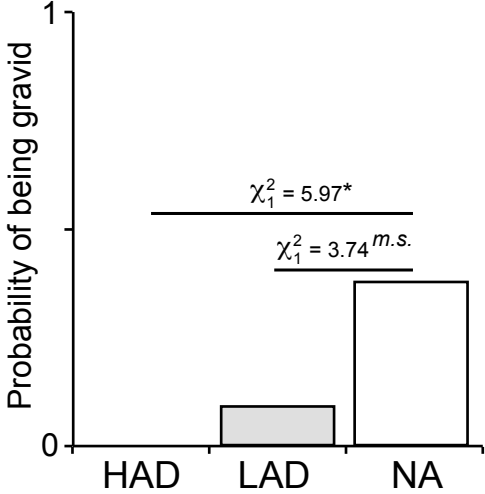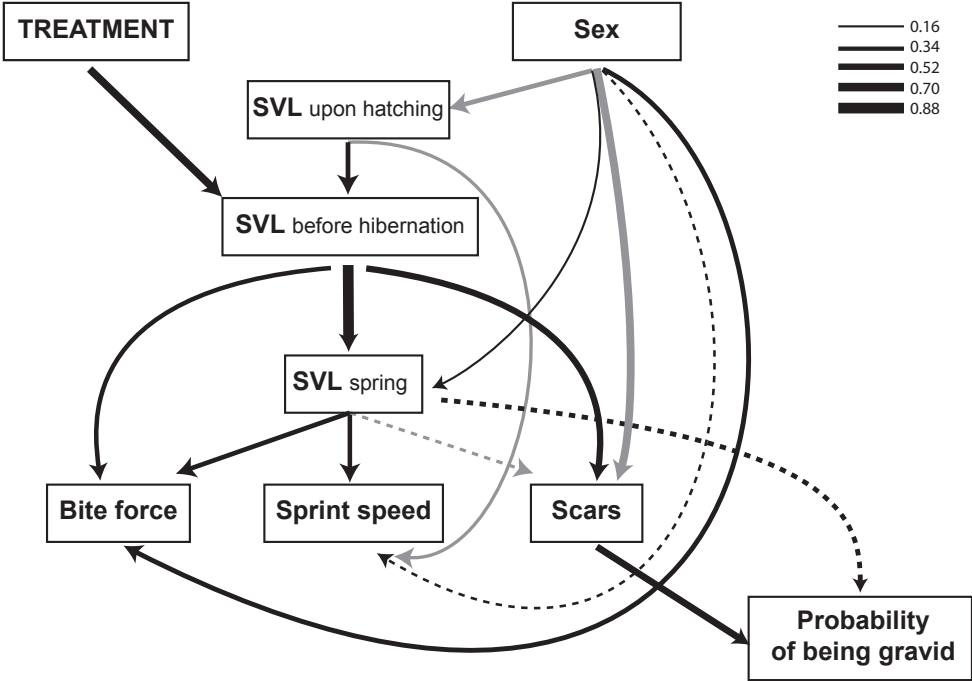**Figure 2.**

Figure 3.

(a)

(b)

Figure 4.

(a)

(b)
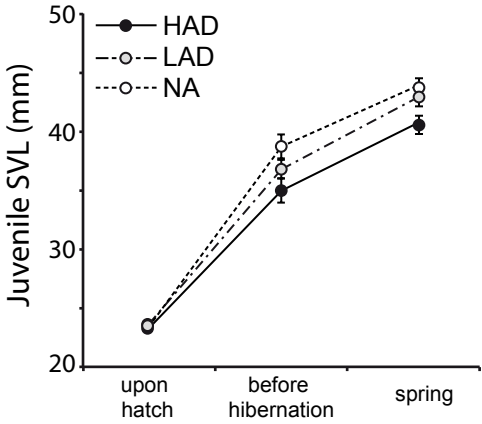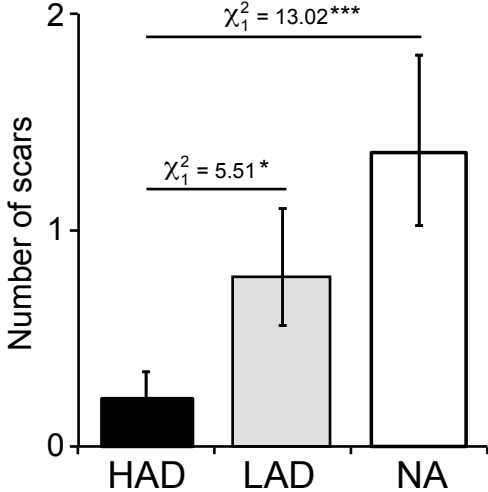
Figure 5.

Confirmatory path analysis

A path analysis was conducted to test if adult density directly affected spring body size, performance, and/or the number of scars of juveniles or if adult density indirectly affected these variables through its effects on pre-hibernation body size. Path analysis were based on the d-sep test described by Shipley (2000), given that juveniles living in the same enclosure are not independent. Consequently, the data had a hierarchical structure. In contrast to classic structural equation models, the d-sep test does allow for hierarchical structures within data sets (Shipley 2009).

We first constructed a hypothetical causal path model using both male and female juveniles in order to test for direct vs. indirect effects of adult density on spring body size, performance traits, and the number of scars. The initial model (full independent model; see Fig. A1) assumed indirect effects of adult density on spring body size, performance traits, and the number of scars mediated by treatment effects on pre-hibernation body size. Sex and snout-to-vent length (SVL) measured at hatching were also considered (Fig. A1a). We first tested whether the full independent model provided a good fit to the data using the C statistic, which follows a chi-square distribution with $2k$ degrees of freedom (k is the number of independent claims, $i.e.$, the number of pairs of variables that are not directly connected in the causal path; Shipley 2000). Because this model was not statistically supported (Table S1), we subsequently excluded all independent claims with a significant null probability (for further details see Shipley 2000, 2009) and tested the goodness of fit of each of the new causal path models. These path models were posteriorly compared using the Akaike information criteria described by Shipley (2013) in order to select the best fitting model

(model with highest, non-significant C value). Note that these models accounted for model complexity (K, the number of free parameters involved in each causal path; Table S1). The final path model was then compared to a path model including the direct treatment effects (Table S1). The same procedures were used to test for direct *vs.* indirect effects of adult density on the proportion of gravid females (see Fig. S2 and Table S2).

Tables:

Table A1: Goodness of fit and model comparisons of the hypothesized causal paths for the direct *vs*. indirect effects of adult density on performance traits and number of scars. A significant *C* statistic indicates that the hypothesized path diagram is not congruent with the data (for further details see Shipley 2000). AIC values and ΔAIC of the different models are given to determine the best fitting candidate model (for further details see Symonds and Moussalli 2010, Shipley 2013). Lower AICs indicate higher support and ΔAIC ≥ 2 indicate significant differences among models (Burnham and Anderson 1998).

Models	*C*	d.f.	*P*	AIC	ΔAIC	Weight	Evidence Ratio
Final model	27.18	28	0.51	75.18		0.38	1
Final model + Direct treatment effects	18.74	20	0.54	78.74	3.56	0.06	5.94
M4	36.34	30	0.20	82.34	7.16	0.01	35.84
M3	45.26	32	0.06	89.26	14.08	<0.01	1140.43
M2	62.91	34	<0.01	104.91	29.73	<0.01	2.86E+06
Full independent model	157.77	42	<0.01	191.77	116.59	<0.01	2.08E+25

Models: Full independent model see Fig. A1, **M2** includes the paths of the full independent model and the direct effects of sex on spring SVL, bite force, sprint speed, and number of scars, **M3** includes the paths of M2 and the direct effect of prehibernation SVL on the number of scars, **M4** includes the paths of M3 and the direct effect of SVL measured upon hatching on sprint speed, the **Final model** includes the paths of M4 and the direct effect of prehibernation SVL on bite force (see Fig. 4 in the main text). **'Direct treatment effects'** refer to the direct effects of adult density on spring SVL, bite force, sprint speed, and scars.

Table A2: Goodness of fit and model comparisons of the hypothesized causal paths for the direct *vs*. indirect effects of adult density on the probability of female juveniles of being gravid. A significant *C* statistic indicates that the hypothesized path diagram is not congruent with the data (for further details see Shipley 2000). AIC values and ΔAIC of the different models are given to determine the best fitting candidate model (for further details see Symonds and Moussalli 2010, Shipley 2013). Lower AICs indicate higher support and ΔAIC ≥ 2 indicate significant differences among models (Burnham and Anderson 1998).

	C	df	*p*	AIC	ΔAIC	Weight	Evidence Ratio
Final model	7.91	16	0.952	35.91		0.84	1
Final model + Direct treatment effects	7.19	14	0.927	39.19	3.28	0.16	5.16
Full independent model	22.68	18	0.203	48.68	12.77	<0.01	592.88

Models: Full independent model see Fig. A2, **Final model** includes the full independent model and the direct effect of spring SVL on the probability of being gravid. **'Direct treatment effects'** refers to the direct effects of adult density on the probability of being gravid.
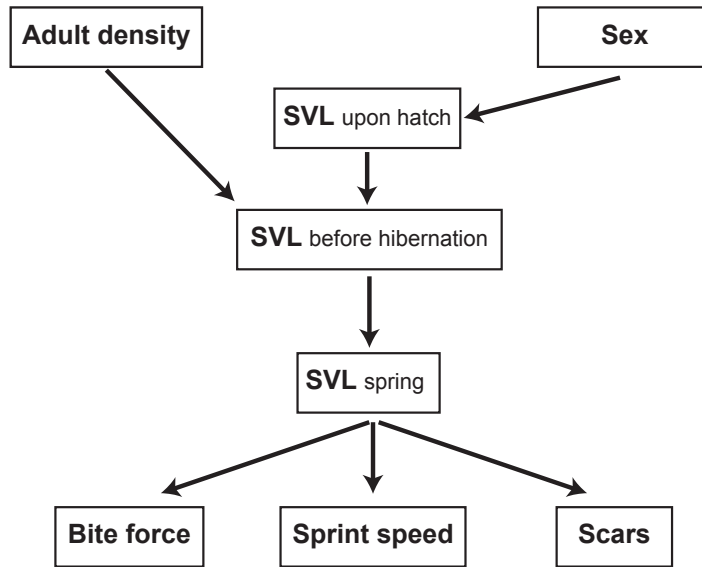
Fig. A1: Initial causal path diagram (full independent model) of adult density effects on performance traits and number of scars.
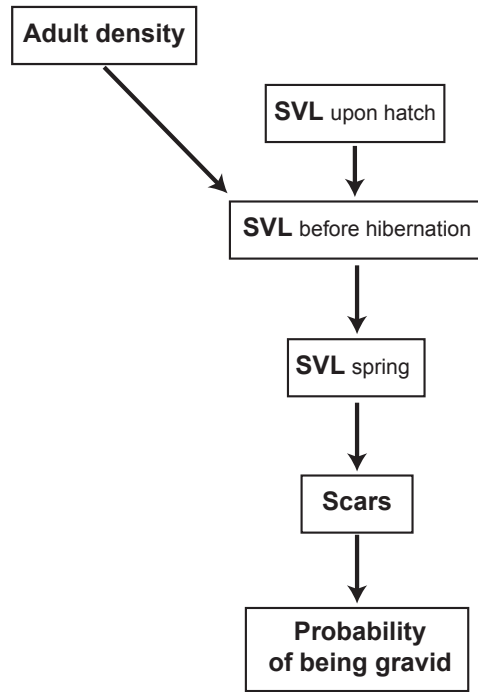
Fig. A2: Initial causal path diagram (full independent model) of adult density effects on the probability of female juveniles being gravid.

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