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Reproductive individuality of clonal fish raised in near-identical environments and its link to early-life behavioral individuality

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ABSTRACT

Recent studies have documented among-individual variation that is unexplained by genetic or apparent environmental differences, but it remains an open question whether such seemingly stochastic variation has fitness consequences. We perform a life-history experiment with naturally clonal fish (*Poecilia formosa*), separated directly after birth into near-identical (i.e., highly standardized) environments, quantifying 2522 offspring from 152 broods over 280 days. We find that (i) individuals differ consistently in the size of offspring and broods produced over consecutive broods, (ii) these differences are observed even when controlling for trade-offs between brood size, offspring size and reproductive onset, indicating individual differences in life-history productivity and (iii) early-life behavioral individuality in activity and feeding patterns, with among-individual differences in feeding being predictive of growth, and consequently offspring size. In this work, we provide experimental evidence that processes unexplained by genetic and apparent environmental differences translate into predictable differences in life-history measures and ultimately fitness.

INTRODUCTION

Phenotypic differences among individuals from the same species abound throughout the animal kingdom [1–3], with substantial consequences for fitness, ecology and evolution [4–8]. It is commonly thought that such individuality (if not minor and inconsequential 'noise' or 'idiosyncrasies') is primarily caused by genetic and/or apparent environmental differences. More recently, however, this long-standing paradigm has been experimentally challenged, with accumulating evidence that even genetically identical individuals raised in near-identical (i.e., highly standardized) environments develop substantial phenotypic differences [9–11]: isogenic fruit flies, for example, develop differences in locomotor handedness and wing-folding, phototaxis, and object-fixated locomotion [12–14]; naturally clonal fish separated directly after birth into highly standardized environments develop repeatable differences in activity levels that are already present from the first day of life [15,16] (see [17,18] for related findings in genetically identical mice and clonal pea aphids).

Such findings are important as they demonstrate that genetic and apparent environmental differences are not the only potent source of variation among individuals, suggesting that factors like pre-birth processes (including epigenetics), development *per se* and/or minor environmental differences may represent other key drivers of phenotypic differences [19–22]. Up to now, however, all recent studies on the emergence of variation in the absence of genetic and apparent environmental differences have focused on characterizing emergent behavioral differences (and their neurobiological underpinnings) and it remains an open question whether or to what extent these differences really matter.

One of the most direct ways to answer this question is to investigate whether phenotypic differences that emerge under genetic and environmental standardization extend to those aspects of the phenotype that directly affect fitness. The goal of the present study is to do exactly this. We performed an experimental study with a live-bearing, naturally clonal freshwater fish, the Amazon molly, *Poecilia formosa*. Directly after birth, we separated genetically identical individuals (N = 34) into near-identical environments and reared them under highly standardized conditions for 280 days (i.e., 40 weeks). We utilized automated high-resolution tracking of activity and feeding patterns to characterize their early-life behavioral profiles over the first 28 days of their lives (daily recordings for 10 hours at 0.2 s resolution, amounting to a total of 9,520 recording hours and 171.4 million data points) [23]. We then characterized reproductive profiles: recording the onset of reproduction, the size of each brood produced (i.e., the number of offspring per brood; in total, N = 152 broods), and the size of all offspring produced (N = 2522 total offspring), thereby observing 4.5 ± 1.1 broods (mean ± SD) per female (gestation takes approx. 30 days [24,25]. Individual body size was measured weekly.

We focus on three key research questions. First, do genetically identical individuals separated at birth into highly standardized environments develop significant among-individual differences in reproductive traits, i.e., repeatable differences in offspring size and/or brood size? Second, are among-individual differences in reproductive traits, if present, indicative of differences in (i) life-history productivity, i.e., the ability to produce new biomass [26,27] and/or (ii) how individuals balance the trade-off between brood size vs. offspring size [28–31]? Third, are reproductive differences, if present, related to early-life

behavioral differences? Such a link could be possible via growth, where behavior (in particular feeding behavior) could be linked to growth and growth, in turn, to reproductive output [28,32,33]. As an underlying assumption, and as shown previously [15,16], we expected repeatable early-life behavioral variation. Whenever appropriate, we focus on repeatability as a key parameter to quantify and test for individuality [3,34,35].

RESULTS

Early-life behavioral individuality

We find that genetically identical individuals separated into near-identical environments on the day they were born exhibit strong behavioral individuality during the first four weeks of life, both in activity (repeatability (R) for activity = 0.371, 95% CI = [0.329, 0.413]) and feeding behavior (R = 0.183, 95% CI = [0.145, 0.224]). These repeatable differences even increase when controlling for within-individual variation caused by individuals growing and becoming older during our observations (adjusted R for activity = 0.571, 95% CI = [0.532, 0.621]; adjusted R for feeding = 0.238, 95% CI = [0.194, 0.285]). Daily activity and feeding behavior are negatively correlated (estimate = -9.134, 95% CI [-10.550 – -7.719] p-value < 0.0001, R^2 = 0.164, **Supplementary Table 7**), this may be explained by more active fish also being more active during the feeding period, thereby having less time to feed at the stationary food resource.

Reproductive individuality and life-history productivity variation

We find consistent among-individual differences in both the average size of offspring (**Figure 1a**, R = 0.396, 95% CI [0.308, 0.484]) and the number of offspring produced (**Figure**

102 **1b**, R = 0.177, 95% CI = [0.117, 0.238]) over consecutive broods. Interestingly, the trade-off
103 between brood size and offspring size explains only a small amount of the variation
104 observed (estimate = -0.013, 95% CI [-0.018, 0.007], p-value < 0.001, partial R^2 = 0.115)
105 (**Figure 1c**, **Supplementary Table 8**). Even when controlling for this trade-off, among-
106 individual differences remain: given the same brood size, onset of reproduction, and size at
107 parturition, some individuals consistently produce larger offspring than others (adjusted R
108 for offspring size = 0.134, 95% CI = [0.085, 0.192]); similarly, when controlling for onset of
109 reproduction, size at parturition, and offspring size, some individuals consistently produce
110 larger broods than others (adjusted R for brood size = 0.077, 95% CI = [0.050, 0.114]).
111 These findings strongly suggest that – next to developing repeatable among-individual
112 differences in offspring size and brood size – these genetically identical individuals, raised
113 individually in highly standardized environments, also differ in life-history productivity.
114
115 We stress that both offspring- and brood size are among the most direct fitness
116 components one can measure, and seemingly small - but repeatable - differences in these
117 traits may have profound long-term consequences. This can be seen, for example, when
118 considering the cumulative number of offspring produced, where even relatively minor
119 individual differences in brood size, when expressed consistently, result in large among-
120 individual differences in total reproductive output (**Figure 1d**).
121
122 All analyses on female reproductive output are controlled for descent (i.e., mother ID) and
123 female size at parturition (see **Supplementary Note 5** 'Effect of female size on reproductive
124 output' for an illustration of the effect of female size at parturition on offspring and brood

125 size and **Supplementary Table 9** for statistical analyses). Moreover, we controlled
126 experimentally for potential effects of breeding tanks and/or males (see 'Reproductive
127 profiles' in Methods). Statistical analyses confirming that our results are robust towards
128 potential male/tank IDs are provided in **Supplementary Note 3** 'Robustness of results with
129 respect to potential male and/or tank effects'.
130
131 *Link between behavioral and reproductive individuality*
132 Despite no direct link between our two behavioral measures, activity and feeding, and our
133 three reproductive traits, i.e., offspring size (**Figure 2 a-b**), brood size (**Figure 2 c-d**), and
134 onset of reproduction (**Figure 2 e-f**) (**Supplementary Table 9**), we find an indirect link
135 between one of our behavioral traits and reproduction: fish that spend more time feeding
136 grow to a larger size (estimate = 0.007, 95% CI [0.003, 0.012], p-value = 0.002, partial R^2 =
137 0.266; **Figure 3b, Figure 3d**), and larger fish, in turn, produce larger offspring (**Figure 3c**;
138 estimate = 0.619, 95% CI [0.299, 0.939], p-value < 0.001, partial R^2 = 0.129). Larger fish also
139 start reproducing later (estimate = 55.537, 95% CI [25.189, 85.886], p-value = 0.001, partial
140 R^2 = 0.310; **Figure 3f**), but there is no effect on brood size (**Figure 3e**) (**Supplementary**
141 **Table 11**).
142
143 In contrast to feeding behavior, we find no indirect link between activity and reproduction
144 (**Figure 3a, Supplementary Table 10**), nor do we find an effect of our behavioral traits on
145 individual growth rates (predicted from fitted growth curves; see Methods) (**Supplementary**
146 **Table 10**). We note growth rate and onset of reproduction are positively correlated: fish
147 that grow faster start reproducing later (estimate = 980.383, 95% CI [235.137, 1725.629], p-

148 value = 0.012, partial R^2 = 0.188), but there is no effect of growth rate on brood- and
149 offspring size (**Supplementary Table 11**). Throughout, qualitatively the same results are
150 obtained when statistically controlling for potential effects of breeding tanks and/or males
151 (see **Supplementary Note 3** 'Robustness of results with respect to potential male and/or
152 tank effects').
153

154 DISCUSSION

155 We find that genetically identical individuals, raised separately and in highly standardized
156 environments, develop repeatable differences in key reproductive characteristics. In
157 particular, when considering consecutive broods, individuals differ consistently in how many
158 offspring they produce and in how large these offspring are. While we find evidence for a
159 weak trade-off between offspring size and number, repeatable among-individual
160 differences are observed even when controlling for this trade-off, as well as for body size
161 and onset of reproduction, providing clear evidence that individuals differ in life-history
162 productivity. While previous studies have provided firm evidence that substantial among-
163 individual variation in anatomical-, behavioral- and neurobiological traits can emerge even
164 in the absence of genetic and apparent environmental differences [10,13,15], the current study
165 builds on and substantially extends these studies by demonstrating that the emerging
166 variation extends to aspects of the phenotype that are directly associated with fitness.
167

168 Interestingly, we find no direct link between early-life behavioral differences and differences
169 in reproductive traits. It is conceivable, however, that a direct link between early-life
170 behavioral and later-in-life reproductive traits may only become apparent in non-benign

171 and/or more complex environments. To give a concrete example, in our experimental set-
172 up, there are only minimal differential costs and benefits associated with different
173 behavioral phenotypes: fish were presented with a stationary food resource, located at a
174 standardized position in the tanks with no additional structures. There was no need to
175 search for food and no cost associated with exploiting the stationary food resource. In
176 contrast, in a more naturalistic context, activity might be linked to the ability to find food
177 and the exploitation of a food resource might be risky [36,37]. That said, it will be interesting to
178 see whether future studies, taking the above and other factors into account, will be able to
179 establish a link between early-life behavioral individuality and reproduction.
180
181 While we do not find a direct link between reproduction and early-life behavior, we find the
182 size of offspring produced to be indirectly linked to early-life feeding behavior: some
183 individuals feed consistently more than others, individuals that feed more grow to a larger
184 predicted final size, and individuals with a larger final size have larger offspring (but not
185 larger broods). The allocation of resources into increasing offspring size, rather than
186 offspring number, may represent an adaptation to environments in which larger offspring
187 have higher fitness, e.g., resource limitation, competition, or high juvenile mortality
188 (cannibalism or size-dependent predation) (reviewed in [29]). All of the above factors may
189 apply to our experimental design: during the reproduction period, individuals were fed a
190 standardized amount of food that they shared with a *P. mexicana* male, which we kept in
191 the female's tank as a sperm donor, potentially causing both resource limitation and
192 competition. Furthermore, offspring were removed from the females' tanks directly after

193 parturition, which decreased the risk of cannibalism but may have caused perceived
194 predation from the female's perspective.
195
196 We find that systematic (i.e., repeatable) among-individual differences in key fitness
197 components can emerge even in the absence of genetic and apparent environmental
198 differences. Future work may compare the observed differences in repeatedly expressed
199 reproductive traits to other iteroparous species, taking genetic and/or apparent
200 environmental variation into account, which will give us a better understanding of the
201 magnitude of the observed differences. Furthermore, we will need to investigate both the
202 causes and consequences of the observed differences. First, all individuals in our study
203 were exposed to one (very specific) environment, and it will be important to investigate
204 whether the observed differences can also be detected in other environments. It will be
205 particularly informative to include predation risk, a key determinant of fitness and major
206 factor shaping life-history trade-offs [38–42], and to investigate, for example, if high-
207 productivity individuals are differently affected by predators than low-productivity
208 individuals. Second, future studies should investigate the mechanistic causes underlying the
209 development of systematic differences in reproductive traits in the absence of genetic and
210 apparent environmental differences. In principle, the same set of factors (stochastic
211 developmental processes, minute environmental differences in combination with positive
212 feedback loops, and pre-birth influences including epigenetic and maternal effects) that are
213 thought to explain the emergence of behavioral individuality in the absence of genetic and
214 apparent environmental differences may also give rise to reproductive individuality [10, 16,19, 20,
215 21]. It is intriguing to speculate that pre-birth processes (e.g., within-brood variation in

maternal egg provisioning or in the exact starting time of embryonic development) initiate the observed reproductive differences, e.g., by creating early-life physiological differences. It is also interesting to note that mechanisms such as developmental instability and stochasticity may themselves be selected for as a means of generating adaptive variation through bet-hedging[43]. Detailed studies are needed to further investigate these and other hypotheses relating to underlying mechanisms driving individuality. Third, in order to evaluate the consequences of the observed differences in brood- and offspring size, it will be important to investigate whether and to what extent these differences are heritable. Do offspring from mothers with larger offspring (or larger brood sizes) sire larger offspring (or large brood sizes) themselves? While all our individuals are genetically identical, such inheritance is still conceivable, for example via epigenetic mechanisms [44–46].

The study of among-individual variation is one of the central themes in ecology and evolution. While such variation – if not minor and inconsequential 'noise' – has traditionally been thought to be caused by genetic and apparent environmental differences, evidence is accumulating that even in the absence of such differences, substantial among-individual variation can emerge. Here, we show that the emergent among-individual variation extends to aspects of the phenotype that directly affect fitness. Put differently, we find that among-individual variation that arises under highly standardized conditions reflects more than just 'idiosyncrasies' or 'noise' – it really matters.

METHODS

All animal care and experimental protocols complied with local and federal laws and guidelines and were approved by the appropriate governing body in Berlin, Germany, the Landesamt fur Gesundheit und Soziales (LaGeSo G-0224/20).

Study species and holding conditions

Amazon mollies used in our experiment were obtained from a stock kept at Humboldt-Universität zu Berlin (Berlin, Germany). The lineage used in our experiment was established prior to the start of the experiment by holding a single Amazon molly from the stock population as well as a *P. mexicana* male and their resulting offspring in a 50 liter tank (approx. 20-50 fish, 12:12h light:dark cycle, air temperature control at approx. 24±1°C, weekly water changes, fish were fed with Sera vipan baby powder food twice a day). Before the experiment, we separated potential mothers (i.e., large females, all of whom were sisters) from the isolated lineage and let them give birth in individual tanks; this allowed us to track the mother ID (N = 3) of individuals used in our experiment.

Early-life behavior

Test fish were transferred to individual observation tanks on the day they were born (see **Supplementary Figure 1** for an illustration of experimental tanks and **Supplementary Table 1** for statistical analyses confirming environmental standardization). Behavioral observations started the next day, i.e., the first full day of life. We recorded individuals daily over the first 28 days of their life from above with a Basler acA5472 camera (5 frames per second). Activity was observed over the first 8 hours of each day, followed by a 2-hour feeding

observation period. During the feeding period, individuals were presented with a 'food patch', that was positioned at a standardized location in the tank (**Supplementary Figure 1**). Food patches were prepared every 2 to 3 days using Sera vipan baby powder food and agar (protocol is provided in **Supplementary Note 2** 'Food patch preparation').

In total, we collected 952 recordings of daily activity and feeding behavior, respectively (34 individuals, each individual recorded over 28 days). To assess activity, we used a total of 941 recordings (mean ± SD recording length: 471.7 ± 29.9 min; 11 days were removed from the data due to technical issues). To calculate how much time individuals spent feeding, we processed 932 feeding recordings (mean ± SD recording length = 120.2 ± 11.2 min; 20 recordings were removed due to technical issues). Recordings were tracked using the software Biotracker [47], and the movement data obtained from Biotracker 3.2.1 (csv-files with xy-coordinates over time) were processed (visualization, calculation of metrics) with a custom-made repository we developed for this purpose [48]. Individual activity was calculated from xy-coordinates over time, in steps of 0.2 sec, as the average distance moved (cm) in one second. Individual time spent feeding was calculated as the amount of time an individual spent in the 'feeding zone', a 5 x 13 cm large zone surrounding the food patch [47][48].

Reproductive profiles

After our early-life behavioral observations, individuals were transferred to individual breeding tanks (11 liters each, visual separation between individual tanks, equipped with a small plastic pipe (length = 4 cm, diameter = 2 cm) and 'sera biofibres', a loose bundle of

green plastic fibers, resembling thread algae). A unified flow-through water system ensured standardized water conditions and a single *P. mexicana* male was placed in each tank. The Amazon molly is a gynogenetic species, i.e., sperm from one of the parental species (*P. mexicana*, *P. latipinna*) is needed to trigger embryogenesis but the male's DNA is not incorporated into the offspring's genome [49–52] (but see [53] for the rare possibility of paternal introgression). Breeding tanks were checked for offspring daily. Once a female gave birth to a brood, all offspring were photographed and counted. Offspring standard length (i.e., the length from the tip of the snout to the end of the caudal peduncle) was measured from the photos using ImageJ [54]. In total, we recorded 152 broods and measured the size of 2522 offspring from 144 broods (no measurements for 8 broods). Individuals produced on average 4.5 ± 1.1 broods (mean ± SD). We excluded all individuals from our analyses with no or partial reproductive data (N = 11 females). Feeding was standardized: twice a day for 5 days a week, fish received 1/64 tsp (up to the age of 70 days) or 1/32 tsp (from the age 70 to 280 days) of powder food.

In order to experimentally control for potential systematic male and/or breeding tank effects on female reproductive output, females were swapped once a week in a randomized manner between the different breeding tanks (while males remained in their tank). Over the course of the experiment, females visited 22 ± 2 males and 19 ± 1 breeding tanks (mean ± SD; the number of males exceeds the number of tanks, as some males were replaced, see **Supplementary Note 3** 'Robustness of results with respect to potential male and/or tank effects'). By providing each female with a series of different tanks (and thus males), we ensured that potential differences between males and/or tanks did not cause systematic

differences in female reproductive characteristics (i.e., repeatable differences in brood size and offspring size). We chose to swap females between breeding tanks rather than males because swapping males would have made it impossible to distinguish between the potential effects of breeding tanks and female identity. As a result of our experimental approach, we cannot isolate the effects of breeding tanks from the effects of males, but we were able to control for both factors simultaneously. See **Supplementary Note 3** 'Robustness of results with respect to potential male and/or tank effects' for further analyses demonstrating that all our results and conclusions are indeed robust with respect to potential variation caused by breeding tanks and/or males.

Long-term growth

Standard lengths of focal individuals were measured from photos once a week, using ImageJ [54] (34 ± 1 measurements per individual, mean ± SD). We fit individual growth curves using the von Bertalanffy growth model [55], a logistic function commonly used to model fish growth. Estimated parameters in this function are the theoretical age when size is zero (t_0), the growth coefficient (K), and the maximum predicted (i.e., asymptotic) size (L_{inf}). For all analyses, we used predicted sizes estimated using individual growth curves rather than raw measurements and characterized individual growth via K and L_{inf} obtained from those individual growth curves.

326 ***Statistical analysis***

327 *General details*

328 Data were analyzed in R version 4.2.1 [56]. Most parsimonious LMs (linear models) and LMMs
329 (linear mixed-effect models; models built using the lme4-package [57]) were fit via stepwise-
330 backward removal of non-significant predictors. Model assumptions were visually assured
331 using residual- and q-q plots. In the main text, we report estimates and p-values for
332 significant predictors only. The effects of covariates are presented in **Supplementary Note**
333 **4** 'Model output main analyses'. Most importantly, individual size at parturition is related to
334 both the number and size of offspring produced (model summaries in **Supplementary**
335 **Table 9**, illustration in **Supplementary Figure 2**); and we found mother ID (N = 3) to be
336 related to individual growth and reproductive output (**Supplementary Table 9** and **10**). We
337 therefore included mother ID as a covariate in all models (LMs and LMMs), and individual
338 size at parturition wherever appropriate. In all LMMs, test fish ID was included as a random
339 term. Individual size on the first day of life did not affect early-life behavior, reproductive
340 output, or growth (**Supplementary Tables 12-14** in **Supplementary Note 6** 'No effects of
341 size at birth on behavior, reproduction, and growth'); and was therefore not considered
342 during analyses. For significant predictors, we calculated partial R^2 using the sensemakr-
343 and r2glmm-package [58,59] (for LMs and LMMs, respectively). Complete model summaries of
344 all full (containing all predictors) and final models (containing significant predictors only) are
345 provided in **Supplementary Note 4** 'Model output main analyses'. Model summary tables
346 (including marginal and conditional R^2 following [60]) were built using the package sjPlot [61].

347

348 *Repeatabilities*

349 We estimated repeatabilities with 95% CIs (confidence intervals) in two ways: first by
350 building LMMs with only the target variable as response and female ID as random term, but
351 no predictors (i.e., raw repeatability), and then by adding fixed effects to the model,
352 allowing us to estimate the amount of variation caused by consistent between-individual
353 differences while controlling for variation explained by other factors (i.e., adjusted
354 repeatability). The significance of consistent among-individual differences was derived from
355 the 95% CI being distinctly different to 0 (95% CI based on 1000 model simulations) [62].

356

357 To test for 'reproductive individuality', we first calculated raw repeatabilities in the size of
358 broods (N = 152 broods) and the size of offspring (N = 144 broods, average offspring size
359 per brood) over all broods produced. Then, to test for among-individual differences in
360 productivity, we adjusted repeatabilities of both brood- and offspring size for onset, female
361 size at parturition, and mother ID. For the model on brood size, we additionally included
362 offspring size as predictor and vice versa (i.e., we accounted for brood size, offspring size,
363 and onset trade-offs).

364

365 To test for early-life behavioral individuality, we calculated raw repeatabilities for activity (N
366 = 941 observations of 34 individuals) and time spent feeding (LMM with N = 932
367 observations of 34 individuals), observed daily over the first 28 days of life. We also
368 adjusted repeatabilities for size and age (week 1-4, categorical variable), i.e., we accounted
369 for variation that was caused by individuals growing and aging over the observation period.
370 We further included a size-age interaction term as predictor (activity was differently affected

371 by size, depending on age). For repeatability calculations, activity was log-transformed for
372 normality. We tested if early-life activity (response) and feeding (predictor) are correlated
373 (LMM N = 931 observations of 34 individuals).
374
375 *Link between early-life behavior and reproduction*
376 To test for a direct behavior-reproduction link, we built three models with either brood size
377 (LMM with N = 152 broods), offspring size (LMM with N = 144 broods), or reproductive
378 onset (LM with N = 34 individuals) as response. In all models, activity and feeding (averaged
379 over 28 days) were modeled as predictors.
380
381 To test for an indirect behavior-reproduction link, we first tested for a link between behavior
382 and growth: we fit one model on the predicted final size L_{inf} (LM with N = 34 individuals)
383 and growth rate K (LM with N = 34 individuals), with activity and feeding as predictors
384 (average behavior over 28 days). When having K as the response, we additionally included
385 L_{inf} as a covariate to control for the effect L_{inf} has on K; i.e., bigger fish grow slower to their
386 final size L_{inf}, (LM with L_{inf} as response and K as well as mother ID as predictors: intercept [CI]
387 = 6.09 [5.8, 6.4]; estimate of K [CI] = -16.9 [-20.0, -13.8], R^2 = 0.89). To test for the link
388 between growth and reproduction, we fit a model on each brood size (LMM with N = 152
389 broods), offspring size (LMM with N = 144 broods), and onset (LM with N = 34 individuals);
390 including K and L_{inf} as predictors and female age at parturition (not in the onset-model) as a
391 covariate.
392

DATA AVAILABILITY

The data generated in this study have been deposited in Figshare (https://doi.org/10.6084/m9.figshare.23971599.v1) [63]. Source data are provided with this paper.

CODE AVAILABILITY

The code used to calculate daily activity and feeding behavior is publicly available on GitHub [48].

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AUTHOR CONTRIBUTIONS

JK and MW acquired funding. All authors conceived and designed the experiment. US conducted the experiment. US, SE, and MW outlined the data analysis. US conducted the data analysis. US and MW wrote the first manuscript draft. All authors commented on the manuscript and contributed to the final version.

COMPETING INTERESTS

The authors declare no competing interests.

FIGURES

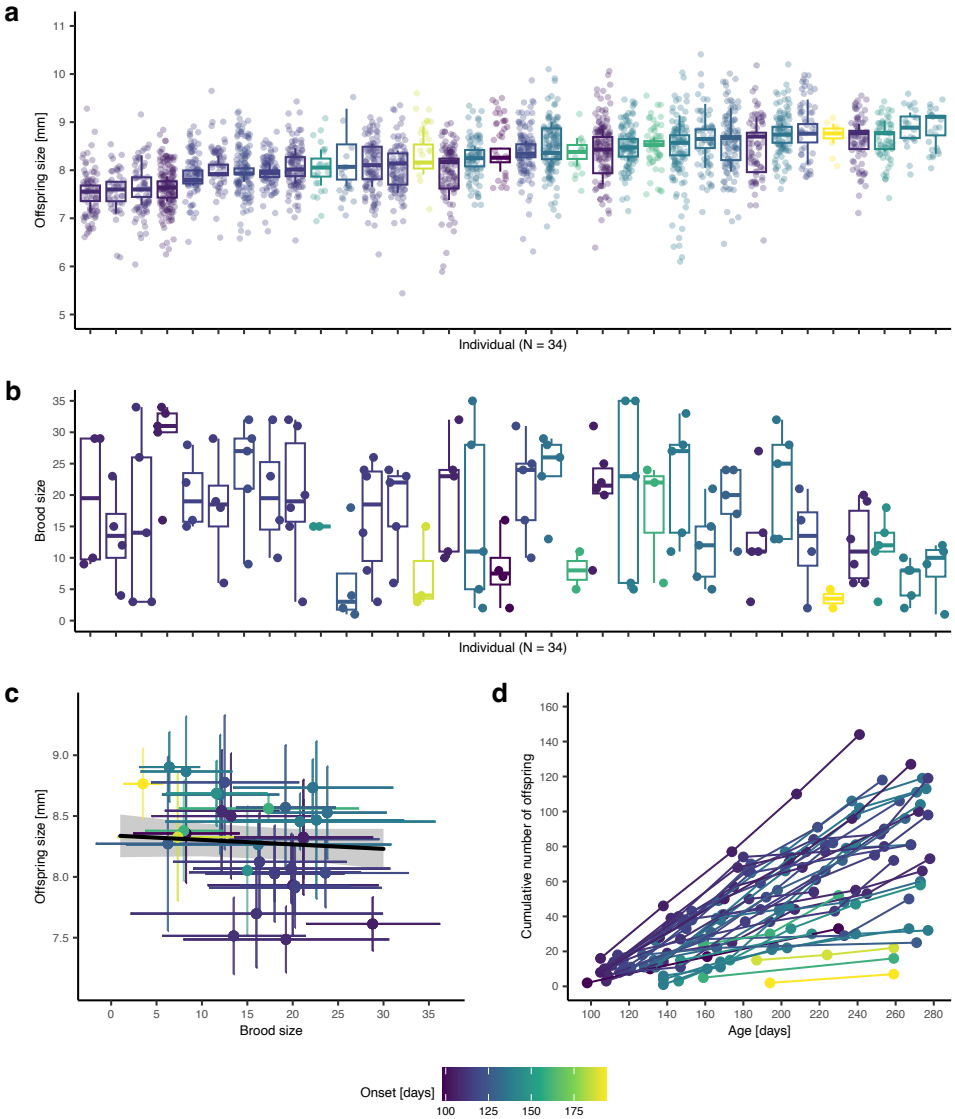
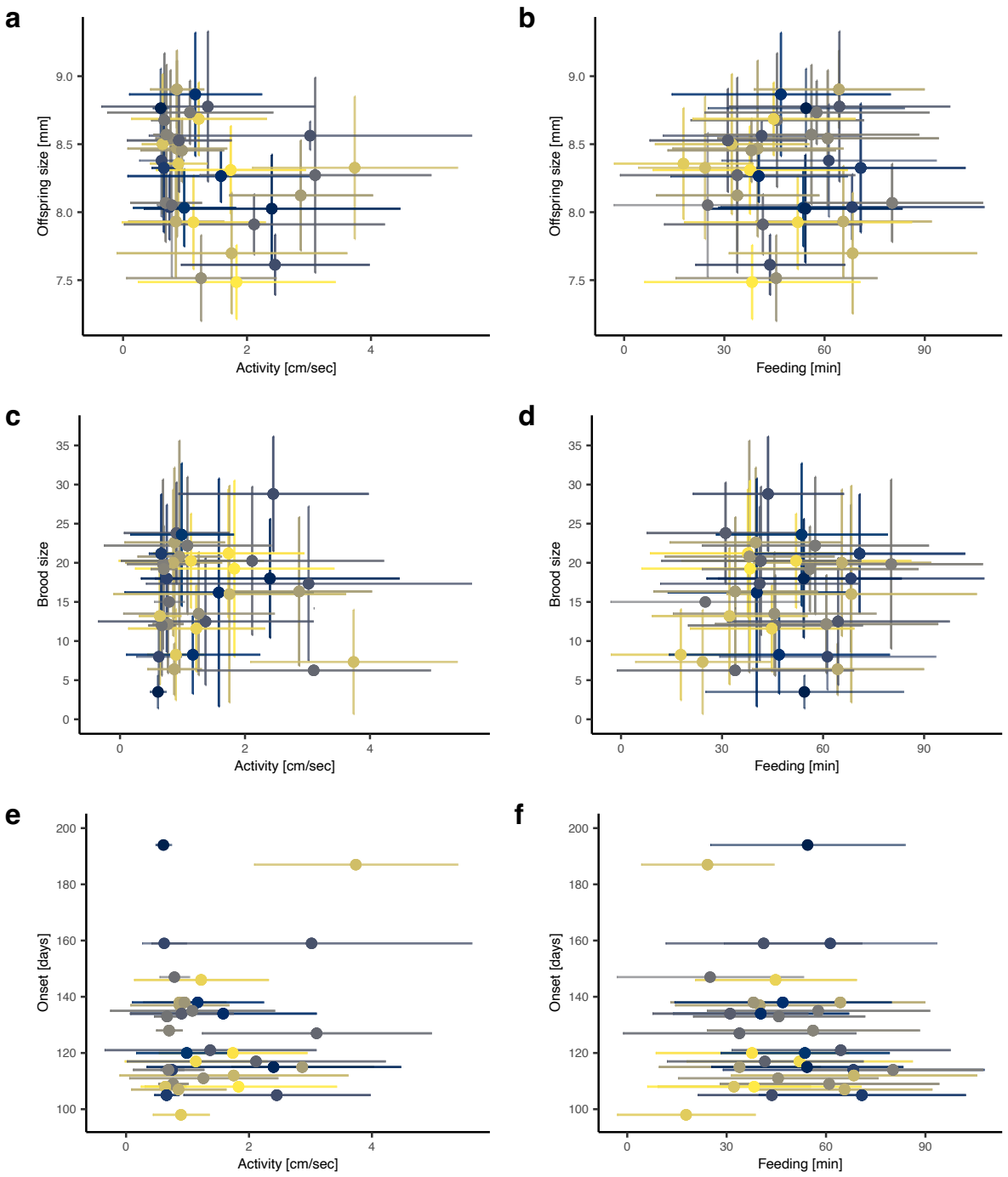


Fig. 1: Reproductive individuality. (a-b) Individuals (N = 34) differ consistently in the size- and number of offspring produced over successive broods (we recorded 152 broods and measured N = 2522 offspring from 144 broods, no size measurements for 8 broods); boxes are sorted by median offspring size; shown are median (middle line), 25th to 75th percentile (box), and 5th to 95th percentile (whiskers) as well as the raw data (points) for each individual. (c) The brood size vs. offspring size trade-off explains only very little of the variation; shown are individual means (points) ± SD (error bars) in brood/offspring size (N = 2522 offspring from 144 broods). The regression line (black) with 95% confidence interval (grey shadow) were estimated via linear mixed-effects model. (d) Differences in reproductive productivity can have profound long-term consequences because reproductive output accumulates over time, shown is the cumulative number of offspring produced by individuals over the first 280 days of life. (a-d) Coloration by onset (yellow represents late onset, purple represents early onset).



570

571 **Fig. 2: No direct link between early-life behavioral individuality and reproductive**
572 **individuality.** We find no effect of early-life behavior (activity and feeding) on offspring size
573 (a-b), brood size (c-d), or onset of reproduction. (e-f) Shown are individual means (points, N
574 = 34 individuals) ± SD (error bars) (N (activity measurements) = 941, N (feeding
575 measurements) = 932, N (size measured offspring) = 2522, N (broods) = 152). (a-f)
576 Individuals are colored differently.

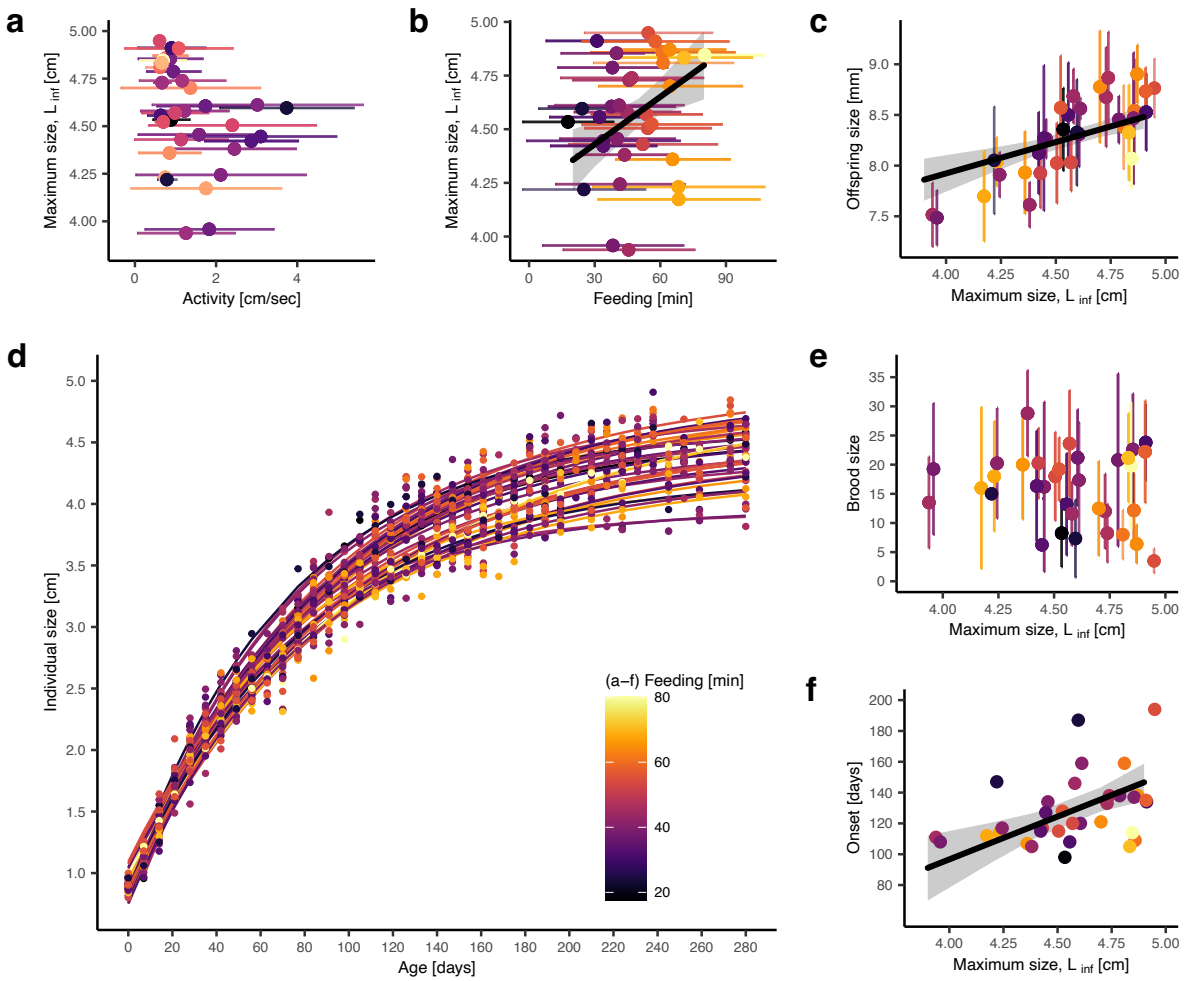


Fig. 3: Indirect link between early-life differences in feeding behavior and offspring size. (a) There is no effect of early-life activity on the maximum predicted size L_{inf}, but early-life feeding behavior and reproductive output are indirectly connected via growth: (b) individuals that feed more grow to a larger size (feeding is presented as mean ± SD, N = 932 feeding measurements), and (c) larger fish produce larger offspring. (f) Larger fish also start reproducing later but (e) individual maximum size and brood size are not linked. (a-c, e) Shown are individual means (points) ± SD (error bars) (N (activity measurements) = 941, N (feeding measurements) = 932, N (size measured offspring) = 2522, N (broods) = 152). (b, c, f) Regression lines (black) with 95% confidence intervals (grey shadow) were estimated via linear mixed-effects models. (d) Shown are individual von Bertalanffy growth curves (lines) with raw data (points). (a-f) Coloration by average time spent feeding (yellow represent long feeding times, black represents short feeding times).

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593 Supplementary information for:
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595 **Reproductive individuality of clonal fish raised in near-identical**
596 **environments and its link to early-life behavioral individuality**
597
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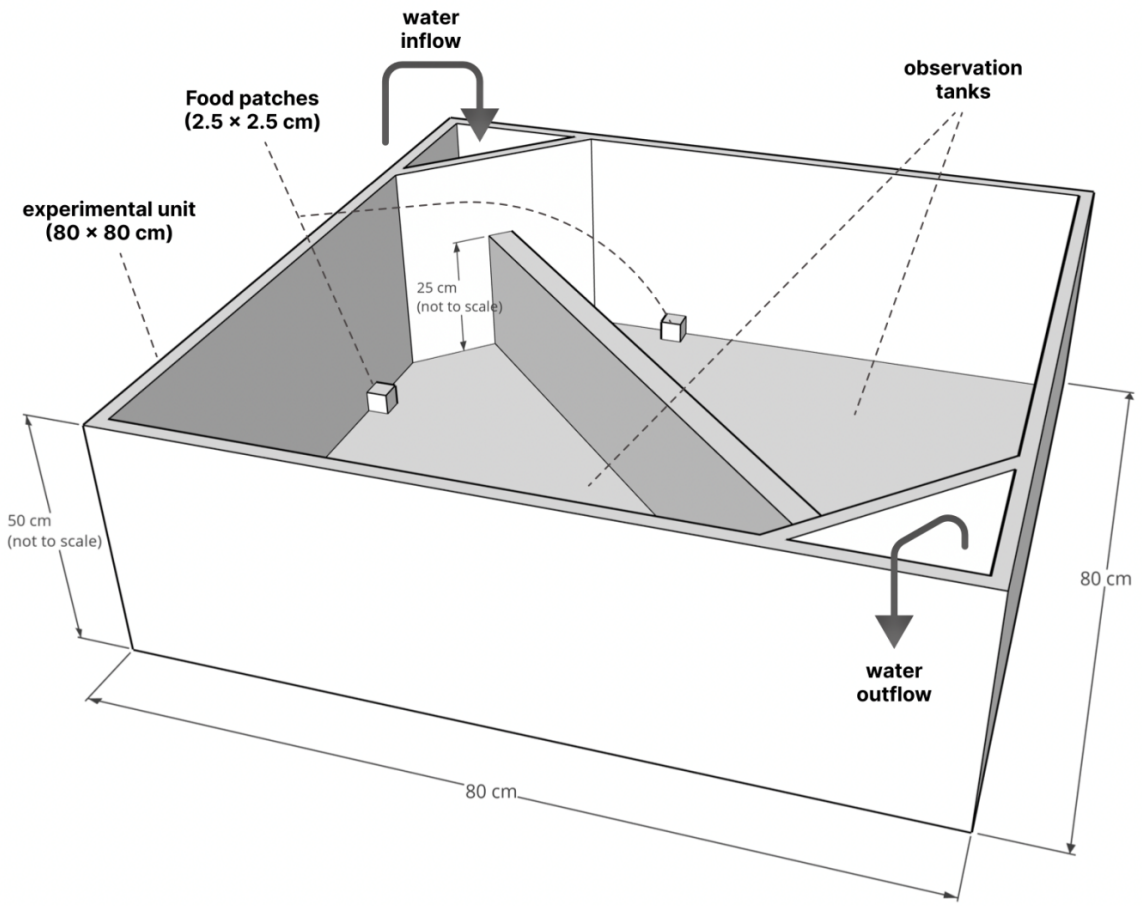
Supplementary Note 1: Behavioral observations



Supplementary Figure 1: Experimental set-up for behavioral observations. One experimental unit with 2 observation tanks. Water level in the tanks: 7 cm. Food patches were present during the feeding only. Observation tanks were illuminated individually from below with 4 LEDs per tank (each LED is 100cm, 12V, color temperature = 5500 K, light output = approx. 1570 lumen; tanks were manufactured from white polyethylene, which allowed light from underneath to get through). There was no visual contact between observation tanks, but tanks were connected via a flow-through water system (24 observation tanks split into 4 flow-through systems). We found no significant effect of the tank system (1-4), distance to the external filter unit (0-2m) or centrality of the tank on individual daily activity or feeding (**Supplementary Table 1**).

Supplementary Table 1 Summaries of linear-mixed effects models testing for potential environmental effects on early-life behavior (activity and feeding). We found no effects of tank system (1-4), distance to the filter (0-2 meters) or centrality (center vs. periphery, referring to a tank's position within a filter system) on individual behavior. Shown are full models (containing all predictor variables; left) and final models (significant predictors only; right).

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Activity [cm/sec]	Intercept	0.103	-0.284 – 0.489	-	-0.027	-0.185 – 0.132	-
	Tank system [2]	-0.219	-0.654 – 0.216	0.699	-	-	-
	Tank system [3]	-0.228	-0.653 – 0.196		-	-	-
	Tank system [4]	-0.119	-0.518 – 0.279		-	-	-
	Distance to filter [m]	-0.125	-0.312 – 0.062	0.195	-	-	-
	Centrality [periphery]	0.189	-0.122 – 0.500	0.238	-	-	-
	Random effects						
	σ^2	0.37			0.37		
	τ_{00}	0.18 Female ID			0.21 Female ID		
	ICC	0.33			0.36		
	N	34 Female ID			34 Female ID		
	Observations	941			941		
	Marginal R^2 / Conditional R^2	0.051 / 0.363			0.000 / 0.363		
Feeding [min]	Intercept	49.614	38.313 – 60.915	-	48.068	43.127 – 53.008	-
	Tank system [2]	4.877	-7.840 – 17.594	0.091	-	-	-
	Tank system [3]	11.747	-0.661 – 24.156		-	-	-
	Tank system [4]	-3.828	-15.486 – 7.830		-	-	-
	Distance to filter [m]	1.127	-4.340 – 6.595	0.686	-	-	-
	Centrality [periphery]	-8.100	-17.191 – 0.991	0.081	-	-	-
	Random effects						
	σ^2	845.77			845.81		
	τ_{00}	134.08 Female ID			184.56 Female ID		
	ICC	0.14			0.18		
	N	34 Female ID			34 Female ID		
	Observations	931			931		
	Marginal R^2 / Conditional R^2	0.049 / 0.179			0.000 / 0.179		

Supplementary Note 2: Food patch preparation

Ingredients

- 0.5g Agar (Bio Agar-Agar, Ruf)
- 100 ml tap water
- 14 g powder food (Sera vipan baby)

Materials

- One fine scale
- One 150 ml beaker
- One small pot
- One stove plate
- One pipette
- Food patch cups (max. volume = 2ml)

Instructions

1. Prepare clean and dry food patch forms.
2. Weigh the amount of agar needed in a 150 ml beaker.
3. Add 100 ml of water.
4. Fill the water-agar mixture into a small pot and cook for 2 min at medium heat.
5. Remove pot from stove and add powder food, mix thoroughly.
6. Let cool down for approx. 5 min at room temperature until agar starts binding.

7. Quickly fill the agar-food mixture into the cups using the pipette.
8. Let the food patches harden in the fridge for approx. 10 min without a lid.
9. Store food patches in a container with a lid (e.g., petri dishes) in the fridge until further proceeding (can be stored for at least 4 days when stored at 4°C).

Note:

The protocol can be modified regarding the amount of food or agar added. Adding more agar will give the mixture a firmer texture. Using less agar is not advised. The amount of agar used here is the least amount possible (resulting in a very soft texture) in order to allow juvenile fish to feed on the food patches. The amount of food can be both decreased and increased allowing for variations in food quality; food variations may require adjustments in the amount of agar used.

665 ## Supplementary Note 3: Robustness of results with respect to
666 potential male and/or tank effects

667

668 We tested whether our results and conclusions are robust with respect to potential
669 variation between males and/or breeding tanks. In order to do so, we used our data
670 to back-calculate the presumed males that triggered embryonic development/tanks
671 where embryonic development was triggered (in the following: male/tank ID) for all
672 broods (see "Assigning male/tank IDs" below). We then repeated all our analyses
673 involving female reproductive output, controlling for male/tank ID. Importantly, we
674 find that there is no effect of male/tank ID on female reproductive individuality
675 (**Supplementary Table 2**) or its link to early-life behavior (**Supplementary Tables 3-**
676 **6**), i.e., we find that all our results are robust and qualitatively the same when
677 controlling statistically for potential variation between males and/or breeding tanks.

678

679 More specifically, we recalculated normal and adjusted repeatabilities using the
680 same models that we used in the main text (for model structures see main text)
681 except that we now additionally included male/tank ID as a random effect. Including
682 male/tank ID has no effect on female repeatabilities (**Supplementary Table 2**). We
683 note that male/tank ID is associated with repeatable differences in offspring size
684 (but not brood size) (see **Supplementary Table 2**). This finding should be treated
685 with caution with respect to interpreting it as a potential male effect, as our

experiment was neither designed to detect potential male effects nor to distinguish between potential male and potential breeding tanks effects but rather to detect female effects while controlling for both male and tank effects.

Similarly, for all other analyses involving brood size or offspring size, we find qualitatively the same results as presented in the main text when including male/tank ID as a random effect: there is a weak brood vs. offspring size trade-off (**Supplementary Table 3**); there is no direct effect of early-life behavior on reproductive output (**Supplementary Table 4**) but larger fish (which feed more) produce larger offspring (**Supplementary Table 5**) (to compare with main text analyses see **Supplementary Table 8**, **Table 9** and **Table 11**). Similarly, we find qualitatively the same results as presented in the main text when testing for a potential effect of female size at birth on reproductive output (**Supplementary Table 6**) (to compare with main text analyses see model summary in **Supplementary Table 13**).

The fact that all our results and conclusions are robust with respect to the above statistical controls of potential effects of males and/or breeding tanks supports the effectiveness of our experimental design, which was aimed at experimentally controlling for both effects of males and breeding tanks simultaneously (see "Reproductive profiles" in the main text), was successful.

707 *Assigning male/tank IDs*

708 Poecilid females typically undergo a reproductive cycle with approx. 2-3 fertile days,
709 which are induced at maturation and immediately after parturition, followed by
710 approx. 30 days during which females are unreceptive to sperm while fertilized eggs
711 are carried internally until parturition [1,2]. For all broods, we thus assigned the
712 male/tank ID to that male/tank a female was with 30 ± 2 days before parturition. If a
713 female was with two different males/in two different tanks within that time frame, we
714 assigned male/tank ID to the male/tank she was with on day 30. If a female was with
715 two different males/in two different tanks on day 30, we assigned male/tank ID to
716 the latter (N = 27 broods).

717

718 Because we have low certainty in male/tank ID (*N* = 100 broods with female access
719 to two males/tanks within 30 ± 2 days prior to parturition), we additionally assigned
720 male/tank ID using two alternative methods: first male/tank ID (assigned to the first
721 male/tank a female was 30 ± 2 days prior to parturition) and last male/tank ID
722 (assigned to the second male/tank a female was 30 ± 2 days prior to parturition),
723 accounting, for example, for potential first or last male precedence or deviations
724 from the average gestation period. All analyses presented (**Supplementary Tables**
725 **2-6**) were carried out with the "exact" male/tank assignment method but all results
726 are robust with respect to the assignment method, i.e., we repeated all analyses

with either the first or last male/tank ID and received qualitatively the same results (not presented here, except **Supplementary Table 2** repeatabilities).

Again, during the reproductive phase of the experiment, females were swapped weekly between breeding tanks, where each breeding tank held a 'resident' male that did not switch tanks (thus tank ID and male ID usually had a one-to-one correspondence). During the experiment, however, some males needed to be replaced, leading to a few incidences where tank ID and male ID were not identical (N = 7 broods). Analyses presented here (**Supplementary Tables 2-6**) were carried out with male ID; however, we repeated all of the above analyses (**Supplementary Tables 2-6**) with tank ID (N = 39 tank where embryonic development was triggered) instead of male ID (N = 45 males that triggered embryonic development) and obtained qualitatively the same results (not presented).

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Supplementary Table 2 Normal and adjusted repeatabilities (accounting for female size and age, onset, and mother ID) for test fish and male/tank ID (N (brood size) = 152 broods, N (offspring size = 144 broods).

Response	*Method to assign male/tank ID*	*Normal repeatability [CI]*		*Adjusted repeatability [CI]*	
		Female ID	*Male/tank ID*	*Female ID*	*Male/tank ID*
Offspring size [mm]	No male/tank ID	0.396 [0.308, 0.484]	-	0.134 [0.085, 0.192]	-
	Exact ID	0.379 [0.279, 0.473]	0.068 [0.042, 0.110]	0.115 [0.073, 0.170]	0.131 [0.086, 0.187]
	First ID	0.405 [0.307, 0.499]	0.039 [0.025, 0.062]	0.117 [0.074, 0.174]	0.109 [0.073, 0.158]
	Last ID	0.338 [0.243, 0.431]	0.126 [0.085, 0.178]	0.126 [0.082, 0.181]	0.143 [0.098, 0.198]
Brood size	No male/tank ID	0.177 [0.117, 0.238]	-	0.077 [0.050, 0.114]	-
	Exact ID	0.212 [0.141, 0.289]	0.000 [0.000, 0.000]	0.085 [0.052, 0.124]	0.000 [0.000, 0.000]
	First ID	0.198 [0.126, 0.275]	0.015 [0.009, 0.023]	0.087 [0.053, 0.126]	0.000 [0.000, 0.000]
	Last ID	0.210 [0.135, 0.297]	0.000 [0.000, 0.000]	0.084 [0.053, 0.127]	0.000 [0.000, 0.000]

752 **Supplementary Table 3** Full (left) and final (right) linear mixed-effect models testing
753 for an offspring size vs. brood size trade-off, controlling for both the test fish ID and
754 male/tank ID.

		Full model			Final model		
Response	*Predictor*	*Estimate*	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Offspring size [mm]	Intercept	5.151	4.333 – 5.968	-	4.540	3.906 – 5.173	-
	Brood size	-0.012	-0.018 – -0.006	<0.001	-0.013	-0.018 – -0.007	<0.001
	Onset [days]	-0.003	-0.007 – 0.001	0.209	-	-	-
	Size at parturition [cm]	0.921	0.739 – 1.104	<0.001	0.970	0.813 – 1.128	<0.001
	Mother ID [m2]	0.026	-0.202 – 0.254	0.078	-	-	-
	Mother ID [m3]	-0.193	-0.364 – -0.022		-	-	-
	Random effects						
	σ^2	0.08			0.08		
	τ_{00}	0.01 Male/tank ID			0.01 Male/tank ID		
		0.01 Test fish ID			0.01 Test fish ID		
	ICC	0.22			0.24		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.583 / 0.675			0.539 / 0.651		

755

Supplementary Table 4 Full (left) and final (right) linear mixed-effect models testing if early-life behavior (activity, feeding) predicts reproduction (brood size, offspring size, onset), controlling for both test fish ID and male/tank ID.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	Intercept	-15.03	-35.58 – 5.53	-	-19.90	-39.82 – 0.03	-
	Activity [cm/sec]	-2.32	-4.88 – 0.25	0.082	-	-	-
	Feeding [min]	-0.07	-0.21 – 0.07	0.312	-	-	-
	Size at parturition [cm]	8.00	3.31 – 12.70	0.001	7.82	3.16 – 12.48	0.001
	Mother ID [m2]	6.11	0.05 – 12.17	<0.001	4.32	-1.61 – 10.26	<0.001
	Mother ID [m3]	10.21	5.71 – 14.71		8.44	4.35 – 12.53	
	Random effects						
	σ^2	70.72			70.53		
	τ_{00}	0.00 Male/tank ID			0.00 Male/tank ID		
		7.54 Test fish ID			10.07 Test fish ID		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.174 / NA			0.155 / NA		
Offspring size [mm]	Intercept	5.176	4.379 – 5.974	-	5.162	4.397 – 5.927	-
	Activity [cm/sec]	-0.039	-0.141 – 0.064	0.459	-	-	-
	Feeding [min]	0.002	-0.004 – 0.007	0.537	-	-	-
	Size at parturition [cm]	0.787	0.607 – 0.967	<0.001	0.799	0.621 – 0.978	<0.001
	Mother ID [m2]	-0.037	-0.284 – 0.209	0.024	-0.086	-0.321 – 0.148	0.014
	Mother ID [m3]	-0.264	-0.453 – -0.076		-0.265	-0.437 – -0.094	
	Random effects						
	σ^2	0.09			0.09		
	τ_{00}	0.01 Male/tank ID			0.01 Male/tank ID		
		0.01 Test fish ID			0.02 Test fish ID		
	ICC	0.20			0.22		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.550 / 0.638			0.539 / 0.642		

Supplementary Table 5 Full (left) and final (right) linear mixed-effect models testing if von Bertalanffy growth parameters (the growth rate K and maximum predicted size L_{inf}) predict reproduction (brood size, offspring size, onset of reproduction), controlling for both test fish ID and male/tank ID.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	Intercept	43.170	-71.776 – 158.117	-	7.187	1.216 – 13.158	-
	L_{inf} [cm]	-4.576	-23.303 – 14.152	0.630	-	-	-
	K	-173.701	-530.521 – 183.119	0.337	-	-	-
	Age at parturition [weeks]	0.205	0.015 – 0.394	0.036	0.215	0.026 – 0.404	0.027
	Mother ID [m2]	5.630	-0.430 – 11.690	0.113	5.085	-0.828 – 10.999	0.011
	Mother ID [m3]	3.808	-4.004 – 11.620		5.875	2.167 – 9.583	
	Random effects						
	σ^2	73.73			73.90		
	τ_{00}	0.00 Male/tank ID			0.00 Male/tank ID		
		8.36 Test fish ID			9.32 Test fish ID		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.132 / NA			0.117 / NA		
Offspring size [mm]	Intercept	5.730	1.557 – 9.903	-	4.895	3.475 – 6.315	-
	L_{inf} [cm]	0.472	-0.206 – 1.149	0.175	0.600	0.297 – 0.904	<0.001
	K	-2.777	-15.764 – 10.210	0.674	-	-	-
	Age at parturition [weeks]	0.029	0.022 – 0.037	<0.001	0.029	0.022 – 0.037	<0.001
	Mother ID [m2]	-0.067	-0.288 – 0.154	0.033	-0.079	-0.292 – 0.134	0.002
	Mother ID [m3]	-0.383	-0.668 – -0.098		-0.333	-0.495 – -0.170	
	Random effects						
	σ^2	0.10			0.10		
	τ_{00}	0.00 Male/tank ID			0.00 Male/tank ID		
		0.01 Test fish ID			0.01 Test fish ID		
	ICC	0.11			0.12		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.580 / 0.628			0.578 / 0.628		

Supplementary Table 6 Full (left) and final (right) linear mixed-effect models testing if size on the first day of life predicts reproductive output, controlling for both test fish ID and presumed male/tank ID.

Response	Predictor	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	Intercept	-1.708	-18.717 – 15.301	-	7.187	1.216 – 13.158	-
	Size at birth [cm]	10.904	-8.549 – 30.357	0.274	-	-	-
	Age at parturition [weeks]	0.208	0.019 – 0.398	0.032	0.215	0.026 – 0.404	0.027
	Mother ID [m2]	4.675	-1.168 – 10.518	0.087	5.085	-0.828 – 10.999	0.011
	Mother ID [m3]	4.561	0.254 – 8.869		5.875	2.167 – 9.583	
	Random effects						
	σ^2	74.06			73.90		
	τ_{00}	0.00 Male/tank ID			0.00 Male/tank ID		
		8.19 Test fish ID			9.32 Test fish ID		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.127 / NA			0.117 / NA		
Offspring size [mm]	Intercept	8.076	7.360 – 8.791	-	7.682	7.446 – 7.918	-
	Size at birth [cm]	-0.484	-1.313 – 0.345	0.255	-	-	-
	Age at parturition [weeks]	0.031	0.024 – 0.038	<0.001	0.031	0.024 – 0.038	<0.001
	Mother ID [m2]	0.007	-0.242 – 0.255	<0.001	-0.016	-0.267 – 0.235	<0.001
	Mother ID [m3]	-0.450	-0.644 – -0.257		-0.509	-0.677 – -0.340	
	Random effects						
	σ^2	0.09			0.09		
	τ_{00}	0.01 Male/tank ID			0.01 Male/tank ID		
		0.02 Test fish ID			0.02 Test fish ID		
	ICC	0.26			0.27		
	N	34 Test fish ID			34 Test fish ID		
		45 Male/tank ID			45 Male/tank ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.527 / 0.651			0.520 / 0.648		

Supplementary Note 4: Model output main analyses

Supplementary Table 7 Full (left) and final (right) linear mixed-effect models testing if early-life feeding behavior and activity are correlated.

Response	Predictor	Full model			Final model		
		Estimate	CI	P-value	Estimate	CI	P-value
Feeding [min]	Intercept	55.554	48.433 – 62.675	-	60.734	55.675 – 65.792	-
	Activity [cm/sec]	-9.222	-10.644 – -7.800	<0.001	-9.134	-10.550 – -7.719	<0.001
	Mother ID [m2]	3.103	-11.814 – 18.020	0.088	-	-	-
	Mother ID [m3]	10.495	0.907 – 20.084		-	-	-
	Random effects						
	σ^2	721.68			721.69		
	τ_{00}	150.82 Test fish ID			165.52 Test fish ID		
	ICC	0.17			0.19		
	N	34 Test fish ID			34 Test fish ID		
	Observations	931			931		
	Marginal R^2 / Conditional R^2	0.174 / 0.317			0.164 / 0.320		

Supplementary Table 8 Full (left) and final (right) linear mixed-effect models testing for an offspring size vs. brood size trade-off.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Offspring size [mm]	Intercept	5.083	4.238 – 5.927	-	4.466	3.827 – 5.104	-
	Brood size	-0.011	-0.018 – -0.005	<0.001	-0.013	-0.018 – -0.007	<0.001
	Onset [days]	-0.002	-0.006 – 0.002	0.335	-	-	-
	Size at parturition [cm]	0.919	0.730 – 1.108	<0.001	0.988	0.830 – 1.146	<0.001
	Mother ID [m2]	-0.038	-0.273 – 0.196	0.061	-	-	-
	Mother ID [m3]	-0.197	-0.359 – -0.035		-	-	-
	Random effects						
	σ^2	0.10			0.10		
	τ_{00}	0.01 Test fish ID			0.01 Test fish ID		
	ICC	0.10			0.13		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.580 / 0.623			0.545 / 0.602		

Supplementary Table 9 Full (left) and final (right) linear mixed-effect models testing if early-life behavior (activity, feeding) predicts reproduction (brood size, offspring size, onset).

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	Intercept	-15.029	-35.583 – 5.524	-	-19898	-39.823 – 0.027	-
	Activity [cm/sec]	-2.317	-4.881 – 0.248	0.082	-	-	-
	Feeding [min]	-0.071	-0.207 – 0.066	0.312	-	-	-
	Size at parturition [cm]	8.002	3.307 – 12.697	0.001	7820	3.157 – 12.484	0.001
	Mother ID [m2]	6.108	0.048 – 12.169	<0.001	4324	-1.608 – 10.256	<0.001
	Mother ID [m3]	10.208	5.706 – 14.710		8444	4.353 – 12.535	
	Random effects						
	σ^2	70.72			70.53		
	τ_{00}	7.54 Test fish ID			10.07 Test fish ID		
	ICC	0.10			0.12		
	N	34 Test fish ID			34 Test fish ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.160 / 0.241			0.138 / 0.246		
Offspring size [mm]	Intercept	5.168	4.359 – 5.978	-	5.147	4.366 – 5.928	-
	Activity [cm/sec]	-0.047	-0.149 – 0.056	0.369	-	-	-
	Feeding [min]	0.002	-0.004 – 0.007	0.513	-	-	-
	Size at parturition [cm]	0.791	0.607 – 0.975	<0.001	0.804	0.622 – 0.987	<0.001
	Mother ID [m2]	-0.058	-0.305 – 0.190	0.018	-0.119	-0.356 – 0.118	<0.001
	Mother ID [m3]	-0.265	-0.446 – -0.084		-0.270	-0.434 – -0.107	
	Random effects						
	σ^2	0.10			0.10		
	τ_{00}	0.01 Test fish ID			0.02 Test fish ID		
	ICC	0.12			0.14		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.552 / 0.607			0.539 / 0.605		
Onset of reproduction [days]	Intercept	126.473	94.420 – 158.526	-	133.786	123.545 – 144.027	-
	Activity [cm/sec]	4.000	-6.139 – 14.138	0.426	-	-	-
	Feeding [min]	0.072	-0.458 – 0.602	0.784	-	-	-
	Mother ID [m2]	15.777	-9.037 – 40.590	0.004	19.964	-1.760 – 41.689	0.002
	Mother ID [m3]	-19.908	-35.944 – -3.872		-17.411	-31.434 – -3.387	
	Observations	34			34		
	R^2 / R^2 adjusted	0.341 / 0.250			0.326 / 0.282		

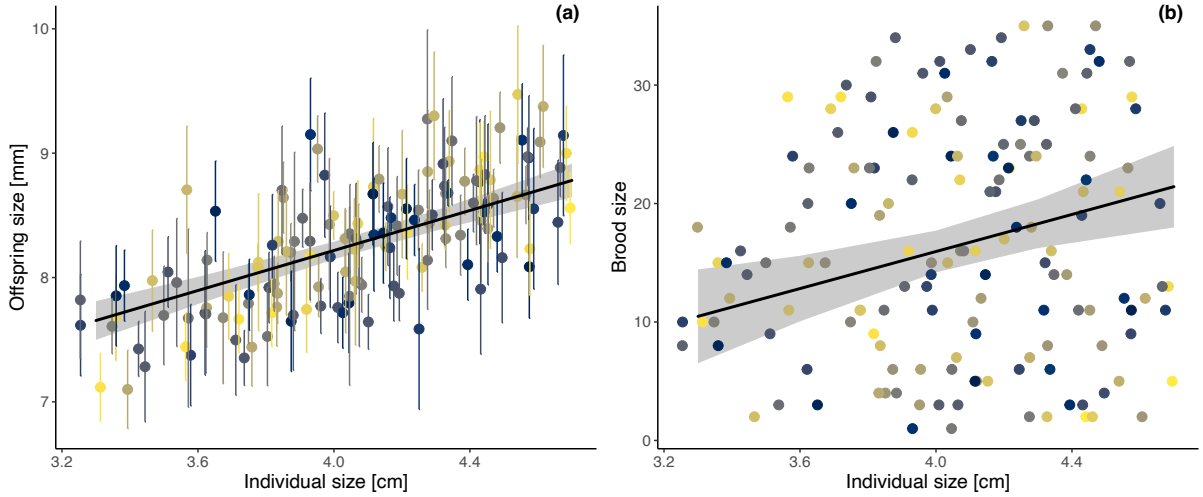
Supplementary Table 10 Full (left) and final (right) linear mixed-effect models testing for an effect of early-life behavior on the maximum predicted size (L_{inf}) and growth rate (K) of individuals.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
L_{inf} [cm]	Intercept	4.465	4.159 – 4.771	-	4.375	4.141 – 4.608	-
	Activity [cm/sec]	-0.045	-0.141 – 0.052	0.354	-	-	-
	Feeding [min]	0.006	0.001 – 0.011	0.015	0.007	0.003 – 0.012	0.002
	Mother ID [m2]	0.144	-0.093 – 0.380	<0.001	0.098	-0.116 – 0.313	<0.001
	Mother ID [m3]	-0.349	-0.502 – -0.196		-0.378	-0.517 – -0.239	
	Observations	34			34		
	R^2 / R^2 adjusted	0.592 / 0.535			0.579 / 0.537		
K	Intercept	0.296	0.247 – 0.344	-	0.305	0.263 – 0.346	-
	Activity [cm/sec]	0.001	-0.001 – 0.004	0.326	-	-	-
	Feeding [min]	0.000	-0.000 – 0.000	0.963	-	-	-
	L_{inf} [cm]	-0.046	-0.056 – -0.035	<0.001	-0.047	-0.056 – -0.039	<0.001
	Mother ID [m2]	0.004	-0.003 – 0.010	<0.001	0.005	-0.001 – 0.011	<0.001
	Mother ID [m3]	-0.019	-0.024 – -0.013		-0.018	-0.023 – -0.014	
	Observations	34			34		
	R^2/ R^2 adjusted	0.814 / 0.781			0.807 / 0.788		

Supplementary Table 11 Full (left) and final (right) linear mixed-effect models testing if von Bertalanffy growth parameters (the growth rate K and maximum predicted size L_{inf}) predict reproduction (brood size, offspring size, onset of reproduction).

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	Intercept	43.171	-71.768 – 158.110	-	7.187	1.217 – 13.157	-
	L_{inf} [cm]	-4.576	-23.302 – 14.151	0.630	-	-	-
	K	-173.702	-530.501 – 183.096	0.338	-	-	-
	Age at parturition [weeks]	0.205	0.015 – 0.394	0.035	0.215	0.026 – 0.404	0.026
	Mother ID [m2]	5.630	-0.429 – 11.690	0.111	5.085	-0.828 – 10.999	0.011
	Mother ID [m3]	3.808	-4.004 – 11.620		5.875	2.167 – 9.583	
	Random effects						
	σ^2	73.73			73.90		
	τ_{00}	8.36 Test fish ID			9.32 Test fish ID		
	ICC	0.10			0.11		
	N	34 Test fish ID			34 Test fish ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.120 / 0.210			0.105 / 0.206		
Offspring size [mm]	Intercept	5.739	1.240 – 10.239	-	4.808	3.310 – 6.307	-
	L_{inf} [cm]	0.475	-0.257 – 1.206	0.170	0.619	0.299 – 0.939	<0.001
	K	-3.076	-17.062 – 10.909	0.638	-	-	-
	Age at parturition [weeks]	0.029	0.022 – 0.037	<0.001	0.030	0.022 – 0.037	<0.001
	Mother ID [m2]	-0.081	-0.318 – 0.155	0.026	-0.096	-0.320 – 0.128	<0.001
	Mother ID [m3]	-0.385	-0.689 – -0.080		-0.329	-0.497 – -0.162	
	Random effects						
	σ^2	0.10			0.10		
	τ_{00}	0.01 Test fish ID			0.01 Test fish ID		
	ICC	0.12			0.11		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.568 / 0.618			0.570 / 0.616		
Onset of repro-duction [days]	Intercept	-141.259	-595.812 – 313.294	-	-204.285	-383.856 – -24.714	-
	L_{inf} [cm]	45.090	-29.090 – 119.270	0.224	55.537	25.189 – 85.886	0.001
	K	768.659	-631.930 – 2169.249	0.271	980.383	235.137 – 1725.629	0.012
	Mother ID [m2]	15.631	-7.523 – 38.785	0.393	-	-	-
	Mother ID [m3]	-0.368	-31.794 – 31.058		-	-	-
	Observations	34			34		
	R^2 / R^2 adjusted	0.360 / 0.271			0.317 / 0.273		

Supplementary Note 5: Effect of female size on reproductive output



Supplementary Figure 2: Effects of female size at parturition on reproductive output. Female size at parturition (predicted from individual von Bertalanffy growth curves) is positively correlated with (a) offspring size (shown is mean offspring size (points) per brood ± SD (error bars), N = 2522 offspring from 144 broods) and (b) brood size (N = 152 broods). (a-b) Data points are colored by individuals, regression lines (black) with 95% confidence intervals (grey shadow) were estimated via linear mixed-effects models (**Supplementary Table 9**).

Supplementary Note 6: No effects of size at birth on behavior, reproduction, and growth

Supplementary Table 12 Full (left) and final (right) linear mixed-effect models testing if size on the first day of life predicts early-life behavior.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Activity [cm/sec]	Intercept	1.546	-1.112 – 4.204	-	0.996	0.577 – 1.416	-
	Size at birth [cm]	-0.656	-3.786 – 2.475	0.672	-	-	-
	Mother ID [m2]	1.210	0.301 – 2.118	0.025	1.188	0.298 – 2.077	0.025
	Mother ID [m3]	0.595	-0.079 – 1.269		0.524	-0.050 – 1.098	
	Observations	34			34		
	R^2 / R^2 adjusted	0.218 / 0.139			0.213 / 0.162		
Feeding [min]	(Intercept)	10.888	-38.316 – 60.093	-	48.058	42.847 – 53.268	-
	Size at birth [cm]	42.305	-15.642 – 100.252	0.146	-	-	-
	Mother ID [m2]	-9.241	-26.064 – 7.581	0.454	-	-	-
	Mother ID [m3]	1.021	-11.450 – 13.493		-	-	-
	Observations	34			34		
	R^2 / R^2 adjusted	0.151 / 0.066			0.000 / 0.000		

Supplementary Table 13 Full (left) and final (right) linear mixed-effect models testing if size on the first day of life predicts reproductive output.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	(Intercept)	-1.708	-18.716 – 15.300	-	7.187	1.217 – 13.157	-
	Size at birth [cm]	10.904	-8.548 – 30.356	0.270	-	-	-
	Age at parturition [weeks]	0.208	0.019 – 0.398	0.031	0.215	0.026 – 0.404	0.027
	Mother ID [m2]	4.675	-1.168 – 10.518	0.086	5.085	-0.828 – 10.999	0.011
	Mother ID [m3]	4.561	0.254 – 8.868		5.875	2.167 – 9.583	
	Random effects						
	σ^2	74.06			73.90		
	τ_{00}	8.19 Test fish ID			9.32 Test fish ID		
	ICC	0.10			0.11		
	N	34 Test fish ID			34 Test fish ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.116 / 0.204			0.105 / 0.206		
Offspring size [mm]	Intercept	8.036	7.306 – 8.766	-	7.685	7.448 – 7.921	-
	Size at birth [cm]	-0.431	-1.276 – 0.414	0.315	-	-	-
	Age at parturition [weeks]	0.031	0.024 – 0.038	<0.001	0.031	0.024 – 0.038	<0.001
	Mother ID [m2]	-0.035	-0.288 – 0.218	<0.001	-0.053	-0.307 – 0.201	<0.001
	Mother ID [m3]	-0.462	-0.649 – -0.276		-0.514	-0.674 – -0.353	
	Random effects						
	σ^2	0.10			0.10		
	τ_{00}	0.02 Test fish ID			0.02 Test fish ID		
	ICC	0.18			0.19		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.525 / 0.612			0.519 / 0.612		

Supplementary Table 14 Full (left) and final (right) linear mixed-effect models testing if size on the first day of life predicts the growth rate K and predicted final size L_{inf}.

Response	*Predictor*	Full model			Final model		
		Estimate	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
L_{inf} [cm]	Intercept	4.171	3.473 – 4.870	-	4.716	4.602 – 4.831	-
	Size at birth [cm]	0.650	-0.172 – 1.473	0.117	-	-	-
	Mother ID [m2]	0.019	-0.220 – 0.258	<0.001	0.041	-0.202 – 0.284	<0.001
	Mother ID [m3]	-0.407	-0.584 – -0.230		-0.337	-0.493 – -0.180	
	Observations	34			34		
	R^2 / R^2 adjusted	0.472 / 0.419			0.426 / 0.389		
K	Intercept	0.309	0.268 – 0.350	-	0.305	0.263 – 0.346	-
	L_{inf} [cm]	-0.045	-0.054 – -0.036	<0.001	-0.047	-0.056 – -0.039	<0.001
	Size at birth [cm]	-0.017	-0.037 – 0.004	0.107	-	-	-
	Mother ID [m2]	0.006	-0.000 – 0.011	<0.001	0.005	-0.001 – 0.011	<0.001
	Mother ID [m3]	-0.016	-0.021 – -0.010		-0.018	-0.023 – -0.014	
	Observations	34			34		
	R^2 / R^2 adjusted	0.824 / 0.799			0.807 / 0.788		